**Title**

Biogeography of Australian Camphorosmeae and diversification in climatic space and across arid habitat types

**Authors**

Jessica A. Berasategui1,2, Anže Žerdoner Čalasan1 & Gudrun Kadereit1,3

1Prinzessin Therese von Bayern Lehrstuhl für Systematik, Biodiversität & Evolution der Pflanzen, Ludwig-Maximilians Universität München, Menzinger Str. 67, 80638 München, Munich, Germany

2Institute for Molecular Physiology, Johannes Gutenberg-University Mainz, 55099 Mainz, Germany

3Botanischer Garten München-Nymphenburg und Botanische Staatssammlung München, Staatliche Naturwissenschaftliche Sammlungen Bayerns, Menzinger Str. 65, 67, 80638 München, Munich, Germany

Corresponding author: Jessica Anna Berasategui (née Los) ([J.Los@biologie.uni-muenchen.de](mailto:J.Los@biologie.uni-muenchen.de))

**No. of figures: 7 (Figures 1, 2, 3, 4, 5, 6, 7 should be in colour)**

**No. of tables: 0**

**Word count: 8886**

**Supplementary material: One supplementary figure and three supplementary tables**

**Abstract**

This study investigates the biogeography of the Australian Camphorosmeae (Amaranthaceae *s.l.*) and how it relates to shifts in climatic niche and habitat types of the lineage. Building on previous research and data resources, we integrate molecular phylogenetics, bioclimatic data and biogeographic models to deepen our understanding of the diversification and adaptation of this group across Australia's diverse landscapes in relation to palaeoclimatic changes. For 159 species representing 12 genera, georeferenced distribution points were used to define the most informative bioclimatic variables using principal component analyses. Evolutionary shifts in climatic niches and habitat types were analysed, revealing clade-specific shifts and adaptations to different habitats and climatic conditions. Biogeographic analyses allowed us to infer ancestral areas of Camphorosmeae in Australia and relate their expansion over evolutionary time to habitat shifts. Key periods of aridification in Australia, particularly during the Late Miocene to Pliocene, and the already existing adaptation of this group to warm and dry habitats, were critical in driving its diversification through migration and local adaptation to varied habitats of arid Australia. Our analyses suggest that the “Riverine Desert” habitat that existed already in the Late Miocene and “migrated” eastwards offered suitable conditions for ancestral Australian Camphorosmeae and facilitated their early widespread occurrence in the Western and Eastern Desert. We hypothesise that early diverging lineages such as *Roycea* adapted to the later emerging “Desert Lake” habitat when it spread in Western Australia during the Early Pliocene. Further habitat type shifts occurred from “Riverine Desert” to “Shield Plain”, “Karst Plain” and to “Sand Desert” also during the Pliocene and Pleistocene once these habitat types emerged. This research shows the complex interplay between ecological flexibility and niche conservatism in shaping the biodiversity of Australian Camphorosmeae.

**Keywords**

Camphorosmeae, Australia, Atlas of Living Australia, Biogeography, Ancestral Reconstruction

**1. Introduction**

Australia is characterised by diverse landforms, a wide variety of biogeographic regions, and unique wildlife encompassing fauna and flora. While the northern regions of the continent experience tropical savanna climate with high humidity and a pronounced wet summer and dry winter season, the humidity, temperature and seasonality gradient decline along the eastern coast, which experiences a more moderate oceanic climate (Hadwen et al., 2011). On the contrary, southern and south-western regions are under strong Mediterranean influence with high summer temperatures and a rainfall period during the winter months. The largest portion of the continent, however, experiences a hot semi-arid and arid climate, with annual precipitation below 500 mm and 250 mm, respectively (Hadwen et al., 2011; Pearce et al., 2010). One of the most noteworthy palaeoclimatic events in Australia's history with substantial effects on flora and fauna occurred around 33 million years ago, during the Eocene to Oligocene transition (EOT) when the continent started to experience a continuous period of significant cooling and drying events (Crisp and Cook, 2013; Feakins et al., 2014). This climatic shift led to the spread of arid environments across much of Australia, influencing the evolution of drought-tolerant plant species preadapted to these conditions (Martin, 2006; Crisp and Cook, 2013). Around 30 million years ago, Australia had largely separated from Antarctica and continued to drift northward with increased aridification leading to the transformation of previously abundant rainforest vegetation into sclerophyll woodlands dominated by Proteaceae (*Banksia* L.f.), Myrtaceae (*Eucalyptus* L'Hér.), and Fabaceae (*Acacia* Mill) and Asteraceae (*Olearia* Moench) (Dettmann and Jarzen, 1998; Ladiges et al., 2003; Crisp and Cook, 2013; Jansen et al., 1991).

Australia's diverse habitats and ecosystems, spanning from the Gondwanan remnant rainforests to the much younger outback deserts, are categorised by scientists and ecologists into distinct biogeographical regions. This classification guides conservation efforts, ecological research, land management, and environmental policy. By identifying areas of high biodiversity, researchers can prioritise conservation efforts, study species distribution patterns and develop environmental policies. In essence, the organisation of Australia’s ecosystems into biogeographic regions is a practical tool for understanding, conserving and managing the country's remarkable biodiversity and natural resources. However, this leads to multiple bioregionalizations in Australia, with areas being synonymised or overlapped (Ebach, 2012).

One of the most common classifications is the *Interim Biogeographic Regionalisation for Australia* (Thackway and Cresswell, 1995; IBRA7), which divides Australia into 89 bioregions and 419 subregions. This classification system is based on shared characteristics such as climate, geology, landforms, vegetation, and species distributions (Thackway and Cresswell, 1995). Another well-known bioregionalization is the *Integrated Marine and Coastal Regionalisation of Australia* (IMCRA, Commonwealth of Australia, 2006), which classifies marine and coastal environments into several bioregions based on oceanographic data, biological distributions, and habitat types for marine conservation. The definition of bioregions or subregions, in general, is fundamental to understanding the distribution patterns of biodiversity. By defining regions based on shared ecological characteristics and species distribution patterns, these classifications enable targeted interventions to conserve biodiversity hotspots.

Ebach et al. (2012; 2015) suggested a taxonomy convention for defining and naming the biogeographic areas of Australia. They identified several phytogeographic regions and subregions within Australia based on the distribution patterns of specific taxonomic groups. Each of these regions or subregions is characterised by different ecological traits, biodiversity, and geological characteristics and contributes to the overall diversity of Australia's landscapes and ecosystems. The subregions are divided into twenty phytogeographical regions, including the western, central and eastern deserts; the Great Sandy Desert Interzone; Central and Eastern Queensland; the Nullarbor; Eyre Peninsula and Adelaide areas.

Around 18% of Australia’s landscape is considered a desert, with each desert landscape having its characteristics and attributes (Geoscience Australia, 1994). Mabbutt (1988) described and mapped eight habitat types in arid Australia (Desert Uplands, Shield Plains, Stony Desert, Karst Plain, Sand Desert, Riverine Desert, Desert Clay Plains and Desert Lakes). McDonald (2020) introduced two additional habitat types by studying Australian chenopod species across different arid landscapes to cover adjacent temperate, subtropical, and coastal zones (Mesic Plain, Range, and Coast).

Due to the diversity of Australia’s ecosystems, it is habitat for several large angiosperm families that have evolved in isolation over millions of years. The species richest Australian plant families include Asteraceae, Fabaceae, Myrtaceae and Proteaceae with Amaranthaceae Juss. *sensu lato* present in high numbers particularly in Australian arid regions (Crisp and Cook, 2013; Ladiges et al., 2003; Funk, 2009; Walker et al., 2018; Morales-Briones et al., 2021).

One of the most species-rich Australian tribes within the family Amaranthaceae *sensu lato* is the Camphorosmeae Moq. It comprises around 160 Australian species placed in 12 genera (according to Plants of the World Online, 2024), with the two biggest genera being *Sclerolaena* and *Maireana*. The former genus encompasses 79 currently accepted species, while the latter includes 58 currently accepted species. Australian Camphorosmeae are distributed across different Australian habitats, from coastal dunes to inland deserts. While Australia harbours the highest species diversity of this tribe, there are approximately 35 species across eight genera that occur outside of Australia, and are distributed from the Canary Islands to Asia, mainly in the Old World Desert Belt, North America (e.g. *Neokochia* (Ulbr.) G.L.Chu & S.C.Sand.), and South Africa (Kadereit et al., 2005; Kadereit and Freitag, 2011; Hühn et al., 2024).

The Australian Camphorosmeae species are remarkably well adapted to extreme environmental conditions, including saline soils and arid areas (Kadereit et al., 2005), while presumably performing explicit C3 photosynthesis (Carolin, 1975; Jacobs, 2001; Freitag and Kadereit, 2014). These adaptations include morphological traits such as reduced leaf size, succulence, and hairy or scaly surfaces, which minimise water loss (Kadereit and Freitag, 2011).

This lack of specialised C4 photosynthesis is found in many other species-rich Australian desert plants, such as *Acacia* (Fabaceae), *Eucalyptus* (Myrtaceae), *Eremophila* (Scrophulariaceae) and *Ptilotus* (Amaranthaceae), which indicates that C4 photosynthesis alone cannot explain the evolutionary success of some C4 lineages in water-scarce conditions (Bowman and Cook, 2002; Sage et al., 2007; Kattge et al., 2011). Understanding the evolutionary history and biogeographical patterns of Camphorosmeae is thus essential to understand the mechanisms underlying their diversification and adaptation to diverse ecological niches.

Molecular phylogenetic research has become an important tool to improve the understanding of evolutionary relationships and genetic diversity within this tribe, albeit initially with limited sampling and low support. The taxonomic position of the Camphorosmeae has thus changed several times (Freitag and Kadereit, 2014).

