

INVITED REVIEW

Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota

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Abstract

The integration of phylogenetics, phylogeography and palaeoenvironmental studies is providing major insights into the historical forces that have shaped the Earth's biomes. Yet our present view is biased towards arctic and temperate/tropical forest regions, with very little focus on the extensive arid regions of the planet. The Australian arid zone is one of the largest desert landform systems in the world, with a unique, diverse and relatively well-studied biota. With foci on palaeoenvironmental and molecular data, we here review what is known about the assembly and maintenance of this biome in the context of its physical history, and in comparison with other mesic biomes. Aridification of Australia began in the Mid-Miocene, around 15 million years, but fully arid landforms in central Australia appeared much later, around 1–4 million years. Dated molecular phylogenies of diverse taxa show the deepest divergences of arid-adapted taxa from the Mid-Miocene, consistent with the onset of desiccation. There is evidence of arid-adapted taxa evolving from mesic-adapted ancestors, and also of speciation within the arid zone. There is no evidence for an increase in speciation rate during the Pleistocene, and most arid-zone species lineages date to the Pliocene or earlier. The last 0.8 million years have seen major fluctuations of the arid zone, with large areas covered by mobile sand dunes during glacial maxima. Some large, vagile taxa show patterns of recent expansion and migration throughout the arid zone, in parallel with the ice sheet-imposed range shifts in Northern Hemisphere taxa. Yet other taxa show high lineage diversity and strong phylogeographical structure, indicating persistence in multiple localised refugia over several glacial maxima. Similar to the Northern Hemisphere, Pleistocene range shifts have produced suture zones, creating the opportunity for diversification and speciation through hybridisation, polyploidy and parthenogenesis. This review highlights the opportunities that development of arid conditions provides for rapid and diverse evolutionary radiations, and re-enforces the emerging view that Pleistocene environmental change can have diverse impacts on genetic structure and diversity in different biomes. There is a clear need for more detailed and targeted phylogeographical studies of Australia's arid biota and we suggest a framework and a set of a priori hypotheses by which to proceed.

Keywords: arid biota, Australia, diversity, palaeoclimate, phylogeny, phylogeography

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Introduction

Coarse patterns in the Earth's present climate and geology correspond with distinct constellations of plants and animals. Yet the origin and assembly of these major biomes also reflects unique evolutionary and colonisation histories acted out on a stage of significant global environmental change (Pennington *et al.* 2004; Sanmartin & Ronquist 2004; Poux *et al.* 2005; Crisp 2006; Galley & Lindner 2006). An understanding of the historical processes that have produced today's major biomes is not only of intrinsic interest, but is also relevant to the way we manage them under future environmental change (Moritz 1994; Hewitt 2004a, b).

Our capacity to unravel the histories of the Earth's biomes has taken a quantum leap in the last two decades with key developments in both the biological and physical sciences. First, there has been a revolution in phylogenetics: rigorous phylogenies and phylogeographies are now routinely produced using molecular genetic data, often using divergence time dating techniques. These data sets are critical to tests of biome origin and assembly (Crisp 2006). Second, methods and dating techniques in palaeostratigraphy have also improved, providing a more precise palaeochronology for biologists. The integration of findings from biological disciplines with detailed knowledge of the timing and nature of climatic and geological events has provided new perspectives on the evolutionary history of many of the world's biotas.

Most of the research focus on biome assembly has been in the Northern Hemisphere, especially temperate Europe (Hewitt 2001, 2004a; Taberlet *et al.* 1998), western North America (Soltis *et al.* 1997; Brunfeldt *et al.* 2001; Cook *et al.* 2001; Lessa *et al.* 2003), southeastern North America (Avisé 2000; Soltis *et al.* 2006), the Arctic and Beringia (Weider & Hobæk 2000; Hewitt 2004a; Kadereit *et al.* 2004; Kadereit & Comes 2005), the European Alps (Tribsh & Schonswetter 2003) and the California Floristic Province (Calsbeek *et al.* 2003). A growing number of Southern Hemisphere biomes are also being investigated (see Beheregaray 2008), including the Wet Tropics rainforest (Stork & Turton 2008) and temperate eucalypt forests (Sunnucks *et al.* 2006) of Australia. These studies are painting a general picture of the impacts of geologically recent environmental change on biome assembly and maintenance across the globe, with numerous commonalities emerging as well as idiosyncratic, biome-specific responses. Yet this picture remains incomplete without knowledge of the equivalent patterns and processes in the widespread arid-zone biomes of the planet. Although some individual species have been studied (e.g. Eggert *et al.* 2002; Zink 2002; Bates *et al.* 2003; Murphy *et al.* 2006;

Leaché & Mulcahy 2007), synthetic molecular phylogenetic studies of the evolution of arid-zone biotas are yet to be carried out.

An arid biome ideally suited to broad-scale comparative phylogenetic and phylogeographical analysis is the Australian arid zone, here defined as the region of Australia having a moisture index of less than 0.4 (mean annual rainfall divided by evaporation) (Fig. 1). First, it is the largest biome in Australia, and one of the largest deserts in the world, occupying approximately 70% of Australia's 7.5 million square kilometres. Second, the Australian arid zone's physical origins are well understood: while arid environments were probably present in Australia during the Mid-Tertiary, current arid-zone stony and sandy desert landforms are much younger, with their origin in the Early Pliocene and Mid-Pleistocene (Fujioka *et al.* 2005, 2008). Thus, it is considerably younger than the mesic biomes of Australia's southern, eastern and northern coastlines that stem from the ancestral Mesozoic Gondwanan forests that were widespread until the Mid-Tertiary (Hill 1994; Schodde 2006). Third, the biota of the Australian arid zone is already well described from taxonomic and ecological perspectives (e.g. Barker & Greenslade 1982; Cogger & Cameron 1984; Stafford-Smith & Morton 1990; Dawson & Dawson 2006), with a number of hypotheses already proposed about its evolutionary origins (Schodde 1982; Maslin & Hopper 1982; Cracraft 1986, 1991).

Molecular phylogenetic studies of a diverse array of Australian arid zone plants, invertebrates and vertebrates are beginning to accumulate, and our understanding of the climatic and geological history of the region is continuing to develop. However, a coordinated multispecies approach integrating knowledge from the physical sciences, equivalent to those underway in other regions of the world, is just beginning in Australia. Here we present a synthesis of current knowledge of the history of the Australian arid-zone biota, and the climate and landscape that has harboured it, with an aim to stimulate further coordinated research. First, we review present geological and palaeoclimatic knowledge on the development of the Australian arid zone over the past 20 million years. This provides a vital platform upon which we then proceed to collate the relevant phylogenetic and phylogeographical analyses of arid-zone taxa and look for broad congruence between physical and biological histories. In particular, we consider what light these patterns shed on the processes leading to the origin of the arid-zone biota, as well as the maintenance of that biota as aridity oscillated and intensified over the last two million years. We compare the patterns in the Australian arid zone with those emerging from other biomes, and use these spatio-temporal patterns to generate questions and testable hypotheses to direct future research on the history and conservation of the Australian arid zone.

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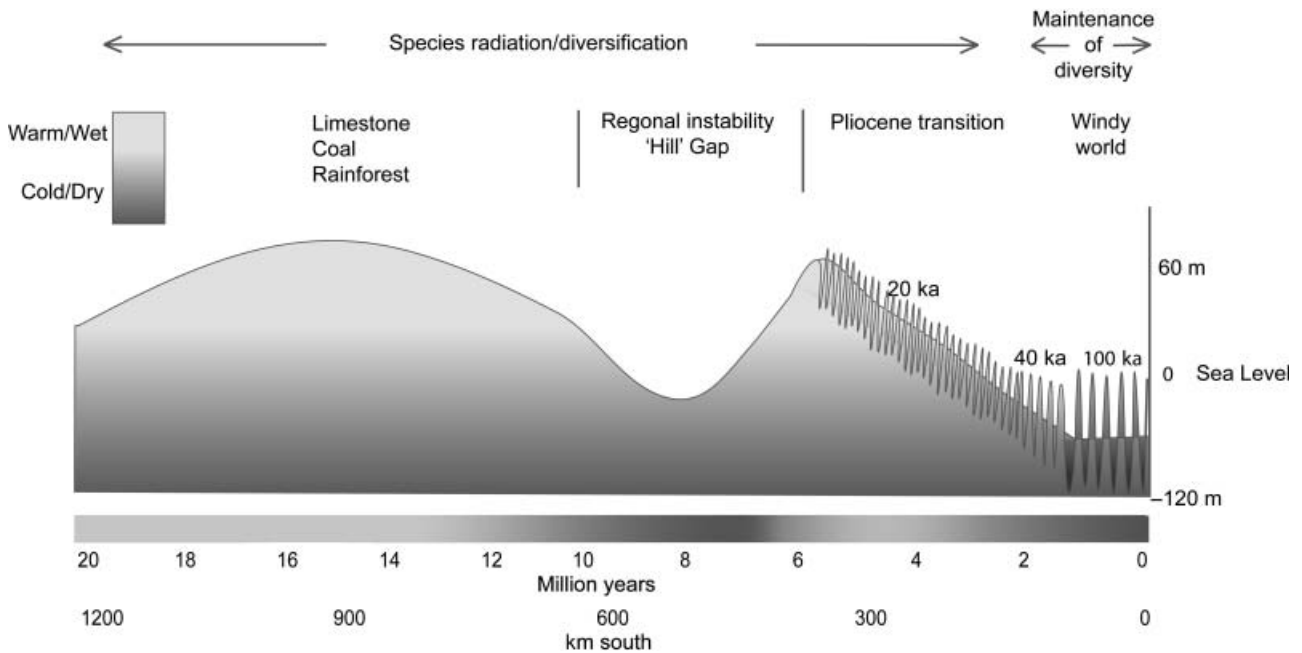


Fig. 1 Summary of the palaeoclimatic conditions in Australia during the evolution of the arid-zone biota from 20 Myr to present. Vertical axis representing sea level not to scale. Horizontal axes represent (i) time in the past, and (ii) distance that the continent of Australia was further south than present during the past. Development of cycling of climatic conditions and sea level changes are evident through the Pliocene and Pleistocene. Shading indicates warm/wet vs. cold/dry climatic conditions. (Modified from a diagram provided by Jim Bowler).

