



Life in the “dead heart” of Australia: The geohistory of the Australian deserts and its impact on genetic diversity of arid zone lizards

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Abstract

Aim: The Australian deserts are home to a remarkable diversity of taxa that might appear to have evolved in the absence of topographic and physical barriers to dispersal. In fact this is a biogeographical illusion, as the dunefields of the modern arid zone obscure the fossil landscapes of the wet desert that existed for much of the Cenozoic. As the geohistory of Australia's arid zone is not widely understood by biologists, we review its geological development and contemporary landscapes in an accessible way, and describe eight biogeographical hypotheses centred on how geomorphology, evolutionary history and contemporary ecological factors interact to shape diversification patterns in the desert lowlands.

Location: Australia.

Taxon: Lizards.

Methods: We review the arid zone landscapes before and after the development of the vast dunefields. As lizards represent a significant component of genetic studies that sample widely across the arid biome, we focus on this taxonomic group to establish emerging patterns.

Results: Recent geological work suggests that the dunefields never formed extensive mobile landscapes such as in the Sahara, but rather were a mosaic of vegetated and stable dune surfaces with scattered bare, mobile patches. Large fluvial systems in the eastern arid zone during the Pleistocene also are at odds with the general perception of an arid landscape during this time. Incorporating this geohistorical insight, understanding where landscape heterogeneity is greatest within the arid zone, and where relative homogeneity might facilitate connectivity and gene flow, are at the heart of our biogeographic hypotheses.

Main conclusions: Patterns are emerging that reflect the underlying influence of geomorphological processes on the genetic structure of Australian desert taxa. Quantifying finer-scale edaphic complexity across the arid zone, widespread genetic sampling from disparate taxonomic groups, and a more detailed understanding of species ecology and life history will greatly improve our understanding of the ecological and historical drivers of diversity gradients in the Australian deserts.



KEYWORDS

aridification, biogeography, endemism, geological history, geomorphology, phylogeography, sympatric sister pairs

1 | INTRODUCTION

"Desert regions, more than most, bear the impact of events distant in time, as well as geologically recent episodes and present processes: the character of an arid land cannot be separated from its past" (Twidale, 1994) pp.28.

Geology and geomorphological processes play a fundamental role in shaping the evolutionary history of organisms. At a broad scale, tectonic uplift can drive diversification both by creating new habitats and isolating populations either side of mountain chains (Hoorn et al., 2010; Hughes & Eastwood, 2006). Other processes such as the dissection of landscapes by river systems (Hall & Harvey, 2002) or the intermittent connection of land bridges (Riddle et al., 2000) also can have a profound impact on evolutionary dynamics. At a finer scale, the importance of geological heterogeneity (i.e., geology, terrain and soil) in shaping plant diversification and distribution patterns via edaphic specialization is widely recognized (Crisp & Cook, 2013; Fine et al., 2005; Kruckeberg, 2002; Mabbutt, 1988), with colour variation in animals also known to coincide to variation in geological substrates (Rosenblum & Harmon, 2011). As a general rule, geological and topographical diversity (and therefore habitat heterogeneity) is positively correlated to species richness (Anderson & Ferree, 2010; Badgley et al., 2017; Rahbek et al., 2019).

Arid zones are some of the most understudied biomes on Earth. While no two deserts are the same, they typically are found in basins and other topographically subdued lowlands (Hesse, 2019), and can appear less geologically diverse than other landscapes because the land surface and bedrock are often obscured by extensive dunefields and sandplains. However, many arid zones are home to extraordinarily rich assemblages of plants and animals that have diversified in these extreme and xeric environments. For example, the iconic Succulent Karoo in southern Africa has exceptional botanical diversity with the richest succulent flora in the world (Mittermeier et al., 1999), while the Great Victoria Desert of Western Australia contains the highest diversity of lizards anywhere on Earth (Pianka, 1989, 1996). Amazingly, arid landscapes as we know them today are geologically young, and while global arid conditions are thought to have arisen during the Miocene, the formation of widespread deserts and dunefields occurred as recently as the late Pleistocene and Holocene (Fujioka & Chappell, 2010; Mason et al., 2011; McLaren & Wallace, 2010; Roskin et al., 2011). Such a youthful geological history of arid landforms makes the high species richness in some arid zones all the more astounding. Because fossil and geological records in arid regions are often poor (Quilty, 1994; Singh, 1988), phylogenetic data can provide an essential means to develop and refine hypotheses about when, and how organisms

adapted to, and diversified in these newly emerged arid biomes. Indeed, dated molecular studies of arid zone taxa across the globe show deep divergences in line with the initial onset and development of arid conditions (Azani et al., 2019; Byrne et al., 2008; Gonçalves et al., 2012; Melville et al., 2009; Metallinou et al., 2015; Riddle & Hafner, 2006), with intensifying aridity and the spread of dunefields and arid habitats thought to drive phylogenetic divergence and phylogeographic structure through persistence in localized refugia (Byrne et al., 2008; Castoe et al., 2007; Portik et al., 2011).

The vast arid zone in Australia is the centrepiece of the continent. It is the largest, and youngest, of Australia's biomes, with the characteristic sand desert landscapes as we know them formed less than a million years ago at the height of the Pleistocene (Fujioka & Chappell, 2010) (Figure 1). In much of the literature, the arid zone is drawn as a homogeneous blob—a rough oval shape comprising the "deserts" (but see Mabbutt, 1988; Smith & Morton, 1990). Indeed, the topography of the region is generally subdued and superficially featureless. However, ancient and isolated rugged mountains occur in the northwest, centre and south. While these ranges are not high enough to have significant orographic effects on climate, they can affect local microclimates, particularly in respect to hydrology and the potential for run-on (Newman & Condon, 1969). In addition, far from being homogeneous, the vast intervening lowlands comprise a discontinuous mosaic of sandy dunefields, stony deserts, clay plains, ephemeral rivers and salt lakes (Mabbutt, 1988) (Figure 1,2). The patterns of rainfall and soil fertility are thus inherently different across the arid zone, both locally, and regionally, and this has important consequences for the distributions of major vegetation formations (Morton et al., 2011) and the biota that inhabit them (Pianka, 1972).

The evolutionary history of Australia's remote and sparsely populated arid zone remains, to a large extent, a scientific enigma. The non-depositional landscape has left continuous on-shore palaeorecords frustratingly incomplete (Quilty, 1994), and extreme climate and inaccessibility means biological collections across much of the arid zone are both limited (How & Cowan, 2006) and far from uniformly distributed. However, the biogeography and composition of the remarkably diverse biotic communities that inhabit the Australian deserts are slowly being pieced together. There are a number of well-tested hypotheses - the drying out of the Australian continent is known to have structured temperate biotas east and west of the Nullarbor Plain, a pattern repeatedly seen in numerous plant and animal taxa (e.g. Crisp & Cook, 2007; Dolman & Joseph, 2016; Foster et al., 2014; Jennings et al., 2003; Morgan et al., 2007; Rix & Harvey, 2012). In addition, broad areas of endemism within the arid zone have been delineated based on congruent patterns of various unrelated vertebrates (birds, mammals, frogs, lizards, snakes [Cracraft, 1991]). More recently these areas have been refined using a biogeographically centred molecular approach

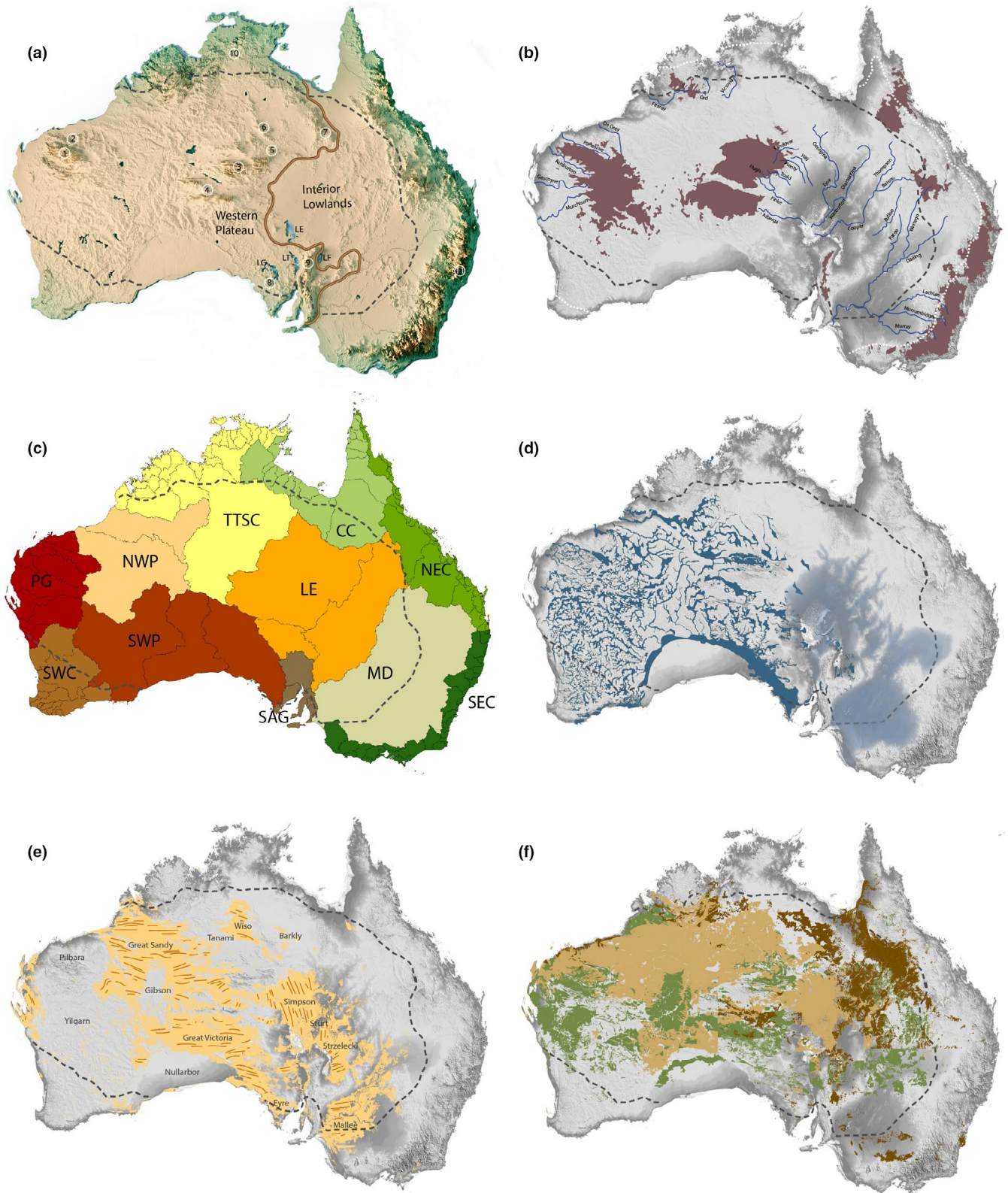


FIGURE 1 Examples of different landscapes and their vegetation communities in the Australian arid zone. Top left shows a dunefield in the Great Victoria Desert near Yulara in the Northern Territory (photo credit: Stephen zozaya); Top right is an aerial drone photo of vegetated dunes in the northern Simpson Desert in the Northern Territory (photo credit: Paul Hesse); Bottom left shows stony desert country with flat-topped mesas from the Kanku-Breakaways near Coober Pedy in South Australia (photo credit: Damien Esquerré); Bottom right shows sand desert country in central Australia in bloom following rain (photo credit: Angus Emmott)

based on major plant groups (Ebach et al., 2015; González-Orozco et al., 2014; Murphy et al., 2019). In 2008, an influential review (Byrne et al., 2008) collated information from existing plant and

animal studies regarding the origin, diversification, maintenance and age of various Australian arid zone organisms relative to earth history. A second review encompassing studies from the following