In 2009, Cabrera et al. conducted the first molecular phylogenetic study for this tribe, including 71 species from all recognised Camphorosmeae genera. Cabrera’s study concluded that although some morphological characters such as fruiting perianth were relevant, the molecular results did not fully support the existing taxonomy, attributing this discrepancy to incomplete lineage sorting and ongoing hybridisation within the Australian Camphorosmeae group. Subsequent biogeographical analyses suggested that the Australian Camphorosmeae migration started in the southwest of Australia via a single long-distance dispersal event from continental Asia during the Miocene, from where this lineage expanded eastward and northward over time. An enhanced diversification took place during the Pliocene, possibly driven by increasing aridity, together with inland migration along palaeodrainage systems especially pronounced in species adapted to coastal conditions (Cabrera et al., 2011; Kadereit and Freitag, 2011).

In 2020, John McDonald published a study on the evolution of chenopods (i.e. former Chenopodiaceae) in Australia, proposing several key hypotheses regarding their diversification and migration. He hypothesised that the primary evolutionary spaces for the range expansion and diversification of most chenopod taxa (including Camphorosmeae) were the Yilgarn and Eyre-Murray centres. These regions, which contain 97% of all Australian chenopod species, are not restricted to the arid zone but represent critical centres for chenopod evolution. He noted that these centres share 43% of all species, indicating widespread initial colonisation from coastlines followed by multiple migrations across these regions. He furthermore identified the inland province of Sandland South (Great Victoria Desert) as an important migration link between the Yilgarn and Eyre-Murray centres, rather than the coastal Nullarbor Plain, dominated by chenopod vegetation today. Finally, he also noted that the chenopod abundance in Riverine Deserts and Desert Lakes underscores the influence of niche conservatism, particularly regarding salinity and flooding in the main inland habitat of chenopods.

Despite these valuable insights, both studies suffered from unresolved phylogenies and limited sampling. A recent study by Hühn et al. (2024) re-evaluated the diversification of the Australian Camphorosmeae using an adapted RADseq approach. Sequence data were generated for 104 species from all 12 Australian genera. A modified NGS-based methodology was used to improve the phylogenetic resolution, identify statistically supported clades, and place the phylogeny into a temporal frame. Seventeen statistically well-supported clades were identified, with their habitat preference demonstrating the influence of landscape change and the emergence of new habitats in arid Australia since the late Miocene, with migration likely following a west-to-east pattern of aridification. The Camphorosmeae arrival coincided with significant palaeoclimatic, landscape, and biotic changes. Possibly aided by preadaptation of their progenitors to coastal (i.e. saline) environments, Hühn et al. (2024) suggested that Camphorosmeae migrated inland along Riverine Desert landscapes (a habitat type defined by Mabbutt in 1988) formed by changes in palaeodrainage systems in southern and western Australia (Hühn et al., 2024).

Those three primary research hypotheses, proposed by Cabrera et al. (2011), McDonald (2020), and Hühn et al. (2024), offer significant insights into the evolutionary history of Camphorosmeae in Australia. While sharing common elements, these hypotheses exhibit unique differences that highlight the complex interplay of diverse mechanisms of dispersal, colonisation, and adaptation.

All of them concur that the ancestors of Australian Camphorosmeae arrived via a long-distance dispersal event from continental Eurasia during the Middle to Late Miocene. This period marks the beginning of significant climatic shifts, leading to the aridification of Australia. The adaptation of Camphorosmeae to arid and saline environments is a central topic across these hypotheses, suggesting that these plants were pre-adapted to such conditions before they arrived in Australia.

Hühn et al. (2024) and Cabrera et al. (2011) share similar results, particularly in their biogeographic patterns and diversification trends. Both propose that initial colonisation occurred in the south and west of Australia, followed by expansion across the continent. They also emphasise the Late Miocene and Pliocene as periods of significant diversification, driven by the intensifying aridification. However, they note a slowdown in speciation during the Pleistocene, likely due to habitat contraction and climatic oscillations.

McDonald's hypothesis introduces the littoral connection hypothesis (Burbidge, 1960; Shmida, 1985), positing that chenopods initially arrived in the coastal regions, from where they expanded inland. This hypothesis underscores niche conservatism, where species retain ancestral ecological characteristics, influencing their migration patterns and habitat preferences. McDonald also explores two scenarios - fragmentation and amalgamation - to explain the development of chenopod diversity in Australia, providing a unique perspective on range expansion and evolutionary centres. The fragmentation scenario involves an initial colonisation and establishment phase with coastal bridgeheads, followed by a landscape spread where chenopods extend their range, particularly towards the west and south coasts, linked through the ancestral Great Victoria Desert. This is followed by two diversification stages, where speciation increases, and distinct lineages form in the western Yilgarn and central-eastern Eyre-Murray centres of diversity. Conversely, the amalgamation scenario begins similarly with coastal bridgehead formation and expansion but follows with separate provincial expansions and early diversification in the west and east. As aridity intensifies, these centres merge, facilitating species exchange and forming the subcontinental Arid-Mediterranean group through further range expansion (McDonald, 2020).

Each of the three approaches has its methodological considerations and challenges. Cabrera et al. (2011) for example highlighted the reliance of molecular data for age estimates in the absence of direct fossil evidence, noting that these estimates are consistent with the fossil record of chenopod-like pollen in Australia. The oldest chenopod-like pollen fossils were discovered at the Oligocene-Miocene boundary (Martin, 1981; Christophel, 1989; Cabrera et al., 2011). However, the study suffered from poor resolution of the phylogenetic tree. McDonald (2020), on the other hand, drew most of his conclusions based on the ecology of the species and the landform evolution of individual habitats on palaeoenvironmental and geological evidence but did not fully resolve the phylogenetic history of the taxon in question. This was succeeded only by Hühn et al. (2024), by using a modified RADseq protocol for sequencing. Their study revealed new clades and at least partially overcame the issue of poor phylogenetic resolution, despite the challenges posed by the high proportion of missing data.

Building on these fundamental hypotheses, our research aims to integrate their strengths and unique aspects through a phylogenetically based ancestral analysis. The aim is to place the evolutionary history of Camphorosmeae into space and to infer its ancestral ecological niche, by using a well-sampled and resolved phylogeny that shows statistically supported clades for credible and significant results. This study explores the role of coastal and inland pathways in the dispersal and diversification of Camphorosmeae, emphasising the impact of climatic fluctuations and ecological niche conservatism.

To validate these hypotheses regarding the climatic niches, habitat types, evolutionary dynamics, and biogeography of Australian Camphorosmeae, mapping habitat type occupations or bioclimatic variables onto the well-resolved dated phylogenetic tree of Hühn et al. (2024), will reveal clade-specific shifts, providing insight into how different Camphorosmeae species have adapted to various habitats or responded to climate change. Additionally, biogeographic analyses will help unravel the complex interplay between evolutionary history, geographic distribution, and diversification events over time.

This study aims to deepen the understanding of Camphorosmeae's evolutionary history in Australia by integrating phylogenetic analyses with biogeographic models, climate data and habitat preferences offering new insights into their distribution and diversification across Australia's diverse landscapes.

**2. Materials and Methods**

**2.1 Taxon Sampling and Occurrence Data**

For this study, the georeferenced distribution points of 159 species, representing all 12 genera of the group, were extracted from Australia’s online species database, the Atlas of Living Australia (ALA), Australia’s most extensive and readily accessible repository of biodiversity data (Belbin and Williams, 2016; Belbin et al., 2021).

Before analysis, manual cleaning steps were required, which included removing records without coordinates, distribution points outside Australia, duplicate coordinates per species, and records categorised under taxonomic ranks such as ‘genus’ or ‘family’. To relate the present analyses to the most recent dated phylogeny of the Australian Camphorosmeae by Hühn et al. (2024), distribution points of 103 Australian Camphorosmeae species included in the phylogeny, except for *Sclerolaena* sp. *yeltacowie* ineditus due to missing coordinates, were selected (Table S1).

**2.2 Bioclimatic Variables and Principal Component Analysis**

All 19 bioclimatic variables were extracted from WorldClim v.2 (Fick and Hijmans, 2017) at a spatial resolution of 2.5 min (~ 4.5 km at the equator), to perform Principal Component Analysis (PCA) aimed at determining the optimal bioclimatic variables for reconstructing their ancestral state based on the dated Australian Camphorosmeae phylogeny. The extent() and crop() methods in R were used to obtain bioclimatic data specifically for the Australian habitat. To achieve this, the extent for Australia was defined, with xmin = 112, xmax = 154, ymin = -44, and ymax = -10. Bioclimatic variable values were extracted for each presence point of the 103 Australian Camphorosmeae. With this dataset, the PCA was carried out to obtain the best bioclimatic variables for further analyses.

To evaluate the proportion of the climatic niche occupied by Camphorosmeae in Australia, we first quantified the climatic space of Australia by selecting 200,000 spatially randomised locations in Australia followed by a PCA for the entire climatic range throughout Australia.

After conducting PCA to identify the major axes of variation, we projected the locations of all occurrences from 103 Australian Camphorosmeae species onto the rotated principal component (PC) space. This transformation enabled us to observe and analyse the distribution patterns of Camphorosmeae in Australia within this modified space. In addition, PCA was conducted on the climatic data of the Australian Camphorosmeae. The principal components, capturing the most significant variation, were identified (PC1 and PC2) for the variable correlation plot, with variables exhibiting high loadings used to determine the orientation of the axes. We selected the variables with the highest loading value for PC1 and PC2, respectively, essentially choosing the variables that contribute the most to the variability captured by PC1 and PC2, respectively. Since they were capturing different sources of variability, they were less likely to be highly correlated with each other. Additionally, a pairwise Pearson's correlation coefficient test was done to evaluate collinearity among these variables.