Setting the stage: development of the Australian arid zone over 20 million years

The first evidence of aridity in Australia dates back to the Late Cenozoic, soon after South America broke free of Antarctica and initiated the Antarctic circumpolar current (ACC; Williams 1984; McGowran *et al.* 2004). The ACC intensified over the Miocene, driving the world's climate into a cold phase, while Australia drifted northward to warmer latitudes (McGowran *et al.* 2004). Thus, Australia was not subject to major glaciations as occurred across much of the Northern Hemisphere – only 0.5% of Australia was glaciated during the Pleistocene (Williams 2000, 2001). Instead, Australia became progressively desiccated over the last 20 million years (Myr) culminating in extreme aridity during glacial cycles (Williams 2000), setting the stage for the evolution of an arid-adapted biota.

Here we summarise the Late Cenozoic environmental history of arid Australia based on a broad range of evidence including plant macro- and microfossils, sedimentology, fossil faunal assemblages, palaeodrainage, geomorphology and isotope analyses. For clarity, we distinguish five major time periods, noting that biotic changes were not always coincident with these boundaries. Figures 1 and 2 provide a schematic summary of the climatic conditions in Australia since the Mid-Miocene and key geomorphological and vegetation features of the arid zone.

Twenty to ten million years, the mild Miocene

In the Middle Miocene, the region that is now the Australian arid zone was warm and wet (Alley & Lindsay 1995; Martin 2006). The most complete data on the climate at this time come from sediments in surrounding regions, which preserve evidence for warm, wet times generally across Australia as well as remarkable climatic stability (Martin 2006). Most dramatically, the Murray, Otways and Gippsland basins, which were then below sea level, contain thick limestones and marls. These sediments preserve foraminifera that today are restricted to warm, subtropical environments (McGowran *et al.* 2004). The deposits date to around 20–16 Myr when continental Australia was located 1200–900 km further south. Thus, the extension of tropical Indonesian faunal assemblages to such high latitudes indicates that sea surface temperatures were at least 6–8 °C warmer than in the same latitudes today.

Evidence for warm wet environments is further documented by the thick coal sequences of the Gippsland Basin, extending from Oligocene to late Miocene time. Australian limestone-coal sequences, probably the largest carbon accumulation of the world at this time, had profound effects on global carbon budgets with possible implications for onset of later climatic cooling (Bowler *et al.* 2006). Regional diversity was low and the biotic communities dominant at this time have no modern analogues. Rainforest

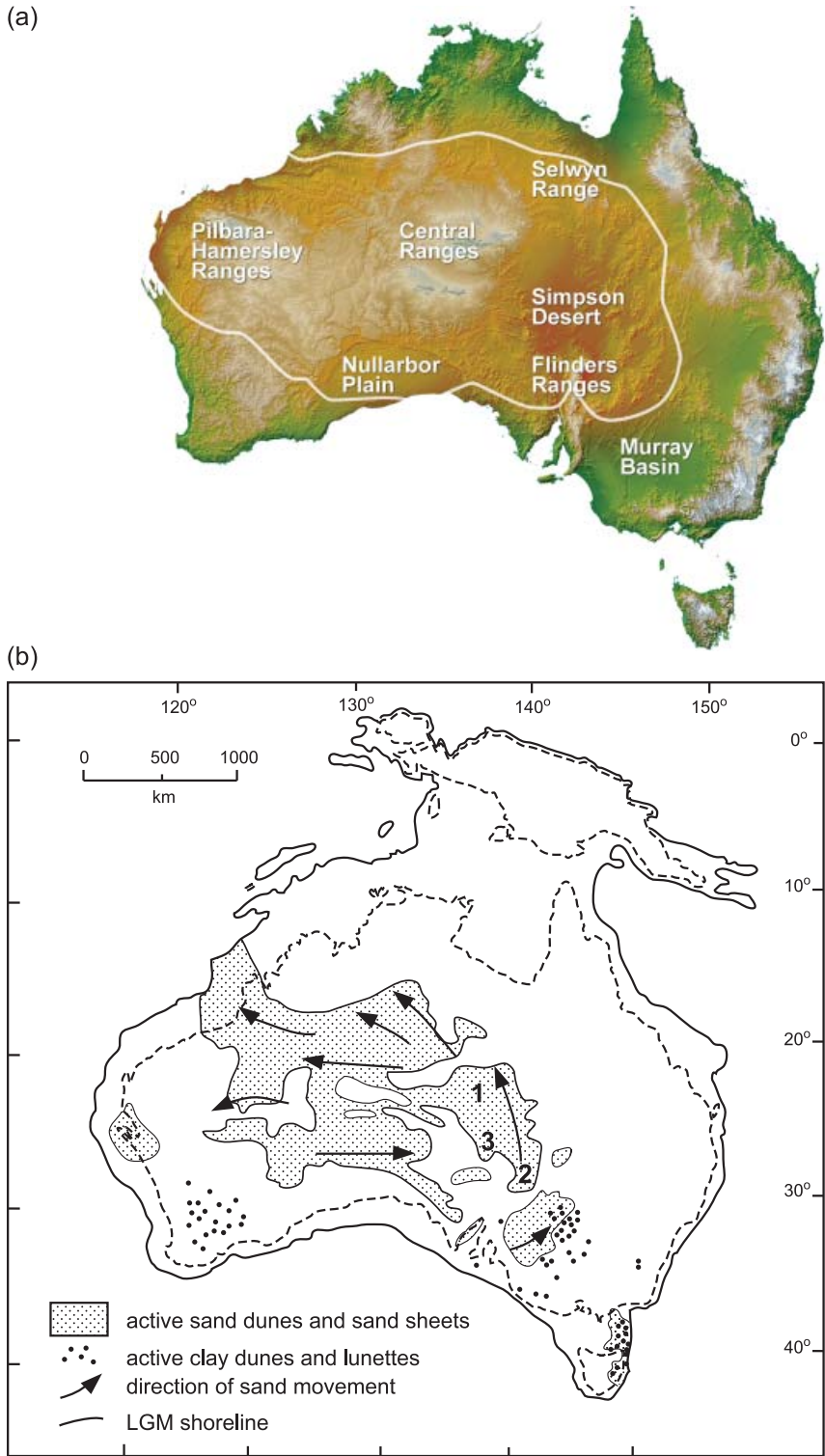


Fig. 2 Geomorphological features of the Australian arid zone. (a) Elevation map of Australia showing the extent of the arid zone (white line) and major geographical features mentioned in the text. (b) Australia during the LGM when sea level was 120 m lower and desert dunes were active (adapted from Williams 2001).

elements were widespread across the continent with some sclerophyllous communities in southern areas (Martin 2006). In central Australia itself, widespread dolomitic limestones extended through the Lake Eyre Basin with faunal and floral elements (flamingos, crocodiles, rainforest) consistent

with warm humid environments (Alley & Lindsay 1995). This long moist interval is reflected in deeply weathered soil profiles on older igneous and sedimentary rocks. In the Mid-Miocene, the great limestone plateau of the Nullarbor Plain was uplifted and the sea retreated (McGowran *et al.* 2004).

Throughout this interval of high sea level and warmer temperatures at high latitudes, there was little or no Antarctic ice. Isotopic evidence shows a significant advance of Antarctic ice ~14 Myr (McGowran *et al.* 2004). At the same time, sea levels began to fall across southeastern Australia, eventually retreating towards the current coastline ~9–10 Myr, heralding the onset of different conditions across continental Australia (Bowler *et al.* 2006). The first signs of aridity were evident in cessation of regular flows in western palaeodrainage channels.

Ten to six million years, the 'Hill Gap'

Following the mild and stable climate of the Mid-Miocene, the Late Miocene was characterised by a cessation of major depositional systems with a concomitant loss of continuous geological records. We refer to this interval of major change with its tantalisingly fragmentary terrestrial evidence as the 'Hill Gap' in deference to Professor Robert Hill (University of Adelaide) who first identified it (Hill 1994). At this time, the oceans retreated from the southeastern marine basins (Murray, Otway and Gippsland).

Terrestrial events of this interval remain poorly defined. Widespread deposition of fluvial gravels marks the end of limestone and coal measure sedimentation in southeastern Australia (Bowler *et al.* 2006). In the Gippsland basin, sheets of quartz gravel spread across land that formerly had rainforest-dominated swamps. In the Murray Basin, gravel sheets extended basinwards from the north-facing highlands of Victoria. Along the margins of the uplifted Flinders Ranges, huge cobble laden streams deposited alluvial fans along basin margins, reflecting major excavation of catchment soils and weathered profiles at least seasonally (Alley & Lindsay 1995).