FIGURE 2 Major geographical features of the Australian arid zone mentioned in the text. Approximate boundary of the arid and zone is always indicated by the dark grey dashed line. (a) 3D Render of Australian topography (source: Frank Ramspott, <https://fineartamerica.com/featured/australia-3d-render-topographic-map-color-frank-ramspott.html>) depicting exaggerated topographic roughness of the landscape. Major mountain range systems are shown, (1) Hammersley Range, (2) Chichester Range, (3) Macdonnell Ranges, (4) Petermann-Mann-Musgrave range complex, (5) Dulcie Range, (6) Davenport-Murchison complex, (7) Selwyn Range, (8) Gawler Ranges, (9) Flinders Ranges, (10) Monsoon Tropics, (11) Great Dividing Range, as well as major arid zone lakes; LE, Lake Eyre; LF, Lake Frome; LG, Lake Gairdner; LT, Lake Torrens. Also depicted is the approximate boundary between the physiographical divisions of the Western Plateau (left) and the Interior Lowlands (right) (from Jennings & Mabbutt, 1977). (b) Modern rivers (including ephemeral systems) of the arid zone depicted by thin blue lines. Land over 500 m above sea level is indicated with dark red shading. The maximum extent of the arid zone based on the inferred distribution of xerophytic vegetation (arid and semi-arid grassland and woodland) during the last glacial maximum is indicated by the white dotted line (c) Drainage divisions (denoted by different colours) from the National Catchment Boundaries (NCB) database (Stein et al., 2014: <https://ecat.ga.gov.au/geonetwork/srv/eng/catalog.search/metadata/73078>). CC, Carpentaria Coast; LE, Lake Eyre; MD, Murray-Darling; NEC, North East Coast; NWP, North Western Plateau; PG, Pilbara-Gascoyne; SAG, South Australian Gulf; SEC, South East Coast; SWC, South West Coast; SWP, South Western Plateau; TTSC, Tanami-Timor Sea Coast. Associated aggregated river basins are shown as thin grey lines within each drainage division. (d) Cenozoic palaeovalleys mapped at high resolution for Western Australia, the Northern Territory and South Australia (Source: <https://portal.ga.gov.au/>). Shaded blue indicates inferred depositional fluvial-lacustrine regions in Eastern Australia during the Early Miocene (modified from Langford et al., 1995). (e) Distribution of dunefields and other desert regions mentioned in the text (from Hesse [2010]). Dune crests are for effect only, for detailed dune crest orientation see Hesse (2010). (f) The current extents of the 3 Major Vegetation Groups (MVG) across the arid zone; MVG16 *Acacia* Shrublands (green), MVG19 Tussock Grasslands (dark brown), MVG20 Hummock Grasslands (light brown). (source: National Vegetation Information System V5.1 © Australian Government Department of Agriculture, Water and the Environment 2020)



decade (Byrne et al., 2018) was published in a compilation of work relating to the ecology of the Australian arid zone (Lambers, 2018). These publications reflect the growing interest in, and understanding of, the evolution of arid zone organisms and their relatively recent adaptation to highly xeric environments (Byrne et al., 2008 has

been cited more than 530 times since publication). While many of the studies referenced are limited in geographic breadth, sampling and/or the number of loci for phylogenetic inference, an overriding theme to emerge is that most arid zone taxa are much older than the desert systems they now live in, and that range shifts and

contractions due to Pleistocene climate fluctuations had diverse impacts on genetic structure.

Understanding the evolution of the Australian arid zone biota presents a challenge - the landscapes and environments that existed for most of their evolutionary history have been buried under a blanket of sand, and they now occupy a region that bears no resemblance to the wet and humid landscapes that characterized the continent for much of the Cenozoic (Martin, 2006). Previous reviews have focused on the origins of Australia's arid zone biota, including from mesic ancestors, using phylogenetic and phylogeographic evidence across all major taxonomic groups (Byrne et al., 2008, 2018). Here, we concentrate our discussion on the evolution of lizard diversity exclusively within the arid biome, using desert geohistory to identify putative current, and historic, biogeographical barriers within the landscapes of inland Australia to help formulate predications regarding where populations may have been able to persist and diversify as the landscapes they inhabited dried out. With our emphasis on broad patterns, we hope to lay accessible geological foundations onto which emerging fine-scale genetic studies can build to further our understanding of biotic diversification in this biome.

Government initiatives have developed a wealth of data relating to different aspects of Australia's desert regions, i.e., Australian Bureau of Statistics' 2006 *Yearbook* (Trewin, 2006), Department of the Environment and Water Resources *Australia's Native Vegetation* (Department of the Environment & Water Resources, 2007), Geoscience Australia's *Shaping a Nation, A geology of Australia*, (Blewett, 2012), *A review of Australian salt lakes and assessment of their potential for strategic resources* (Mernagh, 2013), and *Palaeovalley groundwater resources in arid and semi-arid Australia* (Magee, 2009), Commonwealth Department of Sustainability, Environment, Water, Population and Communities' *Desert Geoheritage*, (Wakelin-King & White, 2016a), and National Water Commission's *Water for Australia's arid zone*, (English, 2012). In addition, a number of books on the Australian arid zone provide valuable prerequisite reading for anyone interested in studying the evolution of arid zone taxa, i.e., *The History of the Australian Vegetation* (Hill, 1994), *On the Ecology of the arid zone* (Lambers, 2018) and *The archaeology of Australia's deserts* (Smith, 2013). We have drawn on these as well as scientific research papers to synthesize general information regarding the evolution of Australia's arid landscapes. After a brief discussion on what constitutes the Australian arid biome, we first review its deep history and provide background to the palaeoclimatic evolution and development of arid conditions on the Australian continent. We then focus on landscape physiography, and outline the major landscape features that existed across the arid zone prior to the development of the vast sand deserts. The timing and formation of the dunefields is then reviewed, followed by descriptions of major elements of the modern arid zone landscape. This provides the foundation for the second section of our review, which concentrates on the evolution of arid zone biodiversity. With a focus on lizard molecular studies and the biogeographic patterns revealed through detailed sampling across the different desert systems, we explore how the distribution of genetic diversity may relate to

regional variation in geology and geomorphology. Finally, we describe eight biogeographic hypotheses to be tested as additional fine-scale data become available.

2 | DEFINING THE ARID ZONE

"the dead heart of Australia" (Gregory, 1906).

Australia is the flattest and driest vegetated continent in the world, with 33% of the landmass lying within the arid zone *sensu stricto*, and 75% within the arid and semi-arid boundaries (Bowler, 1976) (Figure 2). For the purposes of this review, we consider these regions collectively as the "arid zone" and use the term "desert" interchangeably. The arid zone is essentially a climatological boundary, defined in simple terms by a moisture index (precipitation divided by potential evapotranspiration) of less than 0.4 (Morton et al., 2011). However, given the immense latitudinal gradient encompassed by the arid zone (~18° from north to south), it is unsurprising that broad climatic differences exist across the region, with the southern margins falling in the winter rainfall zone, the south-centre in the "persistently dry" or uniformly distributed rainfall zone, and the northern arid zone under the influence of the Australian summer monsoon (Ash & Wasson, 1983; Hesse et al., 2004; Australian Government Bureau of Meteorology). Mackey et al. (2008) use climatic, terrain and substrate variables to create a series of climatic and environmental classification maps that illustrate differences across and between the arid zone and other Australian biomes. Today, the Australian deserts are only moderately arid, and they are mostly well-vegetated (Ash & Wasson, 1983; Smith, 2013). Most of the desert regions receive up to 250 mm average annual rainfall, while the Simpson and Strzelecki deserts in the driest core of the arid zone receive less than 125 mm (for comparison, some deserts such as the Atacama in South America receive <15 mm a year). In the southeast arid zone there are dunefields that extend into areas that receive 400 mm a year, and up to 625 mm in the northwest (Ash & Wasson, 1983). However, it is the extreme temporal variation in rainfall across the Australian arid zone that makes it unique on a world scale, with yearly totals typically skewed towards lower values and only occasional years of very high rainfall (Smith & Morton, 1990). As cloud cover across the arid zone is generally low, radiation is high and temperatures show a high diurnal range. Summer temperatures can soar into the high 40°Cs, and parts of the Pilbara in the northwest can reach 50°C (Sudmeyer, 2016). At the other extreme, light frosts occur during winter over much of the arid zone, with temperatures falling as low as -7.5°C in the higher elevations of central Australia (Trewin, 2006).