**2.3. Ancestral State Reconstruction with Key Climatic Variables and Ancestral Habitat Type Reconstruction**

To investigate the evolutionary history and ecological adaptations of Australian Camphorosmeae two different reconstructions were made: Ancestral Bioclimatic Reconstruction with the two most relevant environmental bioclimatic variables (Bio05 - Maximum Temperature of Warmest Month; and Bio13 - Precipitation in the Wettest Month) and Ancestral Habitat Type Reconstruction based on defined habitat types. The dated maximum clade credibility (MCC) tree by Hühn et al. (2024) was used for that.

For the Ancestral Bioclimatic Reconstruction, the mean value of each bioclimatic variable for 103 species was calculated. To determine the optimal number of clusters for each of the two bioclimatic variables and prevent under- or over-clustering, the partition around medoids (PAM) approach was used, employing the average silhouette method implemented in the R function fviz\_nbclust() (R package ‘factoextra’, Kassambara and Mundt, 2016). This clustering approach was essential to facilitate the visualisation and interpretation of the bioclimatic variables within the phylogenetic context. By identifying clusters, we could discern distinct patterns or groupings that might not be readily apparent when treating the climatic variables as continuous. This clustering approach enhances the resolution of ancestral character state reconstruction by providing a more structured representation of the data, enabling clearer identification of ecological niches or adaptive strategies across the evolutionary history of the taxa under study.

Following the publication by Hühn et al. (2024), which inferred the ancestral status of habitat types based on chronological order, this study conducted a formal analysis using 'Ancestral Habitat Type Reconstruction' to test their assumptions. To do so, ten habitat types defined by Mabbutt (1988) and McDonald (2020) were used. The specific habitat types corresponding to the individual species were derived from the work of Hühn et al. (2024).

For both Ancestral Reconstruction Models, the maximum parsimony method following the topology of Hühn et al. (2024) was employed in Mesquite (v3.81, www.mesquiteproject.org).

**2.5 Biogeographical Analysis**

To investigate the biogeographical history of Australian Camphorosmeae, again, the dated MCC tree by Hühn et al. (2024) was used in the R package ‘BioGeoBEARS’ v.1.1.2 (Matzke, 2013) and its dependencies. BioGeoBEARS presents a versatile, likelihood-based system, designed to characterise the dynamic shifts of branches within phylogenies across discrete biomes over evolutionary time. These biome shifts encompass both anagenetic events, occurring within a single branch, such as dispersal and extinction processes (DEC; Ree and Smith, 2008), and cladogenetic events, which transpire at branching points and involve sympatric (BAYAREALIKE; Landis et al., 2013), vicariant (DIVALIKE; Ronquist, 1997), and founder-event speciation processes (DEC+J, BAYAREALIKE+J, DIVALIKE+J; Matzke, 2014, Van Dam and Matzke, 2016).

A large-scale analysis based on an almost complete sampling by Hühn et al. (2024) was performed. For the distribution data, twenty Australian phytogeographic subregions were selected following the ranges identified by Ebach et al. (2015). Subregions were chosen for each species only if more than 10% of their occurrence points were present within those areas. Any subregion with less than or equal to 10% of occurrence points per species was treated as insignificant. This enables the main occurrences of the respective species to be analysed and avoids potential identification biases. The required subregion shapefile from Ebach et al. (2015) was downloaded for this purpose. However, since some species in Camphorosmeae occur very close to the coast, adjustments to the shapefile were necessary. The edges of the shapefile did not always align precisely with the coast, leading to the exclusion of some coastal occurrence points in the initial attempt. Consequently, the shapefile was overlaid on an Australian landscape map via QGIS V3.30 (QGIS, 2024) and the coastal boundaries were extended accordingly. This adaptation allowed the inclusion of many distribution points near the coast in the biogeographical analysis for certain species (*Threlkeldia diffusa* R.Br., *Maireana oppositifolia* (F.Muell.) Paul G.Wilson, *M. brevifolia* (R.Br.) Paul G.Wilson, *Sclerolaena uniflora* R.Br., *Dissocarpus biflorus* (R.Br.) F.Muell.).

As a result, there are one to a maximum of four main subregions for most of the species. A table showing this reduction can be found in the supplement (Table S2). Nine subregions in total for 103 species were selected: Central Desert, Central Queensland, Adelaide, Eyre Peninsula, Nullarbor, Southwest Interzone, Southwestern, Eastern Desert, and Western Desert. The maximum range size was set to 4, as the most widely distributed Australian Camphorosmeae species covered a maximum of four subregions. Six models have been tested (DEC, BAYAREALIKE, and DIVALIKE and their +J alternatives). The best‐fit model was chosen by comparing the corrected Akaike information criterion (AICc) and Akaike weight (AICc\_wt).

**3. Results**

**3.1 Data Compilation and Cleaning**

A total of 228,875 occurrence points from ALA were compiled (Atlas of Living Australia, 2021; Atlas of Living Australia occurrence download at https://doi.org/10.26197/ala.a4134452-6171-4ad7-8da0-46682199a2d8. Accessed 30 May 2023). Manual data cleaning reduced the total number of records to 195,758. Distribution points of 103 Australian Camphorosmeae species included in the most recently dated phylogeny by Hühn et al. (2024) were specifically selected for the analyses (Table S1). This results in 178,355 included distribution points.

**3.2 Bioclimatic Characterisation and Niche Occupancy**

This analysis aimed to identify the bioclimatic variables driving the distribution patterns of Australian Camphorosmeae and to assess the proportion of climatic niches occupied by the species within the Australian habitat. Through the Principal Component Analyses (PCA) of 19 bioclimatic variables, significant axes of climatic variation could be identified. The PCA was conducted with all distribution points of 103 Australian Camphorosmeae species together (Figure 1).

The resulting correlation circle, displayed in Figure 1, represented the distribution of 19 environmental variables (Bio01 to Bio19) across the first two principal components, PC1 and PC2, and revealed strong relationships between those variables based on their distance from the centre and orientation relative to each other. Bioclimatic variables located far from the centre and close to each other exhibited strong positive correlations (r-value close to 1), while those far from the centre and orthogonal were not correlated (r-value close to 0). Variables positioned on opposite sides of the centre demonstrated significant negative correlations (r close to -1).

**(--FIGURE 1--)**

PCA analysis of 103 species together, explained a substantial portion of the variability among all climatic variables, with both PC axes accounting for 65.91% of the total variance (Figure 1). PC1 and PC2 explained 43.37% and 22.54% of the total variance, respectively. Interpretation of the loading values highlighted the dominant climatic axes captured by each principal component. PC1, primarily reflecting the temperature axis, was strongly influenced by variables such as Bio05 (Maximum Temperature of the Warmest Month; loading value of 0.333) and Bio10 (Mean Temperature of the Warmest Quarter; loading value of 0.328). On the other hand, PC2, representing the precipitation axis, was mainly driven by variables including Bio13 (Precipitation in the Wettest Month; loading value of 0.437) and Bio18 (Precipitation in the Warmest Quarter; loading value of 0.422), indicating their substantial contribution to this component.

In addition to the correlation circle, the Pearson correlation coefficient test also showed strong correlations between the variables Bio05 and Bio10, and between Bio13 and Bio18. Therefore, only the variable with the highest loading value per PC was selected for further analysis (Bio05 and Bio13). Initially, they were used to project the distributions of Australian Camphorosmeae species onto their rotated PC space (Figure 2).

**(--FIGURE 2--)**

The climatic niche occupied by the Camphorosmeae species in Australia was evaluated by conducting a PCA on the entire climatic range of Australia. Figure 2 shows the PCA of the climatic range across Australia, based on 200,000 spatially randomised points for each of the two bioclimatic variables. The PCA space is rotated, with PC1 and PC2 accounting for 44.71% and 37.80% of the total variance, respectively. These components were used to project the occurrence of 103 Australian Camphorosmeae species onto the rotated PC space. The Camphorosmeae species predominantly occupy areas with high maximum temperatures, as indicated by the clustering of occurrence points in the warmer regions of the climatic space. The species occurrences are concentrated in areas with low to moderate rainfall, with a notable presence in regions experiencing lower precipitation.

Figure 3 represents the rotated principal component (PC) space, with colours representing the subregions of Australia as defined by Ebach et al. (2015). Only subregions with more than 10% of occurrence points per species are displayed. These visualisations provide insights into the main axes of climatic variation and the spatial distribution of climatic conditions across the continent. PC1 explains a significant portion of the variance, capturing a broad climatic gradient across Australia. PC2 represents another important climatic gradient, orthogonal to PC1.

**(--FIGURE 3--)**

**3.3 Ancestral estimation and transitions**

The clustering analysis revealed a variation of the optimal number of clusters across the two selected key bioclimatic variables, Bio05 and Bio13. Specifically, two clusters were identified for Bio05, while three clusters for Bio13. Clusters were defined in the following ranges: Bio05: ≤ 34.2°C and > 34.2°C; and Bio13: ≤ 36 mm, 37 – 52 mm, and ≥ 52 mm. The bioclimatic niche evolution of those two selected bioclimatic variables is shown in Figure 4, and the Ancestral Habitat Type Reconstruction in Figure 5. To facilitate the evaluation and discussion of these patterns and results, the same clade numbers as assigned by Hühn et al. (2024) were utilised.