Thus, although environmental changes in this interval remain poorly defined, certain conclusions may be drawn. First, there was the major termination of warm, wet environments of earlier Miocene time. Second, there is evidence for unprecedented levels of erosion across a landscape previously stabilised by an effective vegetation cover. The vegetation that remained shows contraction of rainforest and expansion of sclerophyllous taxa like *Eucalyptus* and *Casuarina* (Martin 2006). In central Australia, dry, open woodlands and chenopod shrublands expanded. The demise of once extensive lakes points to a fall in the water table, either through uplift of the adjacent ranges and/or through reduced rainfall. The development of extensive aridity in central Australia had begun.

Six to two and a half million years, a mesic pulse in the Pliocene

The Pliocene saw a temporary return to warm, wet conditions. In the marine sequences, sea level rose to levels akin to those of the early Miocene, but instead of carbonates,

shoreline facies were quartz dominated, probably reflecting the abundance of detrital materials following the earlier phase of erosion (McGowran *et al.* 2004). The Murray Basin contains the world's best record of sea level retreat with more than 170 shoreline ridges preserved by slow tectonic uplift and a progressively falling relative sea level (Bowler *et al.* 2006). Although composed of fine to medium quartz sand, ideal for dune generation, the smooth arcuate outline of shoreline ridges shows a complete absence of simultaneous dune formation indicating a weak wind regime, in contrast to the deflation of sand associated with present-day shorelines (Bowler *et al.* 2006).

Soils developed on the marine shorelines were deeply leached with ferruginous and kaolinitic profiles of a type more commonly associated with subtropical environments. Sandy shorelines grade to marine marls at shallow depth across the greater part of the Murray Basin, a feature that specifies a wind wave regime of moderate energy (Bowler *et al.* 2006). Sea level ridges (more than 170 in 4 million years) reflect 20 000 to 40 000-year cyclic oscillations consistent with the marine isotope record (Williams *et al.* 1998), a rhythm pointing to orbitally controlled contractions and expansions of Antarctic ice superimposed on a state of progressive or incremental ice growth. An enormous inland lake, Lake Bungunnia, formed due to the tectonic damming of the Murray River in South Australia ~3–4 Myr. The formation of this lake resulted in huge expansion of surface waters, and the deposition of the acidic Bungunnia Clays, followed by deposition of the Bungunnia Limestone in alkaline environments, reflecting increasingly dry conditions (Bowler *et al.* 2006).

Although data from other parts of Australia are sparse for this interval, the available local and global evidence points to environments both warmer and wetter than today's, a feature consistent with major contraction or collapse of Antarctic ice which triggered the major sea level rise and basin flooding. The early Pliocene (5–3 Myr) saw a return of rainforest elements although never repeating the organically rich swamps and lakes of early Miocene time. Generally, however, the vegetation at this time was sclerophyllous forest and woodlands with shrublands and grasslands becoming common (Martin 2006; Sniderman *et al.* 2007).

Two and a half million to four hundred thousand years ago, the periodic Pleistocene¹

The beginning of the Pleistocene is well known to represent the initiation of major oscillations between glacial and interglacial climates. These cycles developed concurrently

¹Correction added after online publication 8 September 2008: the title 'Two and a half to four hundred thousand million years, the periodic Pleistocene' was corrected to 'Two and a half million to four hundred thousand years ago, the periodic Pleistocene'.

with the rapid growth of the Northern Hemisphere ice caps ~2.5 Myr (Williams *et al.* 1998). The tropics also became drier at this time, with the first stony desert pavements appearing in central Australia by 3–2 Myr (Fujioka *et al.* 2005). Thereafter, sea level fluctuated as the northern ice caps waxed and waned in 40 000-year cycles. Glacial sea levels were 40–50 m below present level. The transition from the low-energy, shallow wave-base shorelines at 2 Myr to high-energy shorelines indicative of a deep wave-base is evinced by the first appearance of wind-blown calcareous ridges at ~1.3 Myr, a result of strong winds and ample sand supply (Bowler *et al.* 2006).

At ~800 000 years, glacial–interglacial climates changed to a periodicity of 100 000 years, and for the first time glacial sea levels dropped more than 120 m (Williams *et al.* 1998; Bowler *et al.* 2006). Frosts were more common during glacial times and aridity was accentuated by less evaporation from cooler seas and greater land area when sea levels fell. The environment had entered an entirely new system involving lower temperature thresholds never previously experienced by the biota. The arid zone expanded during the glacial intervals, although the speleothem isotopic record from Naracoorte in South Australia suggests that the interglacials may have been relatively dry (Ayliffe *et al.* 1998). The marsupial fossil fauna recovered from the Naracoorte caves persisted through successive glacial maxima, indicating that they were already well adapted to cold and aridity (Prideaux *et al.* 2007).

*Four hundred thousand years to present: the dusty world*²

The amplitude of the Pleistocene climatic oscillations peaked over the last 0.4 Myr. Thresholds for stabilised vegetation were exceeded in many areas during glacial maxima, resulting in widespread erosion and a dusty world. The climatic extremes between full interglacial and full glacial maxima resulted in extreme temporal and spatial variability of late Quaternary environments (Williams *et al.* 1998). Hydrological conditions began to change at ~0.4 Myr. Lakes on the northern desert margins were much larger around 300 000 years than they are at present and shrank during subsequent interglacials (Bowler *et al.* 1998). Progressive drying of the continent is evident in the wind-blown dust records from the Tasman Sea and Antarctica (Revel-Rolland *et al.* 2006). This time period also provides an insight into the geographical variations across the continent, notably the differences between the summer rainfall climatic zone in the tropical north (Bowler *et al.* 2001; van der Kaars *et al.* 2006) and the winter rainfall zone in the temperate south (Ayliffe *et al.* 1998; Williams *et al.* 2001).

Palaeoenvironmental evidence suggests higher rainfall and slightly warmer temperatures during last interglacial (~130 000–120 000 years) and Lake Eyre attained an elevation 25 m above present floor level that has never since been exceeded (Magee 1998). The last glacial maximum (LGM) at 21 000 ± 2000 years was a time of widespread and locally extreme aridity. Sea level was ~120 m lower than present and land area increased by 25% (Fig. 2b) (Williams 2000, 2001). Previously freshwater lakes became saline or dried out altogether. Formerly vegetated dunes became active again (Fig. 2b). Extensive areas were effectively treeless, and streams draining the Eastern Highlands ferried substantial volumes of sand and gravel during periods of high seasonal discharge. Estimates of temperature depression for this time range between ~–10 °C and –5 °C (Williams 2000). These estimates give little insight into biologically significant factors such as seasonal variations and extreme events. Of the latter, severe frosts are likely to have been more frequent during drought and would have aggravated climatic stress as the Australian biota in general is not well adapted to frost.

The current arid zone of Australia is generally less than 300 m above sea level, and of low relief, with a remarkably flat plain centred on west-central Australia. Two-fifths of arid Australia consists of dune fields and sand plains in contrast to the Sahara that is only one-fifth sand (Williams 1984). The region is defined by rainfall between 100 mm and 250 mm per year. One of many unique features of the Australian arid zone is rainfall unpredictability, and only moderate rainfall seasonality (Stafford Smith & Morton 1990). The extensive dune fields have been stabilised by the modern flora in all regions except some very arid parts of the Simpson Desert. The major vegetation formations of arid Australia are semi-arid shrub woodlands, chenopod, *Acacia* and mallee eucalypt shrublands, hummock and tussock grasslands. While covering the vast majority of the Australian landscape, the arid-zone biota is relatively depauperate as the following examples show. The arid zone provides habitat for 15% of Australian bird species, which includes some 16 endemic genera of birds (Schodde 1982, 2006) and 10% of Australian plants (Barker & Greenslade 1982). However, it provides habitat for 43% of Australia's nonmarine reptiles (H. Cogger, Australian Museum, personal communication, 2007) and a similarly large proportion of termites and ants.