The geographical boundaries of the arid zone are poorly defined (see Ebach & Murphy, 2020). It is limited to the east by the uplifted Great Dividing Range, and to the north, the red desert sands of the Great Sandy and Tanami deserts grade into the rugged sandstone-capped plateaus of the Kimberley and Arnhem Land. In the west, the arid zone extends all the way to the continental fringe, as



does the southern margin that extends to the treeless plains and cliffs of the Nullarbor plain. In practical terms, however, because vegetation cover is limited, even from space the arid zone is highly visible, delineated by the characteristic red hues from the high iron oxide mineralogy of the heavily weathered regolith (Pillans, 2018). In the past, people have categorized variation across Australia's arid zone in different ways, depending on the subject of interest. For example, from a geological perspective, Mabbutt (1969) delimits the arid zone into six physiographic types, including mountain and piedmont desert, riverine desert, shield desert, desert clay pans, stony desert and sand desert. Smith (2013) on the other hand categorizes diversity in the arid zone into five geographical regions, providing eloquent summaries of the Pilbara, Western Deserts (Great Sandy, Little Sandy, Gibson and Great Victoria deserts), the Central Australian Ranges, the eastern "arid rivers" region (the large low-gradient ephemeral riverine system draining into Lake Eyre and associated Simpson, Strzelecki and Sturt deserts), and the Nullarbor Plain. Analysis of floral species turnover illustrates two major phytogeographical regions in the arid zone—the southern Eremaean and to the north the Northern Desert (Gonzalez-Orozco et al., 2014). These are divided into nine phytogeographical sub-regions, with changes in vegetation communities occurring in the western, central and eastern deserts, the Pilbara and Great Sandy Desert interzone, Central Queensland and the Nullarbor, Eyre Peninsula and Adelaide areas (Ebach et al., 2015). At a much finer scale, the Interim Biogeographic Regionalisation for Australia [IBRA] (Thackway & Cresswell, 1995) delimits the arid zone into 34 (out of a total of 89) bioregions, each of which is divided into numerous, smaller subregions. These various delineations are sometimes comparable (for example Mabbutt's [1969] riverine desert refers to the arid rivers region of Smith [2013]), however, other times they can appear unrelated (for example the main phytogeographical division of Gonzalez-Orozco et al. [2014] correlates to a major climatological transition rather than a correspondence to geology or landforms). It is important to note that all these various divisions apply to the modern arid zone. However, biomes are not fixed in space or time. Rather, they evolve continuously as landscapes and climates change. Since the end of the Miocene, the margins of the arid and semi-arid zones have waxed and waned with variation in global temperatures (Bowler, 1976; Smith, 2013). As we outline below, major changes to the central Australian landscape have taken place in the last 15 million years.

3 | PALAEOCLIMATIC HISTORY

"One of the paradoxes in Quaternary research is that the history of deserts is commonly a history of lakes and rivers..." Smith (2013), pp. 52.

At the beginning of the Cenozoic, the Australian continent lay 35–40° of latitude further south, adjoining a largely unglaciated Antarctica (Martin, 2006). In the following 55 million years, changes in

the Australian climate were largely driven by major rearrangements in southern oceanic circulation as Australia slowly became isolated from Antarctica, as well as the changing latitudinal position of the subtropical high pressure cells relative to the Australian continent (Pillans, 2018). The separation of Australia and Antarctica allowed circum Antarctic oceanic flow for the first time. This resulted in the increased cooling of Antarctica and adjacent oceans, with the large-scale development of Antarctic ice sheets implicit in the major shift to a much drier climate over large parts of Australia, particularly in the interior (Wilford & Brown, 1994). Excellent summaries of Cenozoic climate history and the development of aridity in Australia can be found in Alley (1998), Bowler (1976), Byrne et al. (2008), Fujioka and Chappell (2010), Macphail and CRC LEME (2007), Martin (2006), Quilty (1994) and Pillans (2018), with a particularly detailed and thorough review in Smith (2013).

Through the Cenozoic eons, the face of the Australian continent has been subtly modified—ancient rivers eroded the western plains leaving dendritic scars etched across the landscape; shield volcanoes and lava fields erupted along the eastern margin as the Australian Plate moved over a series of mantle plumes; and large inland seas in the south have encroached and retreated, leaving behind an enormous fossilized limestone reef. But by far the greatest Cenozoic environmental change in Australia has been the development of the immense arid biome. Over a very short period of geological time, this climatic discontinuity transformed the landscapes across the central landmass; there was wide-scale contraction of temperate rain forests, unprecedented levels of erosion, cessation of drainages and the disappearance of extensive inland lakes (Bowler, 1976; Frakes et al., 1987; Martin, 2006) with intensifying aridity culminating with the development of vast dunefields across the central continent (Fujioka et al., 2009; Hesse, 2010).

Despite the scale of this environmental transformation, the stratigraphic evidence for onshore palaeoclimatic change is sparse. This largely relates to the general lack of study sites in the arid zone, the poor preservation potential of organic material (such as pollens and microbial lipids) in arid environments, and the difficulties in dating desert landforms and obtaining chronologies beyond the late Quaternary (Fitzsimmons et al., 2009; Fujioka & Chappell, 2011; Sniderman et al., 2019). The chronology of arid zone development has therefore been pieced together largely using sedimentological and palaeontological data from southern marginal and inland basins (Fujioka & Chappell, 2010; McLaren & Wallace, 2010). Based largely on the inferred timing of contraction of palaeo mega lakes, as well as documented changes in fauna and flora, Bowler (1976), Martin (1978, 2006) and others have suggested the onset of aridification began sometime in the mid-late Miocene (~15 Mya). There is some evidence suggesting parts of northwestern and central Australia may have had relatively dry climates earlier than this (Mao & Retallack, 2019; Weston & Jordan, 2017). Nonetheless, fossil records generally indicate that climates progressively dried during the Neogene, with arid conditions intensifying dramatically in the Pleistocene (Bowler, 1976; Fujioka et al., 2009; Hesse et al., 2004; Kershaw et al., 2003; McLaren & Wallace, 2010; Pillans & Bourman, 2001).

These two main phases of aridification are evident in stratigraphic records, with many of the freshwater palaeolakes making the transition to saline conditions 15–12 Ma, their subsequent dessication paving the way for the diversity of arid features that formed in response to the extreme climatic oscillations of the Quaternary (Bowler, 1976; reviewed in Smith, 2013). Timing of the aridification process was not uniform across the arid zone. Bowler (1982) recognized the growth of the Antarctic ice sheet in the Pliocene changed the equator-pole temperature gradient and caused the subtropical high belt (associated with present-day hot subtropical deserts) to move northwards, overtaking the Australian continent from the south (see Pillans, 2018). Fujioka and Chappell (2010) also suggest the initiation of arid conditions was regionally variable, with diminishing precipitation inferred in central Australia in the middle Miocene, whereas wet conditions persisted in SE Australia until the late Miocene. Limited micro and macrofloral evidence from central Australia appear to support this (see Greenwood, 1996).

Despite the overall trend of increasing aridity from the late Miocene, records from radiometrically-dated fossil pollens indicate an abrupt onset of warm and wet climates in the early Pliocene which were sustained for ~1.5 My, driving complete biome turnover in southern Australia (Sniderman et al., 2016). This interval of warmth has been inferred at a number of other localities and using various sources of reconstruction. For example, Woodhead et al. (2019) showed the main phase of speleothem growth (indicative of wetter climates) in caves beneath the Nullarbor plain occurred during the Early Pliocene, with growth declining rapidly after 2.5 Ma. In addition, using chemical analyses of marine sediment cores, Stuu et al. (2019) suggest an increase in precipitation in northwestern Australia from 5.3 Ma, with run-off related to monsoonal rains peaking between 4.4 and 3.6 Ma, followed by a rapid return to drier conditions.

Arid conditions intensified significantly with the initiation of glacial-interglacial cycles of the Quaternary (Fujioka & Chappell, 2010), and climatic variation achieved its maximum amplitude and frequency during this time. In their stratigraphic analysis of palaeo Lake Bungunnia in SE Australia, McLaren and Wallace (2010) review variation in timing of the onset of major arid climatic regimes across Australia, and conclude that in SE Australia this began around 1.5 Ma. This is broadly consistent with dates reported from elsewhere and using various types of data, lending strong support for intensifying aridity from ~2 Ma (Stuu et al., 2019; Woodhead et al., 2019). Cosmogenic exposure age dating suggests the gibber pavements such as in Sturt's stony desert formed earlier, around 2–4 Ma, while dated playas and dunes in central Australia indicate they probably formed within the last million years (Fujioka & Chappell, 2010; Fujioka et al., 2009). A final major pulse to "fully arid conditions" is inferred around 0.5 Ma (Martin, 2006). This shift is reflected in palaeoclimatic data such as the switch from an oxide to carbonate dominated weathering regime in southern Australia (Pillans & Bourman, 2001), the shift from clay to gypsum-dominated sediments in freshwater systems in the southwest (Zheng

et al., 1998), and expansion of reef systems and ooids off the west coast of Australia (Gallagher et al., 2014). Aridity during the last glacial cycle is thought to have been particularly extreme, intensifying in the centre of the continent before gradually spreading to the margins (Nanson et al., 1992). The climate was significantly colder than present, up to 9°C lower than today in inland and southern Australia (Barrows et al., 2001; Miller et al., 1997). Sea level was as much as 130 m lower (Pillans & Bourman, 2001), exposing the continental shelf and extending the sandplains of the arid Pilbara coast up to 40 km (Veth et al., 2014). The boundaries of the arid zone also were greatly expanded elsewhere (Bowler, 1976; Hesse, 2010; Thom et al., 1994), with arid and semi-arid grassland and woodland inferred to extend across the entire continent, with the exception of a narrow continental fringe in the east, north and southwest (Bowler, 1976; Hope et al., 2004) (see Figure 2b). There is widespread agreement that at the height of the Last Glacial Maximum (LGM) ~20–18 ka, dune fields were partially reactivated in the Strzelecki Desert, Simpson Desert, and northern central Australia (see Fitzsimmons et al., 2007; Fujioka & Chappell, 2010), and that new dunes formed in areas of the humid continental fringes where conditions are no longer suitable (Bowler, 1976; Hesse, 2010; Hesse et al., 2003, 2004; Hope, 1994; Jennings, 1975; Thom et al., 1994). For detailed reviews of late Quaternary climates across the arid zone see Cupper (2005), Fitzsimmons et al. (2013) and Hesse et al. (2004).

4 | PALAEOLANDSCAPES & FOSSIL RIVERS

The landscapes of central Australia are topographically subdued, and have been for a long time (Taylor, 1994; Twidale & Campbell, 1995). The geological stability of the continent coupled with its low relief, lack of Quaternary glaciation, low rainfall and resistant rocks have all contributed to Cenozoic geological landforms being particularly well-preserved (Pillans, 2018; Twidale, 1976). Excellent descriptions of the palaeohistory of landforms in Australia can be found in Wasson (1982), Mabbutt (1988), Twidale and Campbell (1995) and Taylor (1994), therefore below we present a brief summary of the more basic aspects of physiography in the area now occupied by the arid zone, prior to the development of the Quaternary deserts and dunefields.