Considering the influence of the two bioclimatic variables, a discernible pattern emerges. Firstly, it is apparent that the ancestor of Australian Camphorosmeae and the ancestors of clades 1-6, 9, as well as *M. oppositifolia, M. sedifolia* (F.Muell.) Paul G.Wilson*, M. enchylaenoides* (F.Muell.) Paul G.Wilson preferred lower peak temperatures in the warmest month (Bio05) of ≤ 34.2°C. Subsequently, a multiple transition in numerous clades towards warmer Maximal temperatures of the warmest month is observed in the descendants, namely Clades 7-8, 10-17, *M. cannonii* (J.M.Black) Paul G.Wilson, and *Neobassia proceriflora* (F.Muell.) A.J.Scott. Interestingly, a subsequent return to lower temperatures occurs in some of these clades, e.g. 13, 15-17.

**(--FIGURE 4--)**

Looking at the precipitation of the wettest month (Bio13), the ancestor of Australian Camphorosmeae likely preferred at least 52 mm of precipitation during the wettest month. Ancestors of clades 1-3 and *M. enchylaenoides* were more likely to be found in wetter areas with precipitation values more than or equal to 52 mm during the wettest month, transitioning at the ancestral node of *M. sedifolia an*d Clade 9 into clearly drier conditions (≤ 36 mm). Multiple shifts back to areas with wetter conditions can be observed on at least 10 terminal nodes (Figure 4).

The reconstruction of the ancestral habitat types shown in Figure 5 reveals three main ancestral types, with Riverine Desert being the most prominent and spanning the entire ancestral backbone. For clades 1-3, Riverine Desert and Desert Lake can be recognised as ancestral habitats. Riverine Desert and Karst Plain for *M. enchylaenoides* and *M. sedifolia* and Riverine Desert for all other clades (Figure 5).

**(--FIGURE 5--)**

**(--FIGURE 6--)**

**3.4 Biogeographic history**

For the BioGeoBEARS analyses using a maximum range of four areas, BAYAREALIKE was the best-fit model (AICc = 822.7; AICc\_wt = 0.68), followed by BAYAREALIKE+J (AICc = 824.5; AICc\_wt = 0.28). Both models indicate low rates of dispersal (d = 0.013) but notably higher extinction (e = 0.13) values (Table S3).

**(--FIGURE 7--)**

The biogeography analysis highlights two main combinations of subregions within the phylogenetic backbone as potential ancestral areas (Combination 1 and 2). There is a 47.75% probability that the ancestor of clades 1-6 and 9, along with species *Maireana oppositifolia, M. enchylaenoides* and *M. sedifolia*, inhabited Adelaide, Eastern Desert, and Western Desert (C+H+I, Figure 7). During the end of the Late Miocene, the ancestors of Clade 3 as well as of Clades 7, 8, and 10-17, along with species *Maireana cannonii* and *Neobassia proceriflora*, show a significant presence in the Eastern and Western Desert (H+I, Figure 7) regions, with a probability range of 19-23% for Clade 3 and 60.32% for the rest. Dispersal events to the Eyre Peninsula (D) occurred for clades 2 and 4. These events are represented by the C+D+H+I combination (3) with probabilities of 34.05% and 55.28% at the crown, respectively, contemporaneously during the end of the Late Miocene.

Only during the Pliocene and Pleistocene areas such as the Southwestern (G) in combination with the Western Desert (I) were inhabited. This is evident for Clade 1 at the beginning of the Pliocene. In addition, the Southwestern Interzone (F) was occupied more recently by some species like *Roycea divaricata* Paul G.Wilson, *M. eriosphaera* Paul G.Wilson, *M. carnosa* (Moq.) Paul G.Wilson, *Enchylaena lanata* Paul G.Wilson, *M. suaedifolia* (Paul G.Wilson) Paul G.Wilson, *M. marginata (*Benth.) Paul G.Wilson, *M. amoena* (Diels) Paul G.Wilson, *Didymanthus roei* Endl., *Sclerolaena eurotioides* (F.Muell.) A.J.Scott, *S. fusiformis* Paul. G.Wilson and *S. drummondii* (Benth.) Domin. Additionally, several young species (*Sclerolaena obliquicuspis* (R.H.Anderson) Ulbr*, S. brevifolia* (Ising) A.J.Scott*, S. uniflora, S. holtiana* (Ising) A.J.Scott*,* and *S. diacantha* (Nees) Benth.) from clade 17 migrated into the Adelaide region (C+H, Figure 7) during the early Pleistocene.

**4. Discussion**

Australia's complex palaeoclimatic history has profoundly influenced the evolution and distribution of its flora, including the Camphorosmeae species. The evolutionary history of Camphorosmeae in Australia has been the subject of extensive research over the past few decades, with particular emphasis on the integration of morphological, molecular, and biogeographical data. The main hypotheses put forward by Cabrera et al. (2011), McDonald (2020), and Hühn et al. (2024) offer complementary yet distinct perspectives on the biogeographic patterns and processes driving the diversification and distribution of this group.

Cabrera et al. (2011) pioneered the molecular phylogenetic analysis of Camphorosmeae, highlighting that morphological characters were not fully consistent with molecular data, and suggesting complex evolutionary dynamics influenced by incomplete lineage sorting and hybridisation. Their work underlines the importance of the palaeoclimatic changes that occurred in the Miocene and Pliocene, when aridification processes allowed extensive diversification, particularly in southwestern Australia (Cabrera et al., 2011; Markgraf et al., 1995).

McDonald (2020) extended on this foundation by proposing that the Yilgarn and Eyre-Murray centres served as primary diversification centres for chenopods, with the Great Victoria Desert acting as a critical link for inland migration. His emphasis on niche conservatism, particularly with regard to salinity and flood tolerance, highlighted how these presumably ancestral ecological traits might have influenced the species' distribution and habitat preferences.

The recent study by Hühn et al. (2024) used advanced RADseq techniques to refine the phylogenetic framework of the Australian Camphorosmeae. Their study identified new clades and provided a more nuanced understanding of evolutionary relationships and habitat adaptations within the lineage. Our results confirm the west-to-east migration pattern and the key role of coastal environments in early colonisation, followed by inland expansion facilitated by changing palaeodrainage systems.

While these studies collectively advance our understanding of the evolution of Camphorosmeae, they also highlight persistent challenges. Incomplete taxon sampling, the complexity of Australia's geological and climatic history, and the diverse ecological requirements of different species complicate biogeographical analyses. Overcoming these challenges requires the integration of robust phylogenetic techniques with extensive biogeographic modelling and climate data.

To build on these basic hypotheses, our research aimed to perform an ancestral habitat reconstruction and a biogeographic analysis using an NGS-based phylogenetic tree as the backbones. This approach allowed us to infer more detailed insights into clade-specific ecological shifts.

**Climatic Influence on Evolution and Distribution of Australian Camphorosmeae**

Our study shows significant environmental gradients influencing the occurrence of Camphorosmeae species (Figure 1). The first principal component, driven by Maximum Temperature of Warmest Month (Bio05) and Mean Temperature of the Warmest Quarter (Bio10), explains 43.37% of the variance. This suggests that temperature extremes are crucial in determining and limiting the distribution of these species. The second principal component, linked to Precipitation in the Wettest Month (Bio13) and Precipitation in the Warmest Quarter (Bio18), accounts for 22.54% of the variance, indicating the importance of precipitation minimum and seasonality.

The Camphorosmeae species occupy predominantly areas with high maximum temperatures during the warmest month, as indicated by the clustering of occurrence points in the warmer regions of the climatic space. The maximum temperature in the warmest month for the Australian Camphorosmeae ranges from 27.9°C to 38.0°C, emphasising the adaptation to high temperatures. Additionally, their distribution in areas of low to moderate precipitation during the wettest month (24.3-79.5 mm) highlights their adaptability to different levels of aridity, with a notable presence in regions experiencing moderate rainfall (37-52 mm).

The annual genus *Grubovia* Freitag & G. Kadereit, which is sister to the Australian Camphorosmeae and native to Central Asia (Kadereit and Freitag, 2011; Kadereit et al., 2014), exhibits distinct climatic preferences that closely match those of its Australian relatives. Our analysis of the distribution of *Grubovia* species reveals a preferred maximum temperature in the warmest month (Bio05) ranging from 23.2°C to 27.9°C. This range is lower than the range of the Australian Camphorosmeae, but still overlaps, indicating an adaptation to relatively high temperatures. Regarding precipitation during the wettest month (Bio13), *Grubovia* species thrive in regions with 42.0 mm to 53.3 mm of precipitation. This range is within the wider range of 24.3 mm to 79.5 mm observed for Australian Camphorosmeae. It corresponds to the moderate precipitation conditions of 37 mm to 52 mm where the Australian species are most abundant. Thus, while *Grubovia* occupies a slightly cooler and more consistently moderate rainfall niche compared to Australian Camphorosmeae, both clades show strong adaptability to environments characterised by high temperatures and variable rainfall, particularly moderate conditions.

Looking at the ancestral climatic preferences of the Australian Camphorosmeae, we see that they favoured warmest month temperatures up to 34.2°C and areas with a precipitation during the wettest month of at least 52 mm. This suggests that the ancestors of these two sister lineages were already adapted to this kind of precipitation regime. The milder and lower the temperatures, similar to those preferred by *Grubovia*, furthermore suggest that the ancestors initially thrived in cooler climates. Over time, the lineage that became the Australian Camphorosmeae adapted to the changing climate within Australia since the end of the Late Miocene.

**Habitat evolution**

Reconstruction of ancestral habitat types may reveal critical ecological transitions that facilitated the adaptation and diversification of Camphorosmeae species. Our analysis shows distinct clusters of points in principal component (PC) space, indicating unique climatic conditions in different subregions (Figure 3). This reflects the ecological versatility and/or specialisation of these species, suggesting that they have evolved to occupy different climatic niches.