Responses of the biota to development of aridity in Australia

The patterns of phylogenetic and phylogeographical diversity of plants and animals in the Australian arid zone, documented in Table 1, suggest two general phases in the development of the arid-zone biota. Phase 1 involved the diversification and radiation of lineages through the

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Table 1 Responses of arid-zone biota to increasing aridification of the Australian continent based on molecular phylogenetic and phylogeographical studies

Time frame	Organism	Group	Response	Reference
20–10 Myr	Plant	<i>Gossipium</i>	Australian clade diversified between 24.1 Myr and 9.4 Myr. Divergence of arid sections <i>Sturtia</i> (C genome) and <i>Hibiscoidea</i> (G genome) around 8–15 Myr and tropical sect. <i>Grandicalyx</i> (K genome) 10.5–21 Myr. Diversification within sect. <i>Sturtia</i> earlier (3–6 Myr) than sect. <i>Grandicalyx</i> (1.7–3 Myr).	Liu <i>et al.</i> 2001; Seelanan <i>et al.</i> 1999
	Plant	<i>Acacia</i>	Major lineages include arid and mesic-zone taxa. Higher sequence divergence in arid clades (<i>Acacia victoriae</i> group) compared to mesic clades (sect. <i>Botrycephalae</i>).	Murphy <i>et al.</i> 2003; Ariati <i>et al.</i> 2006; Brown <i>et al.</i> 2006; Ladiges <i>et al.</i> 2006
	Plant	Chenopods	Initial diversification of Australian clade in coastal areas 19–14 Myr.	Kadereit <i>et al.</i> 2006
	Plant	<i>Santalum</i>	Diversification of species between 19 Myr and 6.3 Myr.	Harbaugh & Baldwin 2007
	Marsupial	Dasyurids	Estimated cladogenic dates give common ancestor around 24 Myr. Major radiations of genera and species occurred around 11–16 Myr.	Krajewski <i>et al.</i> 2000; Blacket <i>et al.</i> 1999, 2000
	Reptile	Diplodactyine geckos	Two clades (Pilbara and non-Pilbara) separated approximately 16–27 Myr. Sequence divergences in <i>Strophurus</i> suggest divergence 8–24 Myr. Species divergences in the <i>Diplodactylus vittatus</i> complex 5–15 Myr.	Pepper <i>et al.</i> 2006; Melville <i>et al.</i> 2004; Oliver <i>et al.</i> 2007
	Reptile	Pygopod lizards	Diversification rates peaked early in the group's history (23–10 Myr) before levelling out over the past 10 Myr.	Jennings <i>et al.</i> 2003
	Reptile	Sphenomorphine skinks	Rapid diversification of <i>Lerista</i> and <i>Ctenotus</i> 20 Myr. Diversification rate 2.5–15 times greater than in mesic relatives.	Rabosky <i>et al.</i> 2007
Reptile	Agamid lizards	Diversification of arid taxa from mesic ancestors 22 Myr. Divergence of <i>Amphibolurus</i> and <i>Ctenophorus</i> clades 19 Myr. Radiation of <i>Chenophorus</i> clade from 15 Myr.	Hugall <i>et al.</i> 2008	
10–6 Myr	Plant	Tetratheca	Diversification from rainforest ancestors 6–7 Myr. Increased rate of evolution in the <i>Tetratheca</i> lineage compared to sister lineage of tropical species (<i>Eleocarpus</i> + <i>Aceratium</i> + <i>Sericolea</i>).	Crayn <i>et al.</i> 2006
	Plant	Chenopods	Rapid radiation and expansion of Salicornioideae into arid and semi-arid saline environments around 6–9 Myr.	Shepherd <i>et al.</i> 2004
	Plant	<i>Acacia</i>	Divergence of <i>A. lobulata</i> – <i>A. ixiophylla</i> 3.82 Myr. Divergence of <i>A. oldfieldii</i> – <i>A. acuminata</i> 2.87 Myr.	Byrne <i>et al.</i> 2001, 2002
	Marsupial	<i>Dasyurids</i>	Divergence within <i>Ningau</i> , <i>Planigale</i> and <i>Smithopsis</i> species groups 6–10 Myr.	Blackett <i>et al.</i> 2000, 2001, 2006; Krajewski <i>et al.</i> 2000
	Reptile	Agamid lizards ³	Origin of <i>Ctenophorus</i> 11–12 Myr. Species divergences between 5 Myr and 12 Myr. Divergence of heathlands taxa approximately 10 Myr.	Melville <i>et al.</i> 2001, J. Melville, L. P. Shoo & P. Doughty, in review
	Reptile	Skink	Arid vs. mesic lineage divergence in <i>Egernia whitii</i> species complex around 4–8 Myr. Similar diversification rates in arid and mesic lineages.	Chapple & Keogh 2004
	Invertebrate	Gall-inducing <i>Acacia</i> thrips	Initial diversification of Plurineres-associated thrips around 10 Myr.	McLeish <i>et al.</i> 2007
	Invertebrate	Diving beetles	Later radiation of semi-arid thrips 4 Myr. Transition from surface to groundwater occurred between 3 Myr and 9 Myr. LTT shows increase in diversification rates between 11 Myr and 8 Myr.	Leys <i>et al.</i> 2003
Invertebrate	Subterranean amphipods and isopods	Diversification between species in neighbouring aquifers occurred 3–11 Myr.	Cooper <i>et al.</i> 2007, 2008	
6–2.5 Myr	Marsupial	<i>Dasyurids</i>	Divergence within <i>Planigale maculata</i> species group.	Blackett <i>et al.</i> 2000
	Reptile	Gecko	Diversification of sexual lineages of <i>Heteronotia</i> between 5.5 Myr and 6.5 Myr.	Strasburg & Kearney 2005
	Reptile	<i>Tympanocryptis pinguicollis</i>	Divergence of arid/semi-arid-zone vs. mesic-zone populations during Late Pliocene.	Shoo <i>et al.</i> 2008

Table 1 *Continued*

Time frame	Organism	Group	Response	Reference
	Reptile	Frog	Divergence of northern and southern lineages of <i>Arenophryne rotunda</i> 5.63 Myr.	Edwards 2007
	Reptile	Elapid snakes	Rapid radiation at 10–6 Myr	Sanders <i>et al.</i> 2008
	Bird	Woodswallows	Divergence between arid and mesic taxa in <i>Artamus</i> around 10% sequence divergence.	Joseph <i>et al.</i> 2006; Joseph & Wilke 2006
	Invertebrate	Tiger beetles	Divergence of species from 4 Myr. LTT shows constant diversification between 4 Myr and 0.4 Myr.	Pons <i>et al.</i> 2006
	Invertebrate	Grasshoppers	Diversification of sexual lineages of <i>Warramaba</i> around 2–7 Myr.	M. Kearney & M. J. Blacket, in review
	Invertebrate	Gall-inducing <i>Acacia</i> thrips	Increasing rate of diversification of semi-arid Plurineres-feeding gall thrips at 4 Myr.	McLeish <i>et al.</i> 2007
	Invertebrate	Crayfish	Divergence between arid and mesic drainages.	Hughes & Hillyer 2003; Nguyen <i>et al.</i> 2004
2.5–0.4 Myr	Plant	<i>Lepidium</i>	Genus originated in Australia through hybridisation no more than 1.3 Myr, species radiation 0.3–1.3 Myr.	Mummenhoff <i>et al.</i> 2004
	Plant	Sandalwood	Divergence of arid and semi-arid lineages of <i>Santalum spicatum</i> 0.8 Myr.	Byrne <i>et al.</i> 2003
	Plant	<i>Acacia</i>	Divergence of arid and semi-arid lineages of <i>A. acuminata</i> 1.0 Myr. Speciation of <i>A. sciophanes</i> and <i>A. anfractuosa</i> 0.72 Myr.	Byrne <i>et al.</i> 2002; Byrne <i>et al.</i> 2001
	Plant	<i>Eucalyptus</i> series <i>Subulatae</i>	Divergence among the western, central and eastern clades at 1.25, 1.23, 0.95 Myr. Divergence between western and far-western clades later at 0.49 Myr.	Nicolle 2008
	Plant	Eucalypt	Divergence of southern and northern lineages of <i>Eucalyptus loxophleba</i> 0.7 Myr.	Byrne & Hines 2004
	Plant	Eucalypt	Divergence among populations restricted to granite rocks approximately 1.1 Myr.	Byrne & Hopper 2008
	Marsupial	Dasyurid	Divergence of <i>Sminthopsis crassicaudata</i> clades approximately 1.3–2.1 Myr.	Cooper <i>et al.</i> 2000
	Marsupial	Dasyurid	Divergence of northeastern, southern and western lineages in <i>Sminthopsis macroura</i> .	Blacket <i>et al.</i> 2001
	Reptile	Skink	Divergence between Nullabor and western arid-zone clades in <i>Egernia multiscutata</i> .	Chapple <i>et al.</i> 2004
	Reptile	Skink	<i>Egernia ornata</i> shows six clades with Pliocene divergence and Pleistocene diversification.	Chapple <i>et al.</i> 2004
	Reptile	Gecko	Westward expansion of northerly lineages <i>Heteronotia binoei</i> at 6.0, 3.2 and 1.9 Myr. Major fragmentation event in southern lineage at 2.2 Myr, greater nucleotide diversity in northern vs. southern lineage.	Strasburg & Kearney 2005
	Reptile	Skink	Divergence between lineages of <i>Tiliqua rugosa</i> (~3.2%).	S. Cooper, unpublished
	Reptile	Skink	Origin and expansion of parthenogenetic lineages in <i>Menetia greyii</i> .	Adams <i>et al.</i> 2003
	Reptile	Frog	Divergence within southern lineage of <i>A. rotunda</i> approx 2.05 Ma.	Edwards 2007
	Invertebrate	Grasshopper	Recent range expansion in southern lineages of <i>Warramaba</i> vs. persistence of northern populations multiple small refugia.	M. Kearney & M. J. Blacket, in review
	Invertebrate	Ant	Divergence of three lineages in <i>Nothomyrmecia macrops</i> .	Sanetra & Crozier 2003
	Invertebrate	Snails	Divergence of species of hydrobiid snails in freshwater springs of Great Artesian Basin.	Perez <i>et al.</i> 2005
	Invertebrate	Freshwater prawn	Divergence between arid and mesic drainages ~800 000 years and between catchments within arid drainage ~260 000–50 000 years.	Carini & Hughes 2004; Murphy & Austin 2004
	Invertebrate	Mussels	Divergence between catchments ~1.2 Myr and 0.8 Myr for <i>Velesunio</i> sp. A and ~500 000 years for <i>V. sp. C</i> .	Hughes <i>et al.</i> 2004
	Fish	Bream and smelt	Divergence between arid and mesic drainage basins ~1.5 Myr for <i>Retropinna semoni</i> and ~150 000 years for <i>Nematolosa erebi</i> . Divergence within catchments in <i>R. semoni</i> but not in <i>N. erebi</i> .	Hughes & Hillyer 2006
0.4 Myr – present	Reptile	Gecko	Origin and range expansions of polyploid, parthenogenetic lineages of <i>Heteronotia binoei</i> via hybridisation in western arid zone round 0.3 Myr.	Strasburg & Kearney 2005
	Reptile	Snake	Little structuring in the king brown snake indicates recent expansion across southern arid zone.	Kuch <i>et al.</i> 2005