4.1 | Geological setting

At the broadest scale, the Australian continent comprises three main physiographic divisions; the Western Plateau, the Interior Lowlands and the Eastern Uplands (Jennings & Mabbutt, 1977), and the arid zone occupies an area within the former two (Figure 2a). Geologically speaking, the Western Plateau is broadly coincident with the geographical extent of the Australian Craton (or Western Shield), a vast and ancient geological structure that formed the foundations of the Australian continent (Wasson, 1982), while



the Interior Lowlands correspond to the basins of the central lowlands (Pain et al., 2011). These divisions can be subdivided into provinces, distinguishing major physiographic changes, which can be further divided into regions, representing the most basic geomorphological subdivisions of Australia (see Pain et al., 2011). The provinces and regions of the arid zone tend to be broader in extent than those along the eastern, northern and western margins of the continent, with the smaller size of these peripheral physiographic regions at least in part a reflection of their more complex geological background.

Topographically the two major divisions across the arid zone are very different. The Western Plateau itself is between 300–600 m above sea level, and nearly all the high elevation ranges within and bordering the arid zone are associated with the Archaean and Proterozoic igneous and metamorphic rocks of this division. The topography and rugged characteristics of these upland regions are heavily influenced by the geological composition of the craton, as considerable tectonic and igneous activity in the past has produced a complex mosaic of rock types that are hard and resistant to erosion (Wasson, 1982). The largest of these uplands include the Hamersley and Chichester ranges in the Pilbara, the Macdonnell ranges, Petermann-Mann-Musgrave range complex, the Dulcie Range and Davenport-Murchison complex of central Australia, the Selwyn Range on the northern rim of the Lake Eyre Basin, and the Gawler and Flinders ranges in South Australia (see Figure 2a). The majority of these range systems are ancient and have been tectonically stable for more than 80 million years (Kranendonk et al., 2002), having changed little in their topography and structure during the Neogene and Quaternary. An exception is the Flinders Ranges in South Australia, thought to be a much younger landscape feature that developed in response to tectonism and uplift during the Pliocene and Quaternary (Quigley et al., 2007). Quaternary tectonism also is thought to have influenced uplift in the Peak and Davenport Ranges in the NT as well as the Selwyn Range in western QLD (Twidale & Campbell, 1995). In stark contrast with the adjacent plateau, the eastern arid zone is centred on the Interior Lowlands, a division dominated by much younger Mesozoic and Cenozoic sedimentary rocks, with Late Tertiary and Quaternary sediments at the surface (Habeck-Fardy & Nanson, 2014). The Interior Lowlands division is between 0–300 m in elevation, with the lowest part (Lake Eyre) lying 15 m below sea level.

4.2 | Palaeorivers and lakes

During the Cenozoic, when climates were humid and temperate, rainfall was higher, and rates of evaporation were low (Macphail, 2007), inland river systems were extensive through areas of central Australia that have no modern surface drainage (Figure 2d). These palaeovalleys drained all the Precambrian uplands of the Western Plateau, transporting large volumes of sand from the hills and ranges. Many of these river systems

evolved over tens or hundreds of millions of years (Alley, 1998; English, 2012). Their development was strongly influenced by underlying geological structures (Krapf et al., 2019), and many of the palaeosystems probably originated within pre-existing Mesozoic valleys in response to tectonic stresses following Australia's rifting from Antarctica (Magee, 2009).

Most palaeovalleys evident in the arid zone today are inactive, infilled with Cenozoic sediments and obscured beneath Quaternary sandplains and dunes. Despite their subtle expression in the present day landscape, palaeovalleys often contain elongate chains of playas, aeolian deposits and distinctive soil types or vegetation associations (Magee, 2009) and their distributions can be mapped using remote sensing techniques and geophysical datasets. Detailed palaeovalley mapping was undertaken in Western Australia, the Northern Territory and South Australia (see English, 2012) because these regions lack other reliable water resources. These palaeodrainage maps illustrate Western Australia contains the greatest number of arid zone palaeovalleys in Australia, forming an intricate and interconnected network particularly in the southern half of the State (see Figure 2d) (English, 2012). The distinctive dendritic pattern of palaeovalleys in this region reflects the strong influence of the underlying granite and greenstone basement rocks of the Yilgarn. Along with the palaeovalleys of the northwest Gawler Craton in adjacent South Australia, these systems once mostly discharged into the Eucla Basin (Hou et al., 2008). The dimensions of the valleys vary considerably, with widths ranging from a few tens of meters to more than 30 km and with depths of up to 100 m (Hou et al., 2003). In contrast, other areas of the arid zone contain relatively few palaeovalley systems (for a map showing major geological provinces and associated palaeodrainages see English, [2012]). This is a distinctive characteristic of the Georgina Basin in eastern NT and the contiguous Wiso Basin in the centre of the NT where the geologic environment of extensive "black soil" plains is incompatible with the development of palaeovalleys (English, 2012). Detailed reviews of the evolution of Australia's palaeodrainages can be found in Magee and Geoscience Australia (2009) and English et al. (2012). In the eastern States where surface water is abundant, detailed mapping of the palaeovalleys is not yet available. For these regions, palaeovalley distribution can be loosely inferred via the 1:1 000 000 Surface Geology Map of Australia (<https://data.gov.au/data/dataset/8284767e-b5b1-4d8b-b8e6-b334fa972611>). Because palaeovalleys in the arid zone often have become calcretized, linear distributions of calcrete (Czk) can be a proxy for the presence of palaeovalleys (English pers. comm.). The Palaeogeographic Atlas of Australia (Langford et al. 1995) also provides a series of maps of time slices through the Cenozoic which broadly indicate the distributions of fluvial, lacustrine, erosional, depositional and other features at the continent scale.

Sedimentation within the palaeovalleys is generally uniform across the continent (Magee 2009). The bottom of the valleys is dominated by high-energy fluvial sands, mainly formed in braided river environments under wet climatic conditions of the Eocene,

when mesothermal and megathermal rain forests were widespread (Alley et al., 2009; Magee, 2009). Extensive fluvio-lacustrine sedimentation also is recorded along palaeochannels in the Eucla and Lake Eyre Basins during the warm and wet episodes of the early Pliocene (Alley, 1998; Alley et al., 2009; Krapf et al., 2019). The sedimentation in the valleys was in many cases a source of sand for adjacent dunefields, blown out from the valley floors during dry periods (Hesse, 2019). As such, while the formation of extensive dunefields did not occur until much later in the Quaternary under a considerably more arid regime, there would likely have been corridors of sandy substrates along the palaeovalleys of central Australia periodically throughout the Neogene, as well as isolated dune and sand-sheet patches stabilized by existing vegetation (Hesse pers. comm.).

In addition to these extensive palaeodrainage systems, large perennial lakes also dominated the landscapes of central Australia during humid phases. Using shorelines depicted in DEM's and by virtually filling the Lake Eyre and Frome-Gregory systems using GIS, DeVogel et al. (2004) calculated that at the height of the last interglacial ~125 ka Lake Eyre was a saline lake more than 25 m deep that covered more than three times the area of the current playa. At this depth it is likely that Lake Eyre merged with Lake Frome, and is inferred to have had a volume of 430 km³ of water (by contrast the deepest historical filling in 1974 was 30.1 km³ [Alley et al., 2009]). At the same time, other large lakes also formed concurrently in the Strzelecki, southern Simpson Desert and Mallee areas, probably several times during the Pleistocene interglacials (Alley et al., 2009; Callen & Benbow, 1995; Zhisheng et al., 1986). Mernagh (2013) reviews the evolution, geomorphology and hydrology of Australia's continental salt lakes.

Superimposed on this fluvial and lacustrine history, several extensive marine incursions into the Eucla Basin occurred during the Oligocene and early Miocene (Webb & James, 2006). Limestone was deposited in these shallow seas, periodically exposed to weathering and erosion every time the seas retreated (Webb & James, 2006). Palynological evidence for these marine incursions can be found in palaeovalley sediments, with the influence of marine conditions found as far inland as the foothills of the Musgrave Ranges, more than 400 km NNE of the present coastline (Hou et al., 2008; Krapf et al., 2019). After the final retreat of the sea at the end of the Late Miocene the region now known as the Nullarbor Plain was gently uplifted (Webb & James, 2006). The exposed surface of the extensive limestone is a layer of calcrete ~1 m thick which covers much of the plain as a hard, white, cemented crust (Webb & James, 2006), creating a formidable edaphic barrier (see Crisp & Cook, 2007).

5 | DESERT DUNES AND THE MODERN PHYSIOGRAPHY

"What was the last interglacial like in the interior of Australia? A bird's-eye view across these interglacial landscapes would reveal open, arid woodlands and grasslands across much of the inland. Looking across

the interior, we would see a landscape with significant fluvial and lacustrine systems inset into arid and semi-arid landscapes on the desert margins and in the Lake Eyre basin. Outside of these areas, the interior was a landscape of saltlakes, stabilized desert dunes and xeric vegetation". Smith (2013) pp. 67.

Landforms such as stony and sandy deserts, along with playa lakes and clay pans occur discontinuously across the arid zone. These arid features appeared across the landscape at different times, as progressive steps in the drying of the continent that began in the late Miocene. Excellent summaries of the formation and chronology of these various landforms can be found in Fujioka and Chappell (2010), Mabbutt (1988), and Hesse (2010).

5.1 | Regional drying

The drying up of surface water was the first major expression of aridity in the landscape. Regular flows in the vast palaeodrainage systems in Western Australia had ceased by the mid-Miocene (Quilty, 1994; Van de Graaff, 1977). Here, the valleys and depressions of once well-watered landscapes throughout the Yilgarn and the lowlands of central Australia were reduced to thousands of small playa lakes now found along the remnant palaeodrainages (Hesse, 2010), and previously large perennial lakes transitioned to ephemeral saline playas (Bowler, 1976). While from the late Neogene there was progressively increasing aridity overall, climates oscillated between wet and dry with glacial cycles, and rivers and lakes in the eastern arid zone were periodically reactivated, albeit with increasingly irregular flows (Habeck-Fardy & Nanson, 2014). Somewhat paradoxically, palaeorecords from southeastern Australia during the LGM indicate "... active dunes and dust entrainment from a sparsely vegetated land surface, but with large rivers and enhanced runoff from the highlands..." (Hesse et al., 2004, pp. 95). Indeed, evidence from sand dunes on the Newnes Plateau in the highlands of the Blue Mountains indicate they were active during this time (Hesse et al., 2003). This juxtaposition of active dunes (and sparse vegetation cover) alongside large rivers and perennial lakes has lead Hesse et al. (2003), Hesse et al. (2004) and others to postulate that significantly reduced atmospheric carbon dioxide levels during glacial cycles could induce water stress in vegetation, similar in effect to a climatic drought. Substantially cooler temperatures (and hence lower evaporation) up to 9°C lower than today (Barrows et al., 2001; Miller et al., 1997) across the central and southern interior, the greater influence of snow and periglacialation on runoff, as well as high groundwater tables could have negated the effects of moderately lower rainfall, such that the landscape reflected physiological aridity in attributes such as widespread treeless vegetation cover and active dunes whilst at the same time exhibiting run-off higher than today (Hesse et al., 2004). The severity of aridity also increased from the desert margins to the arid core, so that during glacial cycles when dune development extended well beyond the present arid zone, arid conditions already developed



within the continental core would have been greatly accentuated (Bowler, 1976).