Our results indicate that the diverse range of habitats occupied by Australian Camphorosmeae highlights significant ecological diversity within the group. The habitat type “Riverine Desert” spans the entire backbone of the phylogeny, strongly suggesting it to be the ancestral habitat type of the Australian Camphorosmeae. In the “Riverine Desert”, where vegetation is open and arboreal along channels and floodplains, and where grasses and chenopods are found on broad plains, the climate is characterised by flooding with mild to moderate salinity and variable soil types (McDonald, 2020). This habitat type is well suited to species adapted to high temperatures and arid to semi-arid regions, being consistent with the adaptations observed in many Australian Camphorosmeae species. This demonstrates that “Riverine Desert” landscapes played a significant role as a migration corridor, further facilitating the spread and diversification of these species, as suggested by McDonald (2020) and Hühn et al. (2024), and is supported by our analysis. Certain clades strongly associate with other specific habitats, such as the “Shield Plain” for clades 6 and 16, “Desert Lake” for clades 1-3, 8 and 11, and “Sand Desert” habitats for clade 13. This suggests that habitat specialisation has played a crucial role in the evolutionary divergence of the lineage. The adaptability of Camphorosmeae to semi-arid and arid environments prevalent in Australia is reflected by the strong association between specific clades and particular habitats, indicating that habitat shift might have been one key driver of diversification within this group (Figure 5). The phylogenetic tree and density plots provide additional evidence (Figure 4).

The “Shield Plain” habitats are non-saline and contain a variety of xerophytic plant species (McDonald, 2020). *Sclerolaena drummondii* and *S. densiflora* (W.Fitzg.) A.J.Scott are two examples of a habitat shift from the regularly inundated “Riverine Desert” to the highly exposed rocky “Shield Plain” habitat.

The “Desert Lake” habitat is characterised by a strong salinity gradient, ranging from the bare salt crust to the slightly salty edges with halophytic vegetation (Mabbutt, 1988). A high-temperature tolerance of the species found there allows them to thrive in this environment, while those adapted to moderate amounts of precipitation are likely to be found on the less saline edges where conditions are less extreme. Most of the *Maireana* species tend to occur in the “Desert Lake” habitats.

The very young “Sand Desert” habitat, which was formed less than a million years ago during the Late Pleistocene (Fujioka and Chappell, 2010), characterised by hummock grassland, tall shrubland, or open woodland, generally lacks salinity except in areas where thin sand sheets cover older landscapes and is inhabited by glycophytes that are more competitive in the absence of salinity (McDonald, 2020; Flowers et al., 2010; Waisel, 1972).

It is important to mention that these habitat types are flexible in time and location and are very similar in their overall climatic conditions. They change continuously with changes in geography and climate. The boundaries of the arid and semi-arid areas have changed since the end of the Miocene in response to fluctuations in temperatures (Smith, 2013).

**Biogeography and Historical Processes**

The conducted large-scale biogeographic analysis identifies key dispersal and vicariance events that have shaped the current distribution of Camphorosmeae species. The overlap and separation of habitat types and occupied subregions highlight the diversity of climatic niches occupied by these species, reflecting historical biogeographical processes (Figures 3, 5, 6, 7). These findings provide insights into the evolutionary pressures and ecological dynamics that have influenced the distribution patterns of the Australian Camphorosmeae.

The combination of the Western Desert, Eastern Desert, and Adelaide geographic subregions (sensu Ebach et al., 2015) is identified as the ancestral range of Australian Camphorosmeae. Throughout the evolutionary timeline, particularly from the Late Miocene to the Pliocene, this region served as the core habitat for many Australian Camphorosmeae. The combination of Western and Eastern Desert, the so-called outback, occurs at several points in the phylogenetic tree. In particular, it is retrieved as the ancestral region for clades 3, 7-8 and 10-17. The persistence of this combination may highlight the climatic stability and continuity of the Western and Eastern Desert as key habitats of Camphorosmeae in Australia throughout the Late Neogene. The addition of the Eyre Peninsula to the ancestral range occurs in clades 2 and 4. This expansion likely happened during the Early to Middle Pliocene when the Eyre Peninsula was characterised by open vegetation (Kershaw et al., 1994). This timing suggests a gradual expansion of the distribution area of Camphorosmeae, colonising new habitats as suitable environmental conditions expanded.

In previous studies, it was assumed that the southwest part of Australia could be the area of origin of the Camphorosmeae (Cabrera et al., 2011). However, more recent analyses, including those by Hühn et al. (2024), challenge this view. The new data indicate that the distribution area of Camphorosmeae has not simply shifted from southwest to east, but rather from the west coast of the Western Desert. By considering McDonald's hypothesis, we gain a better understanding of the dispersal and establishment patterns of the Camphorosmeae (McDonald, 2020). The littoral connection hypothesis provides a plausible explanation for the observed distribution, suggesting that chenopods maintained their ecological preferences over time, which directed their spread from coastal regions into the interior deserts.

The recovery of the “Riverine Desert” as an ancestral habitat type adds a layer of complexity. While this habitat type supports the idea of a western origin due to the presence of certain taxa, it appears to contradict the broader biogeographical patterns observed (Figure 6). The data suggests that while there may be taxa in the western part of the Western Desert, the main ancestral range remains more centrally located between the Western and Eastern Deserts and Adelaide, due to the presence of many Late Miocene/Early Pliocene lineages and the greatest diversity of taxa (Figures 5, 6, 7).

Our study of the biogeographical history of the Australian Camphorosmeae reveals a dynamic evolutionary history of their ancestral ranges. Initially centred in the western and eastern deserts, they expanded to the coastline including Adelaide and later the Eyre Peninsula. This challenges previous assumptions of only western origin.

**Migration and local adaptation**

Migration and local adaptation to and in Australia have played a critical role in shaping the continent's biodiversity (Crisp and Cook, 2013; Weston et al., 2017). Plants in arid regions of Australia have developed a variety of complex evolutionary strategies to survive, avoid and persist in hot and water-limited environments (Norton et al., 2016). These strategies include processes of adaptation, in which plants change their structures or functions to better suit their environment (Dörken et al., 2020), and migration, in which they disperse seeds to new areas that offer suitable conditions. The evolution of plant groups in Australia's Eremaean Zone involves vicariance, pre-adapted immigration, and in-situ adaptation (Cauz-Santos et al., 2024). For example, *Eucalyptus* and *Calytrix*, both from the Myrtaceae family, are examples of vicariance (Cauz-Santos et al., 2024; Nge et al., 2022; Martin, 2006). An example of pre-adapted immigration, however, is the genus *Ptilotus*, which was already adapted to thrive in arid environments (Hammer et al., 2021). In-situ adaptation illustrates the evolution of traits specialised for arid conditions within the Eremaean zone. An example of in-situ adaptation in Australia is the persistence of *Banksia* (Proteaceae) species in response to changing climatic conditions, facilitated by adaptive genetic variation within populations (He et al., 2016).

The Australasian grass flora is an example of these processes. The migration and adaptation of grasses is influenced by factors such as climate stability and the suitability of new environments. The spread of grasses to Australia was facilitated by their pre-adaptation to dry, bright conditions, allowing them to outcompete native species (Bryceson et al., 2023). This migration was enhanced by broad land bridges that existed during the Last Glacial Maxima due to lower sea levels (Bryceson and Morgan, 2022).

In our study we observe several transitions from arid ecologies to areas with higher precipitation during the wettest month. Consequently, new traits are required for species to successfully invade these habitats. According to the dated phylogeny, these in-situ transitions are recent and involve comparatively young species and clades.

The two species-rich genera *Maireana* and *Sclerolaena* are known to prefer environments such as lake systems and saline areas. These species are likely to be influenced not only by edaphic factors such as soil type but also by the hydrology of the area, which is highly variable. There have been significant changes during the Pliocene, particularly around the Lake Eyre system, affecting the extent of lakes and saline environments (Habeck-Fardy and Nanson, 2014).

Our formal analyses clarify and detail patterns previously hypothesised, revealing both migration and local adaptation in different species. For example, the *Roycea* group in clade 1, which is one of the early divergent lineages, is nowadays widespread in western Australia, mostly in the subregions Southwestern (*R. pycnophylloides*, *R. spinescens* and *R. divaricata*), Western Desert and Southwest Interzone (*R. divaricata*), with Western Desert (I), the Eastern Desert (H) and Adelaide (C) as the ancestral areas (Figure 7). The ancestors of these three species are likely to have originated in the Riverine Desert habitat and remained in the area while the Riverine Desert migrated eastwards and other habitats arose or changed (Figure 6). The Desert Lake habitat, for example, began to form in the Pliocene, of western Australia. The age of the current habitats in which *Roycea* occurs do not match the age of the lineage. This suggests that *Roycea* did not migrate with the Riverine Desert habitat, which originated in the west of Australia (Cabrera, 2007) and migrated eastwards but instead **adapted** to the Desert Lake habitat in west Australia (Figures 5 and 6). Another example is the two species *Sclerolaena drummondii* and *S. densiflora* that occur in the Shield Plain habitat. That habitat originated in the Yilgran Block in Western Australia and central Australia in the Arunta Block (Mabbutt, 1988) during the Late Miocene. Both species adapted to the Shield Plain habitat in place, while the Riverine Desert habitat migrated eastwards.