Table 1 Continued

Time frame	Organism	Group	Response	Reference
	Invertebrate	Grasshopper	Origin and range expansions of parthenogenetic lineages of <i>Warramaba virgo</i> via hybridisation in western arid zone around 0.3 Myr.	Kearney <i>et al.</i> 2006; M. Kearney & M. J. Blacket, in review
	Invertebrate	Snail	Divergence between catchments ~300 000 years and within catchments ~130 000 years.	Carini & Hughes 2006
	Invertebrate	Crayfish	Little genetic structure within drainages.	Hughes & Hillyer 2003; Nguyen <i>et al.</i> 2004
	Fish	Carp gudgeons	Divergence between arid and mesic drainages in <i>Hyppselotris klunzingeri</i> but not <i>H. sp. 5</i> Midgley's.	Thacker <i>et al.</i> 2007
	Fish	Perch	Little genetic structure.	Bostock <i>et al.</i> 2006
	Bird	Grass finches	Secondary contact in species of <i>Poephila</i> after a period of isolation in Pleistocene.	Jennings & Edwards 2005
	Bird	Grasswrens	Contact between <i>Amytornis barbatus</i> , populations during pluvial lacustrine phases 50 000–20 000 years, and wetter times between 8000 and 6000 years.	Christidis 1999
			Later speciation of <i>Amytornis goyderi</i> .	
	Bird	Woodswallows	Extensively polyphyletic with incomplete lineage sorting, recent range expansion.	Joseph <i>et al.</i> 2006
	Bird	Cuckoo	Recent colonisation and range expansion in <i>Chalcites basalis</i> after 18–16 000 years.	Joseph <i>et al.</i> 2002
	Bird	Fairy-wren, honeyeaters, woodswallow	Recent Pleistocene range expansion across Australia in <i>Malurus leucophaea</i> , <i>Malurus splendens</i> , <i>Lichenostomus virescens</i> , <i>Acanthagenys rufogularis</i> , and <i>Artamus cinctus</i> .	Driskell <i>et al.</i> 2002; Joseph & Wilke 2007; Kearns <i>et al.</i> 2008
	Bird	Australian magpie	Populations of <i>Gymnorhina tibicen</i> diverged 36 000 years associated with Carpentarian and Nullarbor Barriers.	Toon <i>et al.</i> 2007

³Correction added after online publication 23 September 2008: the group name 'Skink' was corrected to 'Agamid lizard'.

Miocene and Pliocene, when arid environments were forming throughout central Australia. Phase 2 involved the maintenance of species diversity through the Pleistocene, when extreme aridity occurred through cyclic climatic conditions. We consider these phases in turn.

Origin and diversification

Origin of arid lineages. The first question to ask of the Australian arid-zone biota is 'From where did it originate?'. Arid biota may have originated through adaptive diversification *in situ* from ancestral forms present in central Australia before the Miocene, or from mesic ancestors through multiple independent divergences over time. The former scenario predicts concordant patterns of sister lineage relationships in phylogenies between the diverging and subsequently expanding arid lineages and their corresponding ancestral mesic lineages. In contrast, under the latter scenario one would expect a pattern of individual arid species or species complexes embedded throughout phylogenies.

Our assessment of molecular phylogenies encompassing a wide range of related taxa shows evidence of both scenarios. A single origin of arid lineages from mesic ancestors is evident in both plant, for example, *Tetratheca* (Crayn *et al.* 2006), *Calotis* (Watanabe *et al.* 2006), *Lepidium* (Mummenhoff *et al.* 2001), *Halosarcia* (Shepherd *et al.* 2004), and animal groups, for example, agamid lizards (Hugall *et al.* 2008), the *Egernia whitii* complex of skinks (Chapple & Keogh 2004), diving beetles and amphipods (Leys *et al.* 2003; Cooper *et al.* 2007), and possibly among *Artamus* woodswallows (Joseph *et al.* 2006). Single origin from tropical ancestors is also evident in the plants *Gossypium* (Seelanan *et al.* 1999; Liu *et al.* 2001) and *Flindersia* (Scott *et al.* 2000), and from the broader Australo-Melanesian region in elapid snakes (Sanders *et al.* 2008).

In contrast, other groups show evidence of multiple independent derivations of arid lineages over time. These include the large plant genus *Acacia* (Murphy *et al.* 2003; Ariati *et al.* 2006), the dasyurid marsupials (Krajewski *et al.* 2000; Crowther & Blacket 2003) and the sphenomorphine skinks (Rabosky *et al.* 2007) that show spectacular diversification within one lineage in particular, the genus *Ctenotus*.⁴

A related question to that of the origin of the arid biota is whether arid-zone lineages were pre-adapted to arid conditions through the environmental associations of their ancestors, or whether adaptation occurred concurrently with the onset aridification. While there is little available evidence at this stage, pre-adaptation is conceivable through a number of avenues. For instance, adaptation to a low-

⁴Correction added after online publication 23 September 2008: the genus name '*Ctenophorus*' in the preceding sentence was corrected to '*Ctenotus*'.

nutrient environment (particularly low phosphorous) has driven the development of sclerophyllous vegetation types that are suited to arid environments (Hill 1994). The evolution of deep encryption of stomata in dry climate members of Proteaceae is hypothesised to represent pre-adaptation to arid climate (Jordan *et al.* 2008). In the arid-zone fauna, for example, reptiles, it could be envisaged that characteristics such as low metabolic requirements and heat and desiccation tolerance could pre-adapt to aridity. Coastal and riparian sand dune habitats could provide substrate for pre-adaptation to arid conditions in plants and animals. It is also possible that the development of more arid conditions during the 'Hill Gap' (10–6 Myr, see above) provided an early expansion of the arid zone that may have caused the increased diversification of arid-adapted lineages observed in many groups (see Table 1). This early expansion may have pre-adapted these groups to the modern arid-zone environments that developed during the Pliocene.

Timing of diversification. A second general question we can ask about the origins of the arid-zone lineages is 'When did they diversify?'. We can address this in part by combining molecular divergence time analyses with recent analytical methods for studying patterns of lineage diversification through time. While there are many difficulties and controversies in placing absolute dates on molecular phylogenies (Graur & Martin 2004), especially regarding their calibration, it is possible to generate broad estimates and analyse the relative timing of events.

Molecular phylogenies of major groups of Australian arid-zone plants and animals show evidence of diversification of lineages through the Mid- to Late Miocene and Pliocene from 20 to 2.5 Myr. Miocene divergences tend to be between genera and infrageneric groups whereas Pliocene-aged divergences include divergence at lower taxonomic levels (species and subspecies). There is also a correspondence between the ancestral derivation of arid lineages and the timing of their diversification. Arid lineages that were derived once from temperate or tropical ancestors tend to have older diversification times, for example, *Gossypium* (Seelanan *et al.* 1999; Liu *et al.* 2001), *Ctenophorus* lizards (Melville *et al.* 2001; J. Melville, L. P. Shoo & P. Docherty, in review), elapid snakes (Sanders *et al.* 2008), than those species or groups with multiple independent evolution from within mesic lineages, for example, *Acacia* (Murphy *et al.* 2003; Ariati *et al.* 2006) and the dasyurid marsupials (Krajewski *et al.* 2000). Interestingly, the major clades in the large plant genus *Acacia* include both arid and mesic-zone species.

The specialised environmental associations of some arid-zone groups have led to very specific responses to environmental change. For example, reduction in permanent surface water appears to have driven a transition from

primarily surface-dwelling organisms to groundwater dwelling in diving beetles, amphipods and isopods between 11 Myr and 3 Myr (Leys *et al.* 2003; Cooper *et al.* 2007, 2008). These groups show high diversification into clades associated with specific aquifers. Similar specific associations with groundwater are seen in the diversification of hydrobiid snails from freshwater springs in the Great Artesian Basin (Perez *et al.* 2005). The diversification of halophytic chenopods also appears highly correlated with the emergence of saline water bodies through arid regions during the Late Pliocene (Shepherd *et al.* 2004).

Overall, there is no evidence that the dramatic climatic oscillations of the Pleistocene have increased speciation rate, at least through orthodox speciation mechanisms (see points in the next section about hybridisation, polyploidy and parthenogenesis). An absence of Pleistocene-aged species divergences has been documented in other biomes and contexts (Schneider & Moritz 1999; Bell *et al.* 2004; Coope 2004). Radiations during the Mid- to Late Miocene indicate that diversification must have begun when the arid zone was much smaller and xeric conditions were not as severe as they are today. Consistent with the late opening up of the arid zone, molecular phylogenies indicate that these radiations commenced much more recently than the Mid-Cenozoic radiations of the sclerophyllous biomes (e.g. Crisp *et al.* 2004).