While not discussed in detail here, major changes to regional vegetation accompanied the drying of the continent. The warm temperate to subtropical rain forests that were extensive across Australia for much of the early Cenozoic became restricted to scattered pockets of lower diversity, while the distribution of sclerophytic vegetation expanded to occupy the hinterlands (Christophel & Greenwood, 1989; Macphail, 1999; Martin, 2006). The forested environments that occupied central Australia in the Eocene (i.e., Greenwood, 1996) became dominated by dry open woodlands and chenopod shrublands by the late Miocene (Mao & Retallack, 2019). Heightened arid conditions in the Quaternary saw a dominance of species of *Poaceae*, *Asteraceae* and *Casuarinaceae* inland, with more eucalypt-dominated communities closer to the mountains (Hope, 1994). The greatly diminished vegetation cover during the most arid periods exacerbated the effectiveness of wind action to remobilize large volumes of sediment from across the continent (see below). For more detailed accounts on Cenozoic climate change and the history of palaeovegetation in the arid zone see Christophel and Greenwood, (1989), Truswell (1993), Kershaw et al. (1994) and Martin (2006).

5.2 | Timing of dune formation

Australian longitudinal dunes are characterized by low mobility and vegetated surfaces, and have accumulated episodically over long periods of time (Hesse, 2016). Geochronological evidence from close to 700 luminescence age estimates largely from the eastern arid zone dunefields (reviewed in Hesse [2016]) suggests dune formation began in the mid to late Pleistocene, with the minimum ages of some dunes in the Simpson and Mallee deserts inferred to be in the order of hundreds of thousands of years (Hesse, 2016). A cosmogenic isotope burial age estimate of up to 1 million years from a drill core in the Simpson Desert potentially extends the history of this dunefield even further (Fujioka et al., 2009). However, despite preservation of these old dunes, the vast majority of age estimates from the most well-sampled Strzelecki and Mallee dunefields are concentrated in just the last glacial cycle (Hesse, 2016). This may partly be an artefact of reworking in the last glacial resulting in a lack of preservation (Fitzsimmons et al., 2007), or depth-bias related due to an under-sampling of dune bases (Hesse, 2016). There is certainly a geographical bias in dune sampling, with an almost complete absence of samples from the large dunefields of western, central and northern Australia. Nevertheless, the strong signal of young dune ages suggest that the late Holocene was a period of substantial accumulation of dunes throughout the arid zone, and that there was regional variation in the timing of dune formation, even within individual desert systems (Cohen et al., 2010; Hesse, 2016). While the lead-up to and duration of the LGM marked a period of dune growth in some deserts, many dunes do not record active growth during this time of major climatic change (Hesse, 2016). As such, the important picture emerging is that the Australian dunefields were never hyper-arid, to the extent that active dunes covered

vast areas (such as in the Sahara). Evidence from both sand dunes and pollen records suggests the persistence of vegetation cover in the Australian dunefields during the last glacial cycle. This implies that even in the face of the heightened arid conditions of the LGM, the dunefields comprised a mosaic of stable dune surfaces and bare mobile patches (Hesse, 2016).

5.3 | Modern landscapes

5.3.1 | Dunefields

Hesse (2010) used satellite imagery to map the distribution of dunefields and sand plains across the arid zone. The areas containing dunefields are extensive, and largely occur in a broad diagonal band stretching from the Mallee Desert in the southeast (though much of this extensive dunefield falls outside the boundaries of the modern arid zone) to the Great Sandy Desert in the northwest (see Figure 2e). However, there are large areas near the centre of the continent where no dunes are found, despite occurring in surrounding areas. For example, the Tanami Desert is largely dune-free while the Gibson Desert comprises a complex mosaic of dunes and ranges (Hesse, 2011). The Yilgarn in the southwest arid zone also conspicuously lacks dunefields. Bedrock topography exerts a strong influence on the distribution of the dunefields (see figure 8.9 in Hesse, 2019). In the eastern arid zone, the Cenozoic Lake Eyre and Murray-Darling basins (within the Interior Lowlands of Jennings & Mabbutt, 1977) underlie the Simpson, Strzelecki and Mallee dunefields. The sands of these deserts is derived from reworking of exposed sand-rich Neogene coastlines when sea levels were low, as well as fluvial sediments from lithologically diverse catchments (Hesse, 2010; Wasson et al., 1988). The low and uniform topography in this region of the eastern arid zone along with the large volumes of sediment in the basins has driven the formation of extensive and continuous dunefields, with “*unwaveringly consistent orientation of the longitudinal dunes*” (Hesse, 2010, pp. 154). In contrast, in the western arid zone, the dunefields of the Great Sandy and Great Victoria deserts cover broad areas of the cratonic Western Plateau, a relict landscape characterized by low hills and shallow valleys. Here, the vast dunefields are largely underlain by Proterozoic to Mesozoic sediments of the Canning and Officer basins and are less continuous than the dunefields in the east, with frequent exposure of the low ridges as bare areas, hills and ranges between the dunes (Hesse, 2010). The sand from these deserts along with the Wiso and Barkly dunefields to the northeast appears to be largely reworked from accumulations in the extensive shallow valleys and piedmonts (Hesse, 2010). The neighbouring Yilgarn block also has preserved a valley and ridge landscape, but lacks extensive dunefields. Here, scattered dunes are widespread but small, and mostly occur along valley floors associated with lakes and playas (Hesse, 2010). Despite the predominantly granite substrate in this region, the absence of dunes is thought to be associated with the cementing effect of widespread laterite

in the soil profile that restricts the release of sand particles, along with steeper valleys that may prevent the accumulation of sand (Hesse, 2010, 2019). Other large dune-free regions within low-relief areas of the arid zone relate to bedrock lithologies not conducive to dune formation, i.e., the limestone Nullarbor Plain, the shales and mudstones of the Georgina Basin, or the clay plains of the Lake Eyre and Murray Darling Drainage Basins (Hesse, 2010).

So what does a typical Australian dune habitat look like? The majority of Australian dunefields are dominated by vegetated linear dunes that can be tens of kilometres long. These mostly range from about 5–25 m in height (Hesse, 2016), and have a spacing mainly in the range of 200–600 m. Dune spacing tends to be inversely related to dune height, and in some areas is closely associated with the characteristics of the interdune surface, being narrowest on sandy surfaces and widest where dunes rest on stony plains (Mabbutt, 1988). Standing in the northern Simpson Desert, the most arid dunefield in Australia, the dunes are 10–35 m high, spaced around 500 m apart, and have crests covered in patchy hummock grass (*Zygochloa paradoxa*) with clumping spinifex grass (*Triodia basedowii*) on the flanks (Fisher & Hesse, 2019; Purdie, 1984). A similar landscape can be found in the Great Sandy Desert, where dunes are typically between 15–20 m high, but can reach heights considerably more than 30 m (Fletcher, 1965). In contrast, in the eastern Mallee Dunefield the weathered red-brown calcareous and clayey sands form short dunes typically 2–6 m in height (Pell et al., 2001) and here there is a greater proportion of vegetation cover that also includes tall shrubs and low trees (Ash & Wasson, 1983).

5.3.2 | Modern Surface drainage divisions & major water courses

Many features of Australia's drainage have a very long history, and the modern landscape and contemporary drainage systems have been greatly influenced by the structural and lithological characteristics of the underlying Mesozoic basins (Nanson et al., 2008). The arid zone encompasses eight major drainage divisions (Argent, 2017) (Figure 2c). In a revision of the drainage basins across Australia, Stein et al. (2014) identified a number of differences from earlier interpretations of Australia's stream and catchment networks. Most significantly, there is now a recognized major drainage divide that splits the Western Plateau Drainage Division in the western arid zone into northern and southern sections, associated with drainage into the Indian Ocean and Great Australian Bight, respectively. In addition, drainage basins previously in the northwest Western Plateau Drainage Division are now linked to coastal basins in the Timor Sea Coastal Division.

River systems and surface water sources in the western arid zone are few compared to the east (Figure 2b). The small systems that do exist all flow to the coast, and most of these do so only seasonally (Pillans, 2018). In contrast, the eastern arid zone is situated largely within the Lake Eyre Basin, the largest internally draining system in the world, and in the southwest portion of the basin, at Australia's

lowest point, lies the very large ephemeral Lake Eyre salt playa (officially named Kati Thanda-Lake Eyre). Habeck-Fardy and Nanson (2014) provide a detailed review of the geological and environmental history of the drainage catchments and primary rivers of the Lake Eyre basin, with the three main rivers feeding Lake Eyre being Cooper Creek, the Diamantina River and the Georgina River. These muddy systems have their headwaters in the monsoon rainfall zone, and intermittently flow across the desert floodplains of the Channel Country in the northeast, carrying a bedload of fine-textured muds and clays. In contrast, the rivers in the northwest of the basin such as the Sandover, Todd, Plenty, Hay and Finke have bedloads dominated by sand (Habeck-Fardy & Nanson, 2014). The floodwaters of these rivers probably never reach Lake Eyre under the current hydrological regime, and instead their flows gradually diminish into the Simpson Desert. The far eastern arid zone also encompasses a section of the lowland rivers and tributaries of the Murray-Darling Basin, Australia's largest modern river system. The Darling and its tributaries also are fed by episodic monsoonal rains, while the southern Murray system with its headwaters in the Snowy Mountains has a cool season dominated precipitation regime (Theobald et al., 2016). The modern river systems within the arid zone are set within larger palaeodrainages that have preserved evidence of their substantially greater flow regimes under past, wetter climates (Hou et al., 2008; Zhisheng et al., 1986). For example, in the Lake Eyre Basin, higher rainfall along the Great Dividing Range in Queensland lead to the development of markedly larger channels during the late Pliocene to Pleistocene (Alley et al., 2009). Alluvial sand excavated from sites along the middle and lower reaches of Cooper Creek indicates the powerful nature of this fluvial system during this time, up to seven times larger than the system today (Nanson et al., 2008). In this same period, the ancestral Murray River extended as a huge estuary far inland (Twidale & Campbell, 1995).