Previous hypotheses suggested that the Southwestern Interzone (F) and the Southwestern (G) habitat types might be ancestral, but this analysis indicates otherwise. Focusing on the Riverine Desert, discussing its age, distribution, and role as a connecting habitat is crucial. These rivers around the Lake Eyre and Murray-Darling Basin, which exist yearly for only 3-4 months before disappearing due to lack of precipitation, follow biogeographic patterns. This demonstrates a balance between niche conservatism and ecological flexibility. Species that retained the Riverine Desert niche migrated east with the habitat, while others that either were ecologically broader and not dependent on the Riverine Deserts, or managed to adapt to the new habitats could remain in the west.

Travelling further east, seasonality becomes more pronounced, and precipitation decreases. In the far southeast, the Australian Alps create a rain shadow, reducing rainfall further inland. Ancestral lineages that **migrated** southeast, such as the clades 9 and 12, as indicated by branches showing precipitation values under and equal to 36.6 mm during the wettest month (Figure 4) adapted to these conditions. The Riverine Desert has long been considered a connecting habitat, and our findings confirm this notion. Hühn et al. (2024) initially hypothesised this and our formal analysis, using ancestral character state reconstruction, supports and extends the conclusions by Hühn et al. (2024). Some species that **migrated** south or towards the coast of Australia like *M. enchylaenoides, E. lanata, M. marginata, D. roei* or *T. diffusa* have branches showing precipitation equal to or greater than 52 mm during the wettest month (Figure 4). Although the ancestors were adapted to survive in areas with precipitation equal to or greater than 52 mm, the descendant species occurred in areas with less than 52 mm precipitation during the wettest month. These mentioned species are presumably more competitive in the regions where 52 mm or more of precipitation falls in the wettest month..

In examining the interplay between migration and adaptation in Australian Camphorosmeae in Australia's dynamic habitats, it becomes clear that distinguishing between the two processes is complex by nature. Habitats and distribution areas of species are both changing constantly, making it difficult to clearly separate migration from local adaptation. In most cases, a mixture of both processes is at work, with one occasionally dominating the other.

Indeed, it is reasonable to question the need for such a distinction, especially in areas that are connected.

**Challenges and further work**

Studying the general biology of the Australian Camphorosmeae is challenging due to several factors, including Australia’s wide and often remote landscapes, which can hinder fieldwork and sample collection, resulting in sampling gaps. Additionally, the complex geological history of the Australian continent, characterised by tectonic activity, climatic fluctuations, and sea level changes, has influenced the distribution and diversification of plant species over millions of years (Dettmann, 1994). Furthermore, the Camphorosmeae tribe comprises species with different ecological requirements and dispersal abilities (Cabrera, 2007), further complicating biogeographical analyses.

The phylogenetic analysis also presents challenges with temporal constraints, especially concerning the Sand Desert habitat. The discrepancy between the estimated age of the sand desert and the migration patterns of Camphorosmeae species, particularly in clade 13, which inhabits the Sand Desert, is shown in Figure 5. This suggests either an error in estimating the age of the habitat, or multiple migrations into the Sand Desert over time. These taxa might have had different ecologies and did only recently migrate into the Sand Desert. Evidence, particularly from groups such as *Triodia* spp., suggests that the Sand Desert habitats are relatively recent (Mabbutt, 1988; Grigg, 2009). The branch length extending back 5 to 4 million years complicates the interpretation, as introducing temporal constraints into the biogeographic model may not significantly affect the state shift estimates. The habitat types, such as Karst Plain, Shield Plain or Desert Lake span multiple geographic regions, making it difficult to perform precise biogeographic reconstructions, a problem exacerbated by the constant shifting of those regions. Similarly, clades 1-3 and the species *M. oppositifolia* show Desert Lake as an ancestral habitat dated to the Late Miocene, whereas the estimated age of these habitats based on palaeogeographic evidence appears to be the Early Pliocene in Western Australia and Late Pliocene in Central Australia (McDonald, 2020). If we accept these estimated habitat ages, only the Riverine Desert could be the ancestral habitat due to its age. However, this raises questions about the true ancestral status given the unresolved backbone of the phylogeny.

The diverse range of habitats occupied by Camphorosmeae species, particularly their association with saline environments and fluctuating hydrological conditions (Cabrera et al., 2011; Hühn et al., 2024), suggests that edaphic factors and hydrology may influence their distribution greatly. This variability, particularly around systems such as Lake Eyre, highlights the need for finer-scale analyses and potentially more nuanced biogeographic coding to capture the dynamic environmental changes over the past eight million years.

Data limitations are another challenge. The partly unresolved backbone and the absence of 56 species (36 *Sclerolaena*, 15 *Maireana*, one *Dissocarpus*, one *Malacocera*, one *Neobassia*, and two *Osteocarpum* species) from the phylogeny limit the scope of the analysis. Although the current phylogeny represents an improvement over previous datasets and does not exhibit significant sampling bias, including these species in future analyses could refine our understanding of their evolutionary and biogeographic patterns. After conducting an additional analysis to account for the missing 56 species by filtering the most important subregions (i.e. areas with more than 10% of occurrences per species), three further subregions (Eastern Queensland, Great Sandy Desert Interzone and Southeastern) were identified to be important (Table S2, Figure S1). It may be that the inclusion of ecologically highly specialised species such as *Sclerolaena hostilis* (Diels) Dominwould be a valuable contribution to a more comprehensive phylogenetic framework, as this species only occurs in the Great Sandy Desert Interzone with a 100% occurrence rate.

All these challenges highlight the complexity of studying the evolutionary and biogeographic history of Camphorosmeae species in Australia. Future research should aim to address these limitations by improving phylogenetic resolution through methods such as target enrichment or genome skimming, conducting finer-scale habitat and biogeographic analyses, and including currently missing species to provide a complete picture of their evolutionary dynamics. The distinction between migration and adaptation can be effectively studied through the combined use of population genetics and ecological niche modelling. These methods provide complementary insights into the processes that drive species distribution and evolution.

**5. Conclusion**

The study of Camphorosmeae in Australia reveals a vibrant evolutionary and biogeographical history shaped by climate change and habitat diversification. The combination of morphological, molecular and biogeographical data has provided insights into the evolutionary dynamics of this lineage, highlighting the influence of temperature and precipitation on species distributions. The ancestral adaptation to warm and moderately humid climates allowed the migration and local adaptation of Camphorosmeae to different habitats, in particular the Riverine Desert, which played a crucial role in their diversification. Despite advances in understanding, challenges such as incomplete sampling and complex geological histories remain, requiring further research to refine phylogenetic frameworks and biogeographic models. Overall, this research highlights the interplay between ecological flexibility and niche conservatism in shaping the biodiversity of Australian Camphorosmeae.

**Acknowledgements**

We thank Atlas of Living Australia for making occurrence data available, and all data collectors and contributors to ALA for their efforts. We thank Dr. Philipp Hühn and Dr. John McDonald for sharing their knowledge and results and engaging in discussions over the last years that significantly inspired this manuscript. This work was supported by the DFG grant KA1816-11/1.

**Conflict of interest**

The authors declare no conflict of interest.

**Author contributions**

**Jessica A. Berasategui:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); visualisation (lead); writing – original draft (lead); writing-review & editing (lead)

**Anže Žerdoner Čalasan:** Conceptualization (supporting); writing – original draft (supporting); writing-review & editing (supporting)

**Gudrun Kadereit:** Conceptualization (supporting); Formal analysis (supporting); writing – original draft (supporting); writing-review & editing (supporting); funding acquisition and project administration (lead)

**Data Availability Statement**

The data that support the findings of this study are available in the supplementary material of this article.

**ORCID**

**Jessica A. Berasategui (née Los):** <https://orcid.org/0000-0002-0375-7397>

**Anže Žerdoner Čalasan:** <https://orcid.org/0000-0003-2081-2076>

**Gudrun Kadereit:** <https://orcid.org/0000-0003-0094-8769>

**Appendix A. Supplementary data**

Supplementary data associated with this article can be found in the online version.

**Table S1:** Coordinates of all species downloaded from ALA.

**Table S2:** Percentage of occurrence points per species across subregions.

**Table S3:** PCA loadings.

**Figure S1:** Occurrence of excluded species.

**References**

Atlas of Living Australia website at [http://www.ala.org.au](http://www.ala.org.au/). Last accessed 18 March 2024.

Belbin, L., Wallis, E., Hobern, D. and Zerger, A., 2021. The Atlas of Living Australia: History, current state and future directions. *Biodiversity Data Journal*, *9*. <https://doi.org/10.3897/BDJ.9.e65023>.

Belbin, L. and Williams, K.J., 2016. Towards a national bio-environmental data facility: experiences from the Atlas of Living Australia. *International Journal of Geographical Information Science*, *30*(1), pp.108-125.<https://doi.org/10.1080/13658816.2015.1077962.>

Bowman, D.M.J.S. and Cook, G.D., 2002. Can stable carbon isotopes (δ13C) in soil carbon be used to describe the dynamics of Eucalyptus savanna–rainforest boundaries in the Australian monsoon tropics? *Austral Ecology*, *27*(1), pp.94-102. <https://doi.org/10.1111/j.1442-9993.2002.tb00156.x.>

Bryceson, S.R. and Morgan, J.W., 2022. The Australasian grass flora in a global context. *Journal of Systematics and Evolution*, *60*(3), pp.675-690.https://doi.org/10.1111/jse.12839[.](https://doi.org/10.1111/jse.12839.)

Bryceson, S.R., Hemming, K.T., Duncan, R.P. and Morgan, J.W., 2023. The contemporary distribution of grasses in Australia: A process of immigration, dispersal and shifting dominance. *Journal of Biogeography*, *50*(9), pp.1639-1652. https://doi.org/10.1111/jbi.14676.

Burbidge, N.T., 1960. The phytogeography of the Australian region. *Australian Journal of Botany*, *8*(2), pp.75-211.https://doi.org/10.1071/bt9600075[.](https://doi.org/10.1071/bt9600075.)