Rate of diversification. A third question relating to the origin of the Australian arid biota is 'Did the rate of diversification of the arid biota vary through time?'. The molecular phylogenies of arid-zone biota clearly show ongoing speciation/radiation following initial diversification of arid lineages. Diversification rates may have been constant throughout the development of arid conditions or may have been episodic if lineages responded to specific climatic conditions. Nonconstant rates of diversification may result from two different scenarios that themselves have several possible causes. There may be increased diversification caused by increased rates of speciation, decreased extinction rates or both. Alternatively, decreased diversification rates may be caused by decreased rates of speciation, increased extinction rates or a combination of both.

Quantitative tests of these alternatives are now feasible with lineage-through-time (LTT) plots or their variants (Nee *et al.* 1992; Rabosky 2006; Rabosky *et al.* 2007) (Fig. 3). However, most of the data sets currently available in the arid-zone biota do not allow for such analyses due to deficiencies in taxon sampling and fossil calibration points, or inappropriate marker choices, although inspection of phylogenies indicates both episodic and more constant diversification patterns. A number of studies are sufficiently rigorous to allow statistical evaluation of the diversification rate and also show evidence of both episodic and constant diversification. For example, the diversification rate of

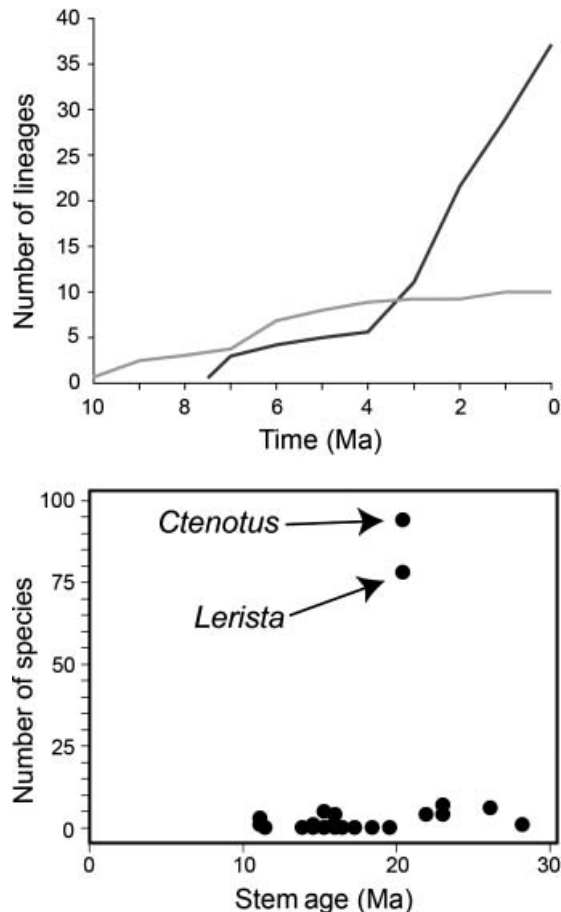


Fig. 3 (a) Lineage through time diversification plot for gall-thrips (*Kladothrips*) that specialise on either semi-arid (sect. *Plurinerves*, black line) or arid acacias (sect. *Juliflorae*, grey line) (adapted from McLeish *et al.* 2007). (b) Relationship between clade stem age and extant diversity for Australian sphenomorphine skinks. The mainly arid genera *Ctenotus* and *Lerista* have an excess of species and the remaining mainly mesic lineages have a deficit of species assuming a constant diversification rate for the entire sphenomorphine clade (modified from Rabosky *et al.* 2007).

salt lake adapted tiger beetles remained constant over the past 4 Myr (Pons *et al.* 2006). Gall thrips (*Kladothrips*) that specialise on arid species of *Acacia* section *Juliflorae* showed relatively constant diversification rates from 10 Myr to the present, in marked contrast to thrips specialising on semiarid species in *Acacia* section *Plurinerves* that showed a later rapid diversification during the Pliocene (McLeish *et al.* 2007). There is a significant increase in diversification rate (between 15 Myr and 5 Myr) of plant lineages occurring on either side of the Nullarbor Plain in comparison to related sclerophyll groups with more mesic distributions (Crisp & Cook 2007). The diversification rate in the arid-adapted *Tetradlea* plant lineage and in the sphenomorphine skinks are greater than that of their respective sister lineages of rainforest elaeocarps (Crayn *et al.* 2006) and

mesic skinks (Rabosky *et al.* 2007). However, the arid lineage of *Gossypium* shows a slower rate of diversification than that in its tropical sister lineage (Seelanan *et al.* 1999; Liu *et al.* 2001). In contrast, the diversification in the *Egernia whitii* group was similar in both mesic and arid lineages (Chapple & Keogh 2004). Clearly, the lineage-specific effects of ecology on diversification rate in an increasingly xeric palaeoenvironment must be taken into consideration when interpreting these studies in the context of biome assembly. Lineage through time analyses are an avenue for further work in this regard.

The birth of the Australian arid zone thus created a stage for some extremely rapid evolutionary radiations (Crisp *et al.* 2004). Many of the well-known and best-studied examples of evolutionary radiations occur in patchy tropical mesic environments or areas with high topographic relief, such as the Hawaiian archipelago (Wagner & Funk 1995). However, despite the relative topographic homogeneity of the Australian arid zone, it has produced the most diverse vertebrate radiation in Australia and one of the most diverse continental radiations across all amniotes, that of sphenomorphine skinks (Rabosky *et al.* 2007), and the world's most diverse radiation of subterranean diving beetles (Leys *et al.* 2003). We now consider how this considerable biotic diversity was maintained through the dramatic environmental change of the Pleistocene to the present day.

Maintenance of the arid-zone biota through the Pleistocene

By the onset of the Pleistocene, most arid-zone lineages and species had radiated within the biome. The main phylogenetic patterns over this period, then, reflect finer scale phylogeographical structuring in response to environmental changes. The few available phylogeographies for Australian arid-zone taxa differ in methodologies and sampling, thus precluding a robust analysis of phylogeographical congruence, as noted by Soltis *et al.* (2006) for eastern North American studies. We can, however, conduct a qualitative evaluation of the patterns observed and these provide a basis for future more rigorous testing of hypotheses, and lead to a number of generalities.

Multiple localised refugia. A common pattern, especially in species of low vagility, is that of geographically structured intraspecific lineages (see Fig. 4(a) and (b) for examples from a tree and a skink). Where these lineages have been dated, Pleistocene divergence has been revealed, most frequently in the Mid-Pleistocene (Blacket *et al.* 2001; Byrne *et al.* 2002, 2003; Sanetra & Crozier 2003; Byrne & Hines 2004; Carini & Hughes 2004; Chapple *et al.* 2004; Hughes *et al.* 2004; Murphy & Austin 2004; Hughes & Hillyer 2006; Edwards 2007; M. Kearney & M. J. Blacket, in review). These studies also show high but not necessarily