5.3.3 | Vegetation

"The natural vegetation here survives extensively.... it continues to reflect geologic, topographic and pedologic influences which, under the broader control of climatic aridity, influence the availability of water to plants and the associated vegetation types.... here sparse vegetation allows a clear expression of underlying geology, landforms, surface soils and patterns of runoff, whilst the prevailing water stress imposes a close accordance between those features and the grouping of perennial vegetation." (Mabbutt, 1988).

There are few regions of the modern arid zone where active dunes prevent the establishment of vegetation (Bowler & Wasson, 1984), though cover can be sparse on hard claypans of ephemeral desert lakes, or on stony gibber pavements. At various geographical scales, the interplay of hydrology, soil and micro-topography creates distinct spatial heterogeneity which is expressed as a mosaic of vegetation



communities of differing patch size and shape across the arid zone landscape (Gillen, 2010). At the continental scale, the vegetation across Australia, including the arid zone, has been classified into 23 Major Vegetation Groups (MVG's) derived from the National Vegetation Information System (NVIS: Australia & Department of the Environment & Heritage, 2007) and the current distributions of each have been mapped and summarized (National Vegetation Information System V5.1 © Australian Government Department of Agriculture, Water and the Environment 2020). The hummock grasslands (MVG20) found throughout much of the arid zone are the most dominant MVG of Australia, occupying 18% of the continental area (Australia's Native Vegetation: A summary of Australia's Major Vegetation Groups 2007). This vegetation group is typified by the spinifex species of *Triodia* and *Plechrachne*, commonly found on the extensive sandy plains throughout the arid zone. The second most dominant MVG in Australia (12% of the continental area) that also is found throughout much of the arid zone is *Acacia* shrubland (MVG16). This vegetation group is typified by an overstorey dominated by the multi-stemmed acacia shrubs *Acacia aneura* (mulga) and *A. cambadjei* (gidgee). Tussock grasslands (MVG 19) represent a third major arid zone vegetation group mainly distributed in the north east. This MVG is typified by perennial grasses with a tufted growth habit, such as *Dichanthium sericeum* (blue grass) and *Astrelia* spp. (Mitchell grass). While mapping of these vegetation groups has been achieved at an extremely coarse scale, and each MVG contains different mixes of plant species within the canopy, shrub and ground layers, the distributions of these three major arid zone vegetation groups are largely non-overlapping (see Figure 2f).

Local variation in vegetation is strongly tied to characteristics of the underlying substrate and the prevailing hydrology (Kruckeberg, 2002). Indeed, Australia-wide bioregionalization mapping is largely based on groupings of similar vegetation along with macroclimate, lithology and landform (IBRA, [Thackway & Cresswell, 1995]). The 34 arid zone bioregions are on average greater in extent than those that make up the mesic periphery of the continent, no doubt in part reflecting the comparatively simplified surface geology and subdued topography of the arid zone. Some substrates such as vertisol or swelling-clay soils have important moisture and nutrient retaining properties not present in sand and gravels (Wakelin-King & White, 2016a). These soils, typical of the Cooper Creek floodplain and the floodplains of other Lake Eyre Basin river systems in the eastern arid zone exhibit deep cracking when they are dry, enabling water to penetrate deeply, and as such can absorb and retain significant moisture. The distribution of these soils amongst some of the driest, nutrient deficient dunefield sands of the Strzelecki desert creates a marked variation in substrate properties over small geographic distances. In the same Cooper Creek system, the moisture gradient from the more mesic channel to xeric outer floodplain exerts a strong influence on vegetation, whereby the more reliably watered parts of the system contain the most structurally and floristically diverse expressions of the region's flora (Gillen, 2010). The powerful influence of moisture availability on vegetation lead Beard (1973, 1975) to demonstrate that palaeodrainage

lines and valleys in Western Australia could be frequently delineated by the occurrence of particular vegetation such as trees, which survive off the limited water retained in the persistent lows created by the former rivers.

At the very local scale, variation in water availability and substrate can promote significantly different vegetation within the dunefields themselves (Ash & Wasson, 1983; Buckley, 1981). Dunes mostly comprise quartz sand, and typically have low fertility and low water retaining capacity, particularly near the crest. Consequently, dunes support both ephemeral herbs which grow after heavy rain, as well as perennials whose growth and survival depends on the availability of water stored within the dune (Ash & Wasson, 1983). In areas of the arid zone that receive more rain, shrubs and trees can grow on the dune crests, but are restricted to the moister, lower dune flanks in drier areas. The topographic zone between the dunes (the swale) can comprise a variety of substrates, including exposed bedrock, saline lacustrine sediments or aeolian deposits. The more arid and saline swales typically are devoid of vegetation (Ash & Wasson, 1983).

6 | THE EVOLUTION OF ARID ZONE BIODIVERSITY

6.1 | Distribution of clades and centres of diversity

Molecular studies of arid zone biota are fundamentally important for understanding the unique diversity that has evolved in concert with progressive and intensifying aridification. This is particularly true given sedimentary palaeorecords and fossil deposits of the Neogene and Quaternary are often inadequate for reconstructing historical diversity. Because genetic data can allow spatial and temporal patterns of diversity to be estimated, these data are a key component to identifying how species have formed and persisted across the landscape. This includes predicting the locations of putative Neogene and Quaternary refugia, highlighting the similar or different responses of populations to past climate change, as well as predicting how and where species might persist in the future. Using detailed sampling only possible through dedicated, extensive (and expensive!) fieldwork, these ideas have been explored in a biome-wide context using reptiles across the Monsoon Tropics (Laver et al., 2017; Moritz et al., 2016; Noble et al., 2017; Oliver et al., 2019; Pepper, Hamilton, et al., 2017; Potter et al., 2016, 2019; Silva et al., 2017), and provide fascinating insights into the long-term, localized persistence of taxa across this topographically complex region. The arid zone shares an almost continent-wide boundary with the Monsoon Tropics, and the historical relationship of these adjacent biomes continues to be explored in light of molecular data using phylogenies of animal (e.g., Catullo & Keogh, 2014; Fujita et al., 2010; Laver et al., 2017; Oliver et al., 2014; Potter et al., 2019; Silva et al., 2017) and plant clades (Crisp et al., 2004; Ebach et al., 2015; Ladiges et al., 2011; Murphy et al., 2019).

Biome-wide studies in the arid zone present a challenge purely on size alone—the arid and semi-arid zones make up 75% of the Australian continent. Numerous authors have suggested rocky uplands provided mesic refuges during periods of extreme aridity (e.g. Byrne et al., 2008; Crocker & Wood, 1947; Heatwole, 1987; Keast, 1961; Morton et al., 1995; Schodde, 1982). Indeed, such mountain systems have preserved abundant archaeological evidence of human occupation during the late Pleistocene, indicating they were important sites allowing hunter-gatherer populations to persist throughout the LGM (Smith, 2013). More recently these arid uplands have been the focus of detailed molecular studies, with results repeatedly identifying substantially higher levels of genetic diversity in rocky upland areas such as in the Pilbara, Kimberley and central Australia compared to adjacent desert lowlands (Blacket et al., 2001; Fujita et al., 2010; Marin, Donnellan, Hedges, Doughty, et al., 2013; Pepper et al., 2011, 2017; Pepper et al., 2011; Umbrello et al., 2017). These findings support the idea that regions of high topographic and geological complexity, which also provided greater associated relative climatic stability, allowed more taxa to persist and diversify in these uplands as the surrounding landscapes dried out.

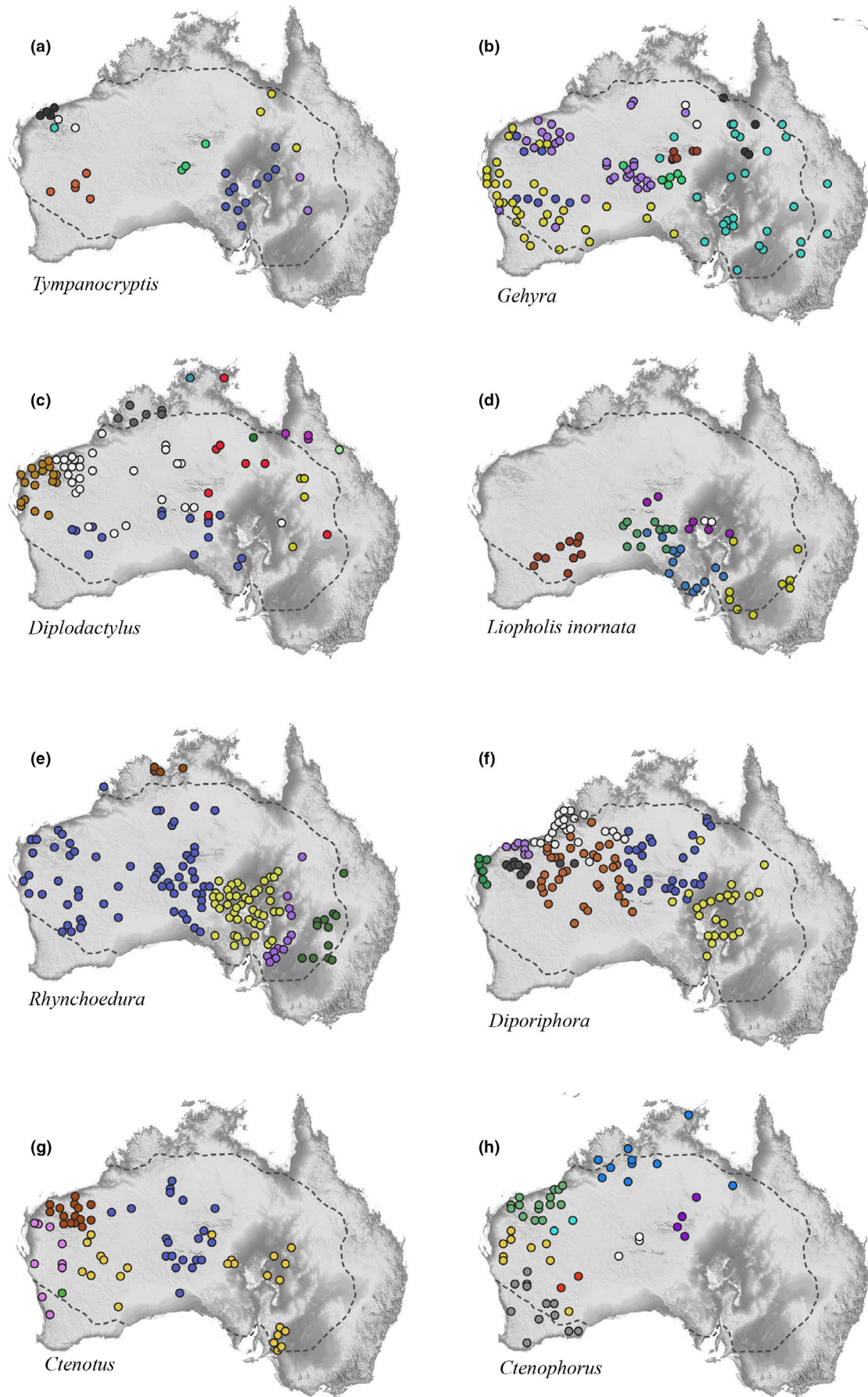
But what of evolutionary patterns across the vast low-lying areas of intervening desert? Genetic studies that sample widely across the arid zone are beginning to emerge that enable us to explore how geohistorical and present-day ecological factors may have shaped the evolution and geographical distributions of desert taxa. An impressive and increasing literature can be found on the biogeography of arid zone birds (i.e., Austin et al., 2013; Dolman & Joseph, 2016; Kearns et al., 2009, 2010, 2014; McElroy et al., 2018; McLean et al., 2017; Mullin et al., 2020; Norman & Christidis, 2016; Toon et al., 2007, 2012). Many of these studies have revealed recent and widespread expansion, with variation in haplotypes and plumage concordant with a number of major biogeographical barriers (reviewed in McLean et al., 2017). However, the high dispersal capability of birds limits the extent to which they might retain the imprint of more localized landscape patterns in their phylogenetic signatures. Reptiles are another taxonomic group increasingly represented in studies of Australian arid zone biogeography, and unlike the avifauna these low dispersal vertebrates have a strong association with the landforms and substrates they inhabit (Pianka, 1972). The diversity of reptiles in Australia's arid zone is staggering, with the Australian deserts thought to harbour the highest number of species anywhere on Earth (Pianka, 1989, 1996). In addition to this extensive species richness, reptiles display remarkable physiological adaptations to life