Cabrera, J.F., 2007. *Phylogeny and historical biogeography of the Australian Camphorosmeae (Chenopodiaceae)* (Doctoral dissertation, Mainz, Univ., Diss., 2007).

Cabrera, J., Jacobs, S.W. and Kadereit, G., 2011. Biogeography of Camphorosmeae (Chenopodiaceae): tracking the Tertiary history of Australian aridification. *Telopea*, *13*(1-2), pp.313-326.<https://doi.org/10.7751/telopea20116023.>

Cabrera, J.F., Jacobs, S.W. and Kadereit, G., 2009. Phylogeny of the Australian Camphorosmeae (Chenopodiaceae) and the taxonomic significance of the fruiting perianth. *International Journal of Plant Sciences*, *170*(4), pp.505-521.<https://doi.org/10.1086/597267.>

Carolin, R.C., 1975. Leaf structure in Chenopodiaceae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, *95*, pp.226-255.

Cauz-Santos, L.A., Samuel, R., Metschina, D., Christenhusz, M.J., Dixon, K.W., Conran, J.G., Paun, O. and Chase, M.W., 2024. Recent speciation and adaptation to aridity in the ecologically diverse Pilbara region of Australia enabled the native tobaccos (Nicotiana; Solanaceae) to colonize all Australian deserts. *bioRxiv*, pp.2024-06. <https://doi.org/10.1101/2024.06.12.598428.>

Christophel, D.C., 1989. Evolution of the Australian flora through the Tertiary. In *Woody plants - evolution and distribution since the Tertiary: Proceedings of a symposium organized by Deutsche Akademie der Naturforscher Leopoldina in Halle/Saale, German Democratic Republic, October 9–11, 1986*, pp.63-78. Springer Vienna.<https://doi.org/10.1007/978-3-7091-3972-1_3.>

Commonwealth of Australia, 2006. Integrated Marine and Coastal Regionalisation of Australia Version 4.0. Environment Australia.

Crisp, M.D. and Cook, L.G., 2013. How was the Australian flora assembled over the last 65 million years? A molecular phylogenetic perspective. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), pp.303-324.https://doi.org/10.1146/annurev-ecolsys-110512-135910[.](https://doi.org/10.1146/annurev-ecolsys-110512-135910.)

Dettmann, M.E., 1994. Cretaceous vegetation: the microfossil record. *History of the Australian vegetation: Cretaceous to Recent*, pp.143-170.

Dettmann, M.E. and Jarzen, D.M., 1998. The early history of the Proteaceae in Australia: the pollen record. *Australian Systematic Botany*, *11*(4), pp.401-438. <https://doi.org/10.1071/sb97022.>

Dörken, V.M., Ladd, P.G. and Parsons, R.F., 2020. Anatomical aspects of xeromorphy in arid-adapted plants of Australia. *Australian Journal of Botany*, *68*(3), pp.245-266. https://doi.org/10.1071/BT19073.

Ebach, M., Murphy, D.J., Gonzalez-Orozco, C. and Miller, J., 2015. A revised area taxonomy of phytogeographical regions within the Australian Bioregionalisation Atlas. *Phytotaxa*, *208*(4), pp.261-277.<https://doi.org/10.11646/phytotaxa.208.4.2.>

Ebach, M.C., 2012. A history of bioregionalisation in Australia. *Zootaxa*, *3392*.<https://doi.org/10.11646/zootaxa.3392.1.1.>

Feakins, S.J., Warny, S. and DeConto, R.M., 2014. Snapshot of cooling and drying before onset of Antarctic Glaciation. *Earth and Planetary Science Letters*, *404*, pp.154-166.<https://doi.org/10.1016/j.epsl.2014.07.032.>

Fick, S.E. and Hijmans, R.J., 2017. WorldClim 2: new 1‐km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), pp.4302-4315.<https://doi.org/10.1002/joc.5086.>

Flowers, T.J., Galal, H.K. and Bromham, L., 2010. Evolution of halophytes: multiple origins of salt tolerance in land plants. *Functional Plant Biology*, *37*(7), pp.604-612. [https://doi.org/10.1071/fp09269.](https://doi.org/10.1071/fp09269)

Freitag, H. and Kadereit, G., 2014. C3 and C4 leaf anatomy types in Camphorosmeae (Camphorosmoideae, Chenopodiaceae). *Plant Systematics and Evolution*, *300*, pp.665-687.<https://doi.org/10.1007/s00606-013-0912-9.>

Fujioka, T. and Chappell, J., 2010. History of Australian aridity: chronology in the evolution of arid landscapes. *Geological Society, London, Special Publications*, *346*(1), pp.121-139.<https://doi.org/10.1144/sp346.8.>

Funk, V.A. ed., 2009. *Systematics, Evolution, and Biogeography of Compositae*, pp.171-189. Vienna: International Association for Plant Taxonomy.

Geoscience Australia, 1994. Geoscience Australia Deserts Database. [*https://www.ga.gov.au/scientific-topics/national-location-information/landforms/deserts*](https://www.ga.gov.au/scientific-topics/national-location-information/landforms/deserts)*,* revised 2022, viewed 14.May 2024.

Grigg, A.M., 2009. An ecophysiological approach to determine problems associated with mine-site rehabilitation: a case study in the Great Sandy Desert, north-western Australia, *University of Western Australia*.

Habeck-Fardy, A. and Nanson, G.C., 2014. Environmental character and history of the Lake Eyre Basin, one seventh of the Australian continent. *Earth-Science Reviews*, *132*, pp.39-66. https://doi.org/10.1016/j.earscirev.2014.02.003.

Hadwen, W.L., Arthington, A.H., Boon, P.I., Taylor, B. and Fellows, C.S., 2011. Do climatic or institutional factors drive seasonal patterns of tourism visitation to protected areas across diverse climate zones in eastern Australia? *Tourism Geographies*, *13*(2), pp.187-208.<https://doi.org/10.1080/14616688.2011.569568.>

Hammer, T.A., Renton, M., Mucina, L. and Thiele, K.R., 2021. Arid Australia as a source of plant diversity: the origin and climatic evolution of *Ptilotus* (Amaranthaceae). *Australian Systematic Botany*, *34*(6), pp.570-586.https://doi.org/10.1071/sb17062[.](https://doi.org/10.1071/sb17062.)

He, T., D’Agui, H., Lim, S.L., Enright, N.J. and Luo, Y., 2016. Evolutionary potential and adaptation of *Banksia attenuata* (Proteaceae) to climate and fire regime in southwestern Australia, a global biodiversity hotspot. *Scientific Reports*, *6*(1), p.26315. https://doi.org/10.1038/srep26315.

Hühn, P., McDonald, J., Shepherd, K.A. and Kadereit, G., 2024. Diversification of Camphorosmeae (Amaranthaceae *s.l.*) during the Miocene-Pliocene aridification of inland Australia. *Perspectives in Plant Ecology, Evolution and Systematics*, p.125811. <https://doi.org/10.1016/j.ppees.2024.125811>.

Jacobs, S.W.L., 2001. Review of leaf anatomy and ultrastructure in the Chenopodiaceae (Caryophyllales). *Journal of the Torrey Botanical Society*, pp.236-253.<https://doi.org/10.2307/3088716.>

Jansen, R.K., Michaels, H.J. and Palmer, J.D., 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. *Systematic Botany*, pp.98-115.<https://doi.org/10.2307/2418976.>

Kadereit, G. and Freitag, H., 2011. Molecular phylogeny of Camphorosmeae (Camphorosmoideae, Chenopodiaceae): Implications for biogeography, evolution of C4‐photosynthesis and taxonomy. *Taxon*, *60*(1), pp.51-78.<https://doi.org/10.1002/tax.601006.>

Kadereit, G., Gotzek, D. and Freitag, H., 2005. Origin and age of Australian Chenopodiaceae. *Organisms Diversity & Evolution*, *5*(1), pp.59-80.https://doi.org/10.1016/j.ode.2004.07.002[.](https://doi.org/10.1016/j.ode.2004.07.002.)

Kadereit, G., Lauterbach, M., Pirie, M.D., Arafeh, R. and Freitag, H., 2014. When do different C4 leaf anatomies indicate independent C4 origins? Parallel evolution of C4 leaf types in Camphorosmeae (Chenopodiaceae). *Journal of Experimental Botany*, *65*(13), pp.3499-3511. https://doi.org/10.1093/jxb/eru169.

Kassambara, A. and Mundt, F., 2016. Factoextra: extract and visualize the results of multivariate data analyses. *R package version*, *1*.<https://doi.org/10.32614/cran.package.factoextra.>

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J. and Cornelissen, J.H.C., 2011. TRY - a global database of plant traits. *Global change biology*, *17*(9), pp.2905-2935.

Kershaw, A.P., Martin, H.A. and Mason, J.M., 1994. 13 The Neogene: a period of transition. *History of the Australian vegetation: Cretaceous to Recent*, p.299.

Ladiges, P.Y., Udovicic, F. and Nelson, G., 2003. Australian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. *Journal of Biogeography*, *30*(7), pp.989-998.<https://doi.org/10.1046/j.1365-2699.2003.00881.x.>

Landis, M.J., Matzke, N.J., Moore, B.R. and Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, *62*(6), pp.789-804.<https://doi.org/10.1093/sysbio/syt040.>

Mabbutt, J.A., 1988. Australian desert landscapes. *GeoJournal*, *16*, pp.355-369.https://doi.org/10.1007/bf00214394[.](https://doi.org/10.1007/bf00214394.)