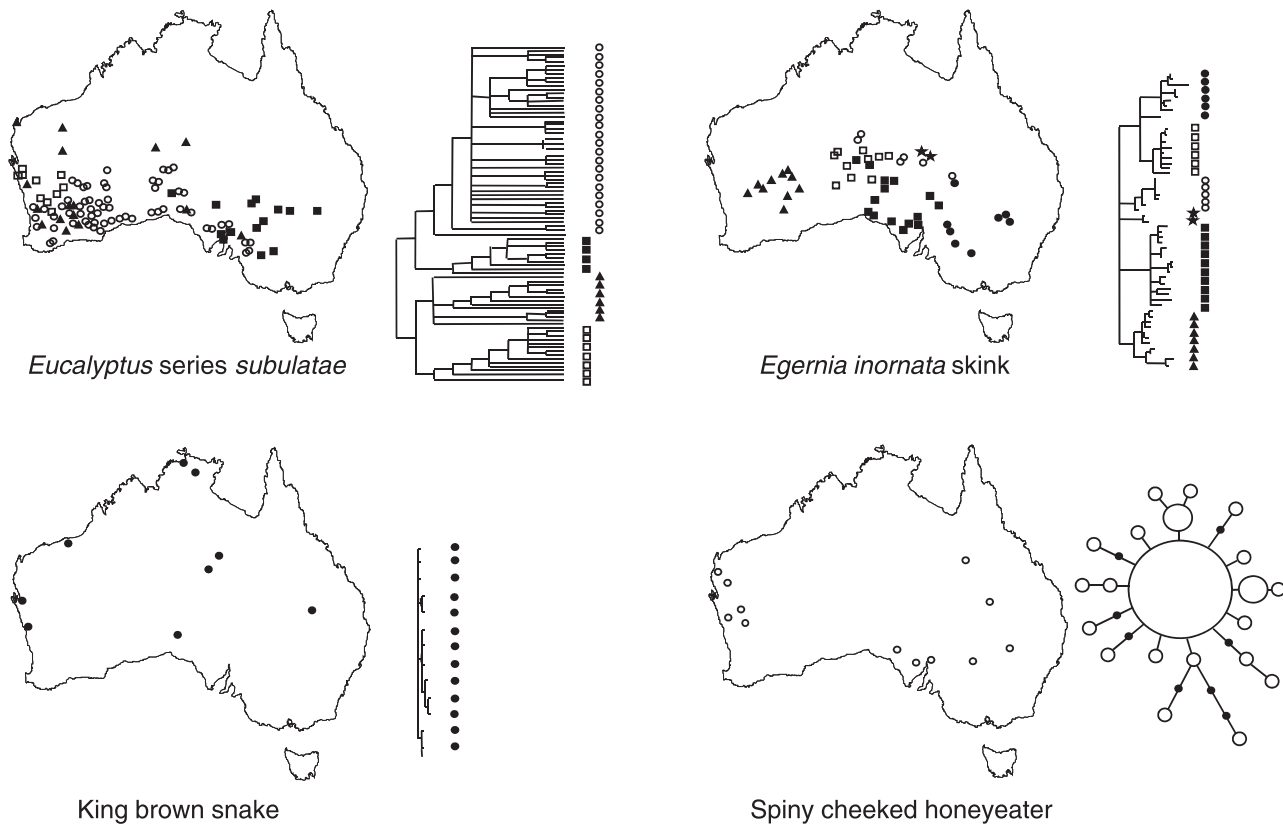


Fig. 4 Examples of phylogeographical patterns in the Australian arid-zone biota. Most biota show multiple clades with high diversity indicative of multiple localised refugia as demonstrated by (a) *Eucalyptus series subulatae* (Nicolle 2008) and (b) *Egernia inornata* skink (modified from Chapple *et al.* 2004). A few more vagile species show very low diversity indicative of recent expansion such as (c) king brown snake, *Pseudechis australis* (modified from Kuch *et al.* 2005) and (d) spiny-cheeked honeyeater, *Acanthogenys rufogularis* (modified from Joseph & Wilke 2007).

shallow diversity within lineages. They do not pinpoint highly localised geographical refugia, as in temperate biotas in Europe and North America. Nor do they reveal molecular genetic signatures of recent leading edge expansion, *sensu* Hewitt (2001), such as would be expected from major recolonisation and expansion episodes during interglacials.

This pattern is instead indicative of multiple localised refugia on a microgeographical scale throughout the distributions of the species, presumably allowing each lineage to rapidly colonise suitable habitat within its range. It is consistent with expectations from a hypothesis of local persistence and extinction with limited migration from localised populations, whereby divergence builds up through repeated cycles of localised contraction and expansion. Such a scenario is similar to the 'refugia within refugia' patterns that have been described in the Iberian and Italian Peninsulas, where phylogeographical lineages remain geographically distinct (Gómez & Lunt 2007; Canestrelli *et al.* 2007). It contrasts with wide-scale contraction to major refugia and subsequent macrogeographical range expansion that has been inferred in temperate Northern Hemisphere biomes.

Extensive range expansion and hybridisation. There is evidence for a second pattern of rapid expansions across large areas in some of the more vagile species (e.g. birds, snakes, lizards, freshwater fish, crayfish), although again not necessarily with a leading edge expansion pattern (see Fig. 4(c) and (d) for examples from a snake and a bird). In these cases, there is evidence for recent expansion across all or part of the arid zone, with little phylogenetic structuring and no specific refugia (Joseph *et al.* 2002, 2006; Byrne *et al.* 2003; Nguyen *et al.* 2004; Kuch *et al.* 2005; Strasburg & Kearney 2005; Bostock *et al.* 2006; Joseph & Wilke 2006, 2007; Toon *et al.* 2007; Kearns *et al.* 2008). Some geographical overlap in refugia, however, is suggested in studies of unrelated birds, for example, east of the Flinders Ranges in inland south-eastern Australia (Joseph & Wilke 2006; Kearns *et al.* 2008).

As observed in the Northern Hemisphere, 'suture zones' (Remington 1968) have been identified in arid Australia where range expanding lineages from a variety of different taxa meet along a broad contact zone (Kearney & Moussalli 2003; Joseph & Wilke 2006; Kearns *et al.* 2008). In one such region, the 'Carnarvon Suture Zone' (Kearney

& Moussalli 2003), hybridisation events have produced parthenogenetic and/or polyploid lineages that have subsequently expanded rapidly across the arid zone (Kearney 2005; Kearney *et al.* 2006; Strasburg *et al.* 2007; M. Kearney & M. J. Blackett, in review). Diversification of lineages through processes of hybridisation, polyploidisation and parthenogenesis lead to instant reproductive isolation (Coyne & Orr 2004), and in the arid zone have also produced diverse and widespread lineages of *Neobatrachus* frogs (Mahony *et al.* 1996), *Heteronotia* and *Menetia* lizards (Moritz 1993; Adams *et al.* 2003), insects (*Sipylloidea*, *Warramaba*) and plants (*Acacia aneura*, *Senna artemisioides*) (Kearney 2005, 2006). This parallels patterns of 'geographical parthenogenesis' and 'geographical polyploidy' seen in northern Europe and North America (reviewed in Kearney 2005) and it is highly likely to have originated through isolating processes in suture zones. Similar patterns are observed in glacially affected Europe and America, and they may reflect strong selective pressure for species to rapidly fill new niches as landscapes and climate change (Ehrendorfer 1980; Kearney 2005).

Mesic relicts. A third pattern shows restriction of species to mesic habitat within the arid zone. The springs of the Great Artesian Basin are classic examples. Species of hydrobiid snails (*Jardinella sp.*), restricted in these habitats to different groups of springs, show high genetic divergence (Perez *et al.* 2005). Molecular genetic data show that arid-zone outliers of the mesic, temperate-adapted skinks in the *E. whitii* complex are best interpreted as relicts of a broader range now contracted to southern mesic areas (Chapple & Keogh 2004). Granite outcrops also represent mesic habitat within the arid zone and would be expected to have acted as mesic refugia during extreme aridity. *Acacia lobulata* is now restricted to two granite outcrops and phylogenetic analysis showed it to be a relictual species with no close relatives, most likely isolated on mesic south-facing slopes during arid cycles (Byrne *et al.* 2001). However, phylogeography of the eucalypt, *Eucalyptus caesia*, which is also restricted to granite outcrops, indicates that it has not been subject to repeated cycles of population expansion and contraction as in the other woodland and heathland plants. Rather, it is adapted to the specific habitat of granite outcrops, so the granite habitat cannot be seen as refugia to which it has contracted (Byrne & Hopper 2008).

Pleistocene speciation. Finally, we found three cases where Pleistocene speciation has been documented. The Australian and New Zealand lineage of the arid shrub *Lepidium* originated through hybridisation between divergent species from South Africa and California no more than 1.3 Myr (Mummenhoff *et al.* 2004). Speciation of Australian *Lepidium* species has subsequently occurred through the Pleistocene. Speciation of the geographically restricted

shrub, *Acacia sciophanes*, at the periphery of the range of its widespread relative occurred during the Mid-Pleistocene (Byrne *et al.* 2001), and a number of gall-forming *Kladothrips* species associated with *Acacia* have evolved during the Pleistocene, according to recent divergence time estimates (McLeish *et al.* 2007).

In summary, we find that molecular genetic evidence mostly supports intraspecific diversification rather than speciation during the Pleistocene in the Australian arid zone, future systematic revisions notwithstanding. It appears that the arid biota that evolved during the Pliocene not only avoided extinction during the dramatic climatic and landscape changes of the Pleistocene, but also underwent major intraspecific diversification.

Comparisons with other biomes

We can now usefully compare and contrast what we know of the assembly and maintenance of the Australian arid-zone biota with studies from other biomes where regional phylogeographies have been compiled. Due to the relative lack of phylogeographical studies in Southern Hemisphere biomes (Beheregaray 2008), we focus particularly on how our understanding of the maintenance of Australia's arid biota across the Pleistocene compares with equivalent studies of northern European and American biomes, as well as tropical and temperate forest biomes within Australia.

Ice sheets vs. sand dunes: did they have analogous genetic impacts? Increasingly extreme climate and large oscillations in temperature and rainfall, particularly over the past 0.8 Myr, saw formation of extensive dunes in arid Australia during glacial periods (Fig. 2). The dunes formed as conditions became so extreme that the vegetation was unable to persist over large regions, perhaps because of extremely low rainfall or frequent and intense frosts. Periodic activation of these dune fields rendered much of the arid zone inhospitable. In that sense, they might have been analogous to the contraction and expansion of glacial ice in the Northern Hemisphere, which also erased biota from large spatial areas. It is well-documented that temperate biota of the Northern Hemisphere responded to glaciation by contraction to peripheral (southern) refugia with recolonisation of large areas during interglacials resulting in low diversity in northern areas (e.g. Hewitt 2001). But is there evidence that hyper-aridity and dune-field formation have had similar genetic consequences as the ice sheets?

The phylogenetic studies we have reviewed here do show evidence for very large-scale range expansions and contractions in taxa such as birds and snakes. However, studies of other groups, for example, plants and invertebrates, suggest that at least part of Australia's present-day arid biota persisted in a patchwork mosaic scattered

across the arid zone during glacial maxima. Subsequent recolonisation from multiple refugia in these taxa may have occurred through rapid dispersal, but was sufficiently restricted to maintain a signal of non-overlapping geographical ranges of lineages (first pattern above). The persistence of many taxa in the arid zone during glacial maxima thus indicates that oases of suitable habitat did persist at these times, in contrast with the more wholesale removal of species from high latitudes in the Northern Hemisphere due to ice sheet formation.