in a xeric landscape (Cox & Cox, 2015), and many species are widespread and overlap across different environments, making them an exceptional group to explore evolutionary patterns and processes across the arid zone.

To date, reptile taxa sampled widely across the arid zone include skinks (Chapple et al., 2004; Rabosky et al., 2009, 2014), dragons (Doughty et al., 2012; Melville et al., 2016, 2019; Shoo et al., 2008), blindsnakes (Marin, Donnellan, Hedges, Puillandre, et al., 2013) and geckos (Eastwood, Doughty, Hutchinson & Pepper, 2020; Fujita et al., 2010; Oliver et al., 2014; Oliver, Smith, et al., 2014; Pepper et al., 2011; Pepper, Ho, et al., 2011; Sistrom et al., 2013; Duckett & Stow, 2013). Notwithstanding the significant collecting effort behind these and other studies, sampling across some of the major sand deserts (e.g., the Great Sandy Desert) is conspicuously absent. For the saxicolous or gibber taxa these sand seas represent real distribution gaps. However, for many other species these empty sand-coloured patches on the map represent a frustrating gap in knowledge, particularly given the phylogenetic picture emerging from other better-sampled parts of the arid zone. While in general the patterns appear to lack the deeply divergent and geographically localized endemism typified in taxa across the adjacent Monsoon Tropics (Fujita et al., 2010; Moritz et al., 2016; Noble et al., 2017; Potter et al., 2019), all show significant genetic variation across the arid zone (see Figure 3). This includes topographically flat areas of low-lying desert where there are no obvious barriers to dispersal and gene flow. For example, the Yilgarn region of Western Australia reflects high diversity and phylogeographic structure in geckos, skinks and dragons (Melville et al., 2016; Oliver, Smith, et al., 2014; Rabosky et al., 2014; Sistrom et al., 2013). This also is seen across the low-lying eastern sand deserts (Chapple et al., 2004; Oliver, Couper, et al., 2014; Pepper, Doughty, et al., 2011; Shoo et al., 2008), and the northwestern sand deserts (Doughty et al., 2012; Marin, Donnellan, Hedges, Puillandre, et al., 2013).

Given the number of studies that incorporate widespread and detailed sampling are still relatively few, it is too early to draw generalities from the phylogeographic patterns exhibited by arid zone reptiles. Differing ecological requirements suggests that taxa are expected to vary in the spatial scale of their response to the onset of aridification and subsequent climatic fluctuations (Zamudio et al., 2016). Indeed, in a study of community structure in six lineages of squamates and marsupials across the Australian arid zone, Lanier et al. (2013) observed highly disparate phylogenetic patterns between groups, and suggested taxon-specific histories were more

FIGURE 3 Examples from published studies showing the geographical distributions of genetic structure within reptile groups sampled across the Australian arid zone. Colours represent different species or mitochondrial clades within a study and should not be compared between maps. These maps have been adapted from the following datasets: (a) *Tympanocryptis cephalus*, *T. intima*, and *T. l. centralis* in Shoo et al., 2008, (b) the *Gehyra minuta*, *G. montium* and *G. variegata* complexes in Sistrom et al., 2013, (c) the *Diplodactylus conspicillatus* complex in Oliver, Couper, et al., 2014, (d) *Liopholis inornata* in Chapple et al., 2004, (e) members of the genus *Rhynchoedura* in Pepper, Doughty, et al., 2011, (f) the arid zone members of *Diporiphora* including *D. pindan*, *D. valens* and *D. winnecke* and close relatives in Doughty et al., 2012, (g) the *Ctenotus inornatus* species group in Rabosky et al., 2014, (h) *Ctenophorus ornatus* and the subspecies of *C. caudicinctus* in Melville et al., 2016. Dashed grey line indicates the approximate boundary of the arid zone



important than climate or historical habitat stability in determining patterns of phylogenetic community relatedness. In our assessment of the squamate literature, contrasting patterns of diversification are emerging. For example, the Pilbara is known to harbour high levels of genetic diversity, with localized, deep phylogeographic structure seen in numerous taxonomic groups including reptiles (Ashman et al., 2018; Kealley et al., 2018; Pepper et al., 2013). However, some studies have found significantly lower genetic diversity in this mesic upland compared to other areas of the arid zone (Laver et al., 2017; Melville et al., 2016; Oliver, Couper, et al., 2014; Pepper, Doughty, et al., 2011), much more indicative of recent recolonization than of long-term persistence. In addition, the hypothesis that arid adapted lineages exhibit wider distributions and shallower divergences than their Monsoon Tropics counterparts, potentially a result of large-scale expansions following relative climatic amelioration during interglacials has been supported by a number of studies (Anderson et al., 2016; Fujita et al., 2010; Jennings et al., 2003; Laver et al., 2017; Oliver & Bauer, 2011; Oliver, Couper, et al., 2014; Pepper, Ho, et al., 2011; Potter et al., 2019). However, taxa such as cf. *Liopholis striata* (Chapple et al., 2004) and cf. *Liopholis kintorei* (Dennison et al., 2015) display high intraspecific divergence across the sand deserts of the northwest. Furthermore, of the studies mentioned above that sample widely across the arid zone, the distributions of lineages are almost exclusively allopatric or parapatric. However, in a phylogenetic study of the fat-tailed gecko *Diplodactylus conspicillatus* and close relatives, broad geographic sympatry across the entire central arid zone is observed in two close relatives, with further sympatry at the eastern and northern arid zone margins with two other, largely mesic, taxa (Oliver, Couper, et al., 2014). This seemingly uncommon pattern of sympatry also was found in two sister pairs of arid zone pygopodid lizards (Jennings et al., 2003), as well as in the sister species cf. *Liopholis striata* and cf. *Liopholis kintorei*, that have sympatric distributions across the sand deserts of western and central Australia (Chapple et al., 2004).

6.2 | Timing and rates of diversification

While widespread aridification, along with the concomitant appearance of the more typical desert landforms was recent, the climatic shift towards drier climates and accompanying changes in vegetation began much earlier. These broad phases of aridification are recorded in the phylogenetic signatures of many taxa as periods of increased diversification. There is growing evidence to suggest much species-level diversification of arid zone lineages is related to events earlier than the glacial cycles of the Pleistocene (see Byrne et al., 2008 and 2018 for a comprehensive review of the diversification history of different taxonomic groups in the arid zone). Many dated reptile phylogenies have inferred late Miocene/Pliocene diversification for major radiations within species groups (e.g., Ashman et al., 2018; Brennan et al., 2016; Brennan & Oliver, 2017; Fujita et al., 2010; Laver et al., 2017; Oliver et al., 2010; Oliver & Bauer, 2011; Oliver,

Couper, et al., 2014; Oliver, Smith, et al., 2014; Pepper, Doughty, et al., 2011; Pepper, Fujita, et al., 2011; Pepper, Ho, et al., 2011), in line with the initial onset of arid conditions. Figure 4 depicts speciation patterns through time for the Australian pygopodoids, sphenomorphine skinks, agamids and elapid snakes (adapted from trees from Brennan & Keogh, 2018 and Lee et al., 2016) and it is clear that for these squamate groups speciation is clustered in the mid to late Miocene and early Pliocene, and slightly later in the Pliocene for elapids. The idea that the appearance of sand dunes facilitated speciation by fracturing the distributions of rock-dwelling organisms does not appear to be supported by molecular dating. While the widespread formation of dunefields within the last million years isolated rocky exposures such as the Pilbara, central Australian ranges and the southern Kimberley, there are a number of examples of saxicolous taxa that were presumably widespread throughout these regions that diversified much earlier (Melville et al., 2016; Oliver et al., 2010; Pepper, Fujita, et al., 2011; Shoo et al., 2008). Even the deeper structure of predominantly sand-dwelling species predates the appearance of the dunefields, which may reflect early adaptation of some lineages to xeric conditions, and supports the existence of sandy substrates and/or pockets of arid or seasonally arid habitats since the late Miocene (i.e., Laver et al., 2017). Indeed there is evidence to suggest that the coastal sandplains in southwestern Australia may have a history that extends to the Miocene ~5.3 MYA (Wyrwoll, Turner & Findlater, 2014).

In addition to speciation processes and patterns of deep cladogenesis of arid zone taxa, the genetic impacts of aridification can be seen in many other ways. For example, despite deep genetic divergences within arid zone lineages, phylogeographic structure within desert clades often is both extremely shallow and young (Laver et al., 2017; Pepper, Doughty, et al., 2011; Pepper, Ho, et al., 2011). Demographic analyses of arid zone lineages repeatedly have revealed signatures of recent population expansion (Fujita et al., 2010; Laver et al., 2017; Oliver & Bauer, 2011; Oliver, Couper, et al., 2014; Pepper, Ho, et al., 2011; Potter et al., 2019), a pattern not as frequently seen in mesic lineages outside the arid zone. Diversification rates also were found to be exceptionally high in the arid-adapted lineages of the Australian skink genera *Ctenotus* and *Lerista* (Rabosky et al., 2007), with the authors suggesting the evolution of traits associated with climate tolerance may have played a role in the explosive diversification of these taxa in response to the expansion of the arid zone since the late Miocene. Elevated speciation rates also were found in arid zone lineages of pygopodoid geckos (Brennan & Oliver, 2017), along with elevated frequency in dispersal from the arid zone into peripheral mesic biomes. In a phylogenomic study of *Gehyra* geckos, Ashman et al. (2018) also found elevated rates of phenotypic evolution in the arid zone compared to counterparts in the Monsoon Tropics. These and other studies highlight the dynamic response of organisms to the catastrophic changes in climate and landscapes across the Australian continent in the Neogene and Quaternary.

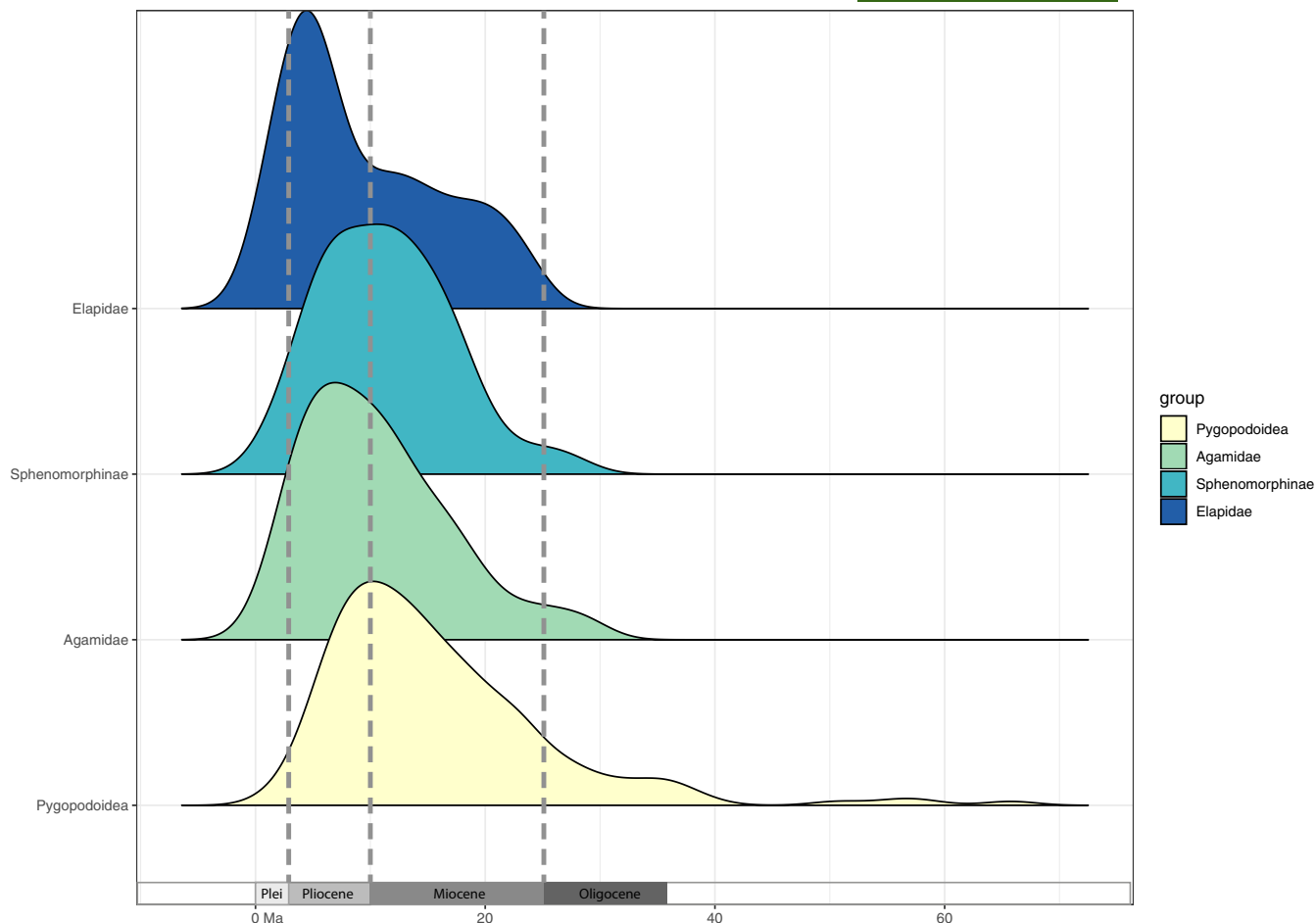


FIGURE 4 Density plots of branching patterns through time for the Australian squamate radiations Pygopodoidea, Agamidae, sphenomorphine skinks and elapid snakes (adapted from phylogenetic trees from Brennan & Keogh, 2018 and Lee et al., 2016)

6.3 | Biogeographical hypotheses

The type and distribution of vegetation in the arid zone is fundamentally linked to the underlying geology, and by extension, the phylogenetic structure of organisms that have evolved with the vegetation might also be expected to reflect underlying geological variation (i.e., Pepper et al., 2013). The IBRA delineations (Thackway & Cresswell, 1995), defined to reflect significant differences in climate, geomorphology, landform, and characteristic flora and fauna, provide a framework for testing spatial predictions about genetic similarity within and between bioregions. Mackey et al. (2008) generated an alternative biogeographical regionalization of the Australian continent based on similarity measures for 11 climatic, terrain and soil attributes, which they termed the “environmental domain classification.” Like IBRA, the environmental domains illustrate the broader environmental similarities within the arid zone when compared to continental margins. However, this classification highlights substantial variation in the western arid zone that is poorly differentiated using the IBRA approach. The spatial predictions using these sorts of bioregionalization frameworks provide important biogeographical hypotheses, and these have been tested

at various geographical scales using species distribution (Burbidge et al., 2008; Virgilio et al., 2014) and molecular (Kay & Keogh, 2012; Lanier et al., 2013; Pepper et al., 2013) data. However, due to the vast geographical area of the arid zone and the many possible fine-scale delineations using these sorts of methods, our approach below is instead to focus on some of the broadest landform and habitat differences within the arid zone that might be relevant to the evolution of phylogeographic structure. Below we describe eight biogeographical hypotheses that could be tested as fine-scale molecular and ecological data become available. The first four relate to discrete features of, or major variation within, the arid zone. Persistent or fluctuating geophysical barriers and habitat heterogeneity across the deserts could provide numerous opportunities for fragmenting ranges and isolating populations, or edaphic specialization. If vicariance or local adaptation followed by diversification of taxa within each region lead to evolutionary patterns, then taxa should exhibit genetic structuring concordant with these major geomorphological and ecological units. The following four hypotheses relate to population demographic responses to climatic and/or landscape change over broad geographical regions, with expectations that include population size contractions and expansions, and relative levels of

genetic diversity. We acknowledge that speciation can be initiated by many evolutionary processes (Butlin et al., 2012) including competition, sexual selection, and hybridization. However, in line with our above review on the geohistory of the arid zone, here our focus is on speciation processes dictated by environmental and landscape aspects.

1. *Does the discontinuity between the Western Plateau and the Interior Lowland basins of eastern Australia structure western and eastern biotas in the central arid zone?* (see Geological Setting & Palaeolandscapes above, and Figure 2a).

The Nullarbor Plain is inferred to have phylogenetically structured many taxa across southern Australia. However, an additional major structural division between the Western Plateau and the Interior Lowlands bisects the entire continent roughly north to south, east of the Nullarbor Plain. Cracraft (1991) identified a division between Eastern and Western desert biotas across the broad centre of Australia. While he implied an association with the occurrence of mulga for this “ill-defined” Western Desert area of endemism, mulga is distributed widely through the west and centre of the continent, with significant stands in the eastern lowland basins (Australian Surveying and Land Information Group (AUSLIG), 1990; Nix & Austin, 1973). Using detailed sampling across the arid zone, Pepper, Doughty, et al. (2011) identified a major phylogenetic split between lineages of beaked geckos along the length of this structural divide, with the distribution of one major lineage clearly limited to the Western Plateau, and another distributed throughout the basins of the Interior Lowlands. While not mentioned specifically as a biogeographical barrier, examination of the published literature reveals coincident geographic patterns of divergence across this topographical divide in a number of other arid zone taxa, for example in pebble-mimic dragons *Tympanocryptis* (Shoo et al., 2008), the geckos *Diplodactylus* (Oliver, Couper, et al., 2014) and *Heteronotia* (Fujita et al., 2010), *Diporiphora* dragons (Doughty et al., 2012) and *Ctenotus* skinks (Rabosky et al., 2014). This is an ancient landscape feature relating to the early Precambrian building of the Australian continent. However, its structure closely influences the distribution of the major drainage divisions. Divergence across this division may therefore relate to the availability of moisture in the landscape, particularly during dry periods (see hypothesis 2 below). There also are major differences in topographic roughness between these two physiographic divisions (see Figure 2a), as well as stark differences in regolith, where cracking clays and stony plains in the eastern Interior Lowlands are reflected in a significantly different vegetation cover (see Figure 2f). This east/west division across the arid zone is at odds with recent work using a large dataset of multiple plant groups. Gonzalez-Orozco et al. (2014) identified the major phyto-geographical split within the arid zone was one that dissects the biome north/south, roughly coinciding with the Tropic of Capricorn and the summer-winter rainfall line. This suggests climate, not geology, was the primary environmental driver of diversity patterns in arid zone plants. Discriminating between these two very

different patterns using molecular studies of arid zone fauna should be straightforward.

2. *Do terrestrial taxa show biogeographical breaks consistent with major drainage divisions in the arid zone?* (see Desert Dunes & the Modern Physiography, above, and Figure 2c).

The structuring of phylogenetic lineages among rivers and drainage divisions is well-documented in arid and semi-arid freshwater biota (Carini & Hughes, 2004; Hughes & Hillyer, 2006; Masci et al., 2008; Murphy & Austin, 2004; Nguyen et al., 2004; Thacker et al., 2007; Unmack, 2001). Because aquatic taxa are biogeographically constrained by spatially and temporally disconnected drainages, they are considered more likely to reflect historical hydrological connections than terrestrial species (Aise, 2000). However, Pepper, Doughty, et al. (2011) showed the distribution of beaked-gecko lineages closely mirrored the major drainage divides within