Markgraf, V., McGlone, M. and Hope, G., 1995. Neogene paleoenvironmental and paleoclimatic change in southern temperate ecosystems - a southern perspective. *Trends in Ecology & Evolution*, *10*(4), pp.143-147.https://doi.org/10.1016/S0169-5347(00)89023-0.

Martin, H.A., 1981. The Tertiary flora. *Monographiae Biologicae*, pp.393-406.<https://doi.org/10.1007/978-94-009-8629-9_13.>

Martin, H.A., 2006. Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of arid Environments*, *66*(3), pp.533-563. <https://doi.org/10.1016/j.jaridenv.2006.01.009.>

Matzke, N.J., 2013. BioGeoBEARS: BioGeography with Bayesian (and likelihood) evolutionary analysis in R Scripts. R Package, Version 1.1.1, 1. <https://doi.org/10.5281/zenodo.1478250>.

Matzke, N.J., 2014. Model Selection in Historical Biogeography Reveals that Founder-Event Speciation Is a Crucial Process in Island Clades. *Systematic Biology, 63*(6), pp.951-970.

<https://doi.org/10.1093/sysbio/syu056.>

McDonald, J.T., 2020. *Biogeography of Australian chenopods: landscape in the evolution of an arid flora* (Doctoral dissertation).<https://hdl.handle.net/2440/126029>.

Morales-Briones, D.F., Kadereit, G., Tefarikis, D.T., Moore, M.J., Smith, S.A., Brockington, S.F., Timoneda, A., Yim, W.C., Cushman, J.C. and Yang, Y., 2021. Disentangling sources of gene tree discordance in phylogenomic data sets: testing ancient hybridizations in Amaranthaceae sl. *Systematic Biology*, *70*(2), pp.219-235. <https://doi.org/10.1093/sysbio/syaa066.>

Nge, F.J., Biffin, E., Waycott, M. and Thiele, K.R., 2022. Phylogenomics and continental biogeographic disjunctions: insight from the Australian starflowers (*Calytrix*). *American Journal of Botany*, *109*(2), pp.291-308.https://doi.org/10.1002/ajb2.1790[.](https://doi.org/10.1002/ajb2.1790.)

Norton, M.R., Malinowski, D.P. and Volaire, F., 2016. Plant drought survival under climate change and strategies to improve perennial grasses. A review. *Agronomy for Sustainable Development*, *36*, pp.1-15. https://doi.org/10.1007/s13593-016-0362-1.

Pearce, M., Willis, E., Wadham, B.E.N. and Binks, B., 2010. Attitudes to drought in outback communities in South Australia. *Geographical Research*, *48*(4), pp.359-369.<https://doi.org/10.1111/j.1745-5871.2009.00639.x.>

Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet;<http://www.plantsoftheworldonline.org/> Retrieved 19 April 2023.

QGIS.org, 2024. QGIS Geographic Information System. QGIS Association. [http://www.qgis.org](http://www.qgis.org/)

Ree, R.H. and Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*(1), pp.4-14.<https://doi.org/10.1080/10635150701883881.>

Ronquist, F., 1997. Dispersal-Vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, *46*(1), pp.195-203. <https://doi.org/10.2307/2413643.>

Sage, R.F., Sage, T.L., Pearcy, R.W. and Borsch, T., 2007. The taxonomic distribution of C4 photosynthesis in Amaranthaceae sensu stricto. *American Journal of Botany*, *94*(12), pp.1992-2003.<https://doi.org/10.3732/ajb.94.12.1992.>

Shmida, A., 1985. Biogeography of the desert floras of the world, in: Evenari, M., Noy-Meir, I., Goodall, D.W. (Eds.), Hot Deserts and Arid Shrublands. *Elsevier, Amsterdam, The Nethlerlands,* pp.23–77.

Smith, M., 2013. *The archaeology of Australia's deserts*. Cambridge University Press.

Thackway, R. and Cresswell, I.D., 1995. *An interim biogeographic regionalisation for Australia: a framework for setting priorities in the national reserves system cooperative*. Australian Nature Conservation Agency, Reserve Systems Unit.

Van Dam, M.H. and Matzke, N.J., 2016. Evaluating the influence of connectivity and distance on biogeographical patterns in the south‐western deserts of North America. *Journal of Biogeography*, *43*(8), pp.1514-1532.<https://doi.org/10.1111/jbi.12727>.

Waisel, Y., 1972. 'Biology of Halophytes.' Academic Press: New York.

Walker, J.F., Yang, Y., Feng, T., Timoneda, A., Mikenas, J., Hutchison, V., Edwards, C., Wang, N., Ahluwalia, S., Olivieri, J. and Walker‐Hale, N., 2018. From cacti to carnivores: Improved phylotranscriptomic sampling and hierarchical homology inference provide further insight into the evolution of Caryophyllales. *American Journal of Botany*, *105*(3), pp.446-462.<https://doi.org/10.1002/ajb2.1069>.

Webb, J., Grimes, K.G. and Osborne, A., 2003. Black holes: caves in the Australian landscape. *Beneath the surface: A natural history of Australian caves*, pp.1-52.

Weston, P., Jordan, G. and Keith, D.A., 2017. Evolutionary biogeography of the Australian flora in the Cenozoic Era. *Australian vegetation*, pp.40-62.

**ALA - Reference**

https://doi.org/10.26197/ala.a4134452-6171-4ad7-8da0-46682199a2d8. Accessed 30 May 2023

**Figure Legends**

**Figure 1: Principal Component Analysis (PCA) Biplot and Loadings for 19 Bioclimatic Variables conducted with all distribution points of 103 Australian Camphorosmeae species together.** The biplot shows the first principal component (PC1) on the x-axis and the second principal component (PC2) on the y-axis. Each vector represents a bioclimatic variable, with the direction and length indicating its contribution to the principal components. Variables Bio05 and Bio13 are highlighted on the biplot as they have significant contributions to PC1 and PC2, respectively. The table on the right lists the loading values of each variable on PC1 and PC2. The bold values indicate the variables with the highest loadings on each principal component. PCA loadings can be found in **Supplementary Table S3**.

**Figure 2:** **PCA biplots for Bio05 (Maximum Temperature of Warmest Month) and Bio13 (Precipitation of Wettest Month) over Australia's climatic space.** Each point represents one of 200,000 spatially randomised locations in Australia, with, for Bio05, coloured according to the maximum temperature of the warmest month (°C). The colour gradient ranges from purple (cooler temperatures) to yellow (warmer temperatures). For Bio13 coloured points according to the precipitation of the wettest month in millimetres (mm). The colour gradient ranges from light blue (lower precipitation) to dark blue (higher precipitation). Inset maps show the spatial distribution of these bioclimatic variables across Australia. Black dots indicate the distribution points of 103 Australian Camphorosmeae species.

**Figure 3: PCA of climate range across Australia.** Each point represents one of 200,000 spatially randomised locations in Australia. Coloured dots represent the subregions with more than 10% of the occurrence points per species. Subregions are shown on the map. PCA loadings can be found in **Supplementary Table S3**.

**Figure 4: Phylogenetic visualisation of bioclimatic niche reconstruction at ancestral nodes for two clustered environmental variables in the phylogenetic MCC tree of Australian Camphorosmeae.** Density plots show the distribution frequency across all clades, with red dashed lines indicating threshold values. Bio05: branches are coloured by temperature: ≤ 34.2°C (green) and > 34.2°C (black). Bio13: branches are coloured by precipitation: ≤ 36.6 mm (blue), 37-52 mm (green), and > 52 mm (black). Outgroup species are marked with a star.

**Figure 5: Ancestral Habitat Type Reconstruction for the Australian Camphorosmeae based on the dated MCC tree.** It represents the evolutionary relationships among 104 (*Sclerolaena* sp. *yeltacowie* included) Australian Camphorosmeae species with ten habitat types defined by Mabbutt (1988) and McDonald (2020). Branch colours indicate each node’s most likely ancestral habitat type, inferred from habitat reconstruction analyses using Mesquite's maximum parsimony method. The right side of the tree shows the current habitat type distributions for each species based on McDonald (2020). Major clades are labelled from 1 to 17 based on Hühn et al. (2024). The phylogeny is calibrated with that time scale at the bottom, divided into the Middle Miocene, Late Miocene, Pliocene, and Pleistocene epochs. The horizontal bars below the time scale show the different habitat types over geological periods based on McDonald (2020). Outgroup species are marked with a star.

**Figure 6: The five important habitat types of the Australian Camphorosmeae.** Riverine Desert (RL), Karst Plain (KP), Shield Plain (SH), Desert Lake (DL), and Sand Desert (SD). Each map shows the geographical extent of a particular habitat type and its evolution over geological periods from the Middle Miocene to the Pleistocene based on Mabbutt (1988) and McDonald (2020). The arrow in the Riverine Desert map indicates the distribution through time. Coloured habitat types are based on Mabbutt (1988) and Webb et al. (2003).

**Figure 7: Biogeography analysis on the time-calibrated phylogenetic MCC tree showing the distribution of Australian Camphorosmeae species across various subregions in Australia over time.** Biogeographic analysis was conducted in BioGeoBEARS v1.1.2 with a maximum range size of four. The colour-coded matrix next to the species names corresponds with the current species distributions. Subregions were chosen only if more than 10% of each species' occurrence points were present within those areas. Squares at nodes represent the ancestral range with the highest probability from the BAYAREALIKE analysis. Colours represent the areas as indicated on the map or combinations of them. The Australian subregion map is based on Ebach et al., 2015. Combined area maps on the right: (1) shows the combination of the subregions C, H, and I in dark red, (2) shows the combination of H and I in light blue, (3) shows the combination of C, D, H, and I in grey. Outgroup species are marked with a star.