The nature of refugia Northern Hemisphere phylogeographical studies, especially in temperate Europe, have identified a small number of highly localised Pleistocene refugia to which northern biotas contracted during ice sheet formation. Molecular genetic signatures recover a relatively small number of simple recolonisation patterns following the retreating ice, with many expanding lineages meeting across common 'suture zones' (Hewitt 2000). There is a growing awareness, however, that a more complex approach to defining refugia is sometimes needed (Taberlet & Cheddadi 2002; Gomez & Lunt 2007) particularly in areas of biogeographical complexity. Indeed, phylogeographical studies of forested areas of tropical and temperate Australia, show more complex and idiosyncratic responses with refugial zones and recolonisation patterns varying considerably according to ecological requirements (Schneider & Moritz 1999; Hugall *et al.* 2002; Yeates *et al.* 2002; Sunnucks *et al.* 2006).

Similarly, for the Australian arid zone, our review of molecular genetic data suggests a species-specific, idiosyncratic basis for refugia. For instance, while there is molecular evidence for broad-scale population expansions in vagile bird species, these studies have not yet permitted ready localisation of refugia from which the expansions started. For these taxa, idiosyncratic ecological requirements of what a refugium was for a given species needs to be considered. For example, if tree-lined watercourses within and beyond inland mountain ranges were limiting, then a refugium may have been spatially diffuse and broad. While there is coarse evidence for suture zones in some regions (e.g. Kearney & Moussalli 2003), recolonisation and expansion, where it has occurred, has not always led to leading edge expansion and concomitant meeting of formerly refugia-specific haplotypes.

We emphasise, however, that phylogeographical studies of species in the Australian arid zone are few in number and there is potential for broad patterns to emerge as studies accumulate. There are some key regions that a priori may be expected to have acted as refugia. For example, because the arid zone was greater in extent during glacial periods, due both to lowered sea level and reduced rainfall over a wider area (Fig. 2b), topographically complex areas on the periphery of the present arid zone may have provided

refugial habitat for some species. The northern edge of the arid zone is likely to have acted as the most important arid/mesic interface of this sort, as species could track both their thermal and hydric niches into this region. Coastal fringes, especially the latitudinally broad west coast, may have acted as refuges due to the buffering effect of the ocean on temperature as well as the higher humidity and rainfall in these areas. The Nullarbor Plain, often regarded as a barrier to southern mesic taxa, is a coastal area that has presumably been a refugium in which some distinctive taxa have evolved, for example, Nullarbor quail-thrush (*Cinclosoma alisteri*, Schodde 1982).

Perhaps the most likely biogeographical features to act as common refugia in the Australian arid zone are the inland ranges. Hewitt (2000, 2004a, b) recognised mountain ranges as important refugia in both temperate and tropical regions expanding on the theory of Fjeldsa & Lovett (1997) that tropical mountains are both reservoirs and generators of lineages and species. In the Australian arid zone, key ranges occur in the region's south, centre, west, and north-east. While not as high as mountains discussed by other authors elsewhere in the world, these ranges nonetheless provide diverse thermal, hydric and edaphic environments. They have long been argued as refugia for birds during peaks of Pleistocene aridity (Keast 1961; Harrison 1973, 1975; Ford 1974; Schodde 1982) and as contemporary refugia (Shurcliff 1980). Relevant ranges include Central Ranges (i.e. MacDonnell, Petermann, Mann, Musgrave and Everard ranges), the Pilbara-Hamersley Ranges, Gawler-Flinders-Mount Lofty Ranges, and the Selwyn Range. All have gorges and permanent waterholes, and today act as refuges for groups that were presumably more widespread in the Miocene such as palms (Wisconsin *et al.* 2004) and snails. The central and western ranges are at lower latitudes than the southern ranges and thus would have been considerably warmer in the Pleistocene. The Pilbara Ranges, being closer to the coast, would also have been considerably wetter and more thermally buffered, perhaps making it the most important inland mountain range.

Some birds show taxonomic distinctiveness between these inland ranges but available molecular studies do not have the sampling necessary to address whether mountain ranges have been major refugia (see Joseph & Wilke 2006, 2007; Kearns *et al.* 2008). We stress that no study has yet been designed to test the hypothesis of ranges as refugia, either in birds or other organisms, and thus the present lack of evidence for distinct refugia may be an artefact of limited sampling. Study of speciation rates in inland ranges and whether many species now more widespread in the arid zone contracted to these regions during glacial maxima will be a fruitful area of further work. Testing whether inland ranges have been refugia provides an excellent opportunity to apply model-based approaches to statistical phylogeography. That is, a priori models would

state different hypotheses of relationships among different inland ranges and these models would then be tested. This model-based phylogeographical hypothesis testing can be carried out in conjunction with explicit ecological and geospatial modelling (Knowles & Carstens 2007; Richards *et al.* 2007).

Conclusions

Our review of the origin, radiation and diversification, and maintenance of the biota of the Australian arid zone provides a tantalising view of the evolution of an arid biome. As in many other parts of the world, widespread aridity is relatively recent with most arid landforms emerging in the past few million years. While many species level divergences occurred within arid Australia during this time, we have also provided evidence that some of the major arid-zone radiations, in both plants and animals, originated before this during the Mid- to Late Miocene. It is possible that the environments inhabited by the ancestors of some arid-zone lineages may have pre-adapted them to invasion of arid environments as they developed. But it is also likely that many older arid zone lineages diversified when spatially restricted precursors of the modern arid zone developed and expanded, most likely in central and northwestern Australia. The ill-defined environmental changes during the highly erosional period known as the 'Hill Gap' may have also played an important role in the origin of Australia's arid biota. Our review thus emphasises that the relatively young nature of many present day arid environments does not necessarily reflect a relatively young biota.

The Pleistocene saw major changes in relative rates of diversification and extinction of Australian arid-zone lineages. Speciation declined in most groups although there are an increasing number of examples of speciation through hybridisation, polyploidy and parthenogenesis. Pleistocene environments in the arid zone were characterised by dramatic fluctuations in aridity and temperature as well as expansion and contraction of vast regions of barren ground and dune fields. While these dramatic environmental changes parallel the development of extensive ice sheets in the Northern Hemisphere, the genetic consequences in arid Australia appear to have been more idiosyncratic and subtle than the repeated cycles of widespread population contraction and expansion in response to waxing and waning of ice sheets. Phylogeographies of many arid-zone species reveal a complex pattern of multiple localised refugia along with localised expansion indicative of a diversity of evolutionary processes. This diversity shows similarities with phylogeographical patterns in the Iberian and Italian Peninsulas (Canestrelli *et al.* 2007; Gomez & Lunt 2007) that contrast with the typical northern temperate pattern of major refugia with large-scale re-

colonisation of significant geographical areas. There has already been considerable effort in identifying refugia in the Australian arid zone from a more present-day ecological perspective. Here we have highlighted the relevance of many of these refugial areas from a palaeoclimatic perspective, and have shown the enormous potential of modern phylogeographical approaches, especially model-based ones, to identify refugia from a longer term, evolutionary perspective.

In describing the rich picture already emerging of the origin and maintenance of the Australian arid biome, we also emphasise that it is far from complete. Our analysis suggests the following eight hypotheses and questions as fruitful areas for further study:

- The closest relatives of arid-zone taxa will be found in Australia's mesic zone.
- The oldest lineages probably diversified when small precursors of the modern arid zone developed and expanded; expansions began in central and northwestern Australia.
- The 10–6 Myr 'Hill Gap' was an early period of diversification of arid-zone taxa.
- The rapid and recent expansion of Australia's arid zone has led to very high rates of diversification in the organisms that are endemic to the region.
- The dramatic climate changes of the Pleistocene did not lead to an increase in speciation rate through orthodox, gradual processes, but have instead in some groups promoted instantaneous speciation events through hybridisation, parthenogenesis and polyploidy.
- Inland ranges have been refugia for some groups, for example, birds, fish, aquatic insects, and tests of this should use a priori models of relationships among different ranges, for example, populations in the Selwyn Ranges in the arid zone's northeast are more closely related to those in the Central Ranges than to those in the western Pilbara-Hamersley Ranges.
- An individual species' ecology strongly determines the size and distribution of refugia, which may not necessarily have well-defined geographical regions but rather are dispersed and cryptic, for example, riparian woodland, mesic microhabitat niches in gorges and caves.
- The genetic signatures of taxa should vary from high to low genetic structure as one moves from small, low-vagility organisms with modest spatial requirements (e.g. plants and insects), to highly mobile taxa capable of maintaining genetic connectivity across patches (e.g. birds) to larger taxa requiring larger home ranges (e.g. kangaroos and emus). Sampling in such studies of widespread taxa should be designed to allow testing of model-based hypotheses of refugia appropriate to the ecology and environmental envelope of the organism(s) involved.

Our review highlights the potential gains from interdisciplinary approaches combining data sets from the fields of molecular systematics, molecular ecology and palaeo-environmental research. Searching for congruence in the relative timing of biotic and abiotic events can lead to a more comprehensive understanding of the origins, evolution and assemblage of biomes. Rigorous phylogenetic and phylogeographical studies of the arid-zone biota in Australia are still few and scattered. We hope this review will stimulate further concerted and focused research effort to develop phylogenetic and phylogeographical studies of arid-zone biota. This should further extend and deepen our understanding of the origin and maintenance of this fascinating and unique Australian biome, and enlighten our understanding of the evolution of biota in other arid zones worldwide.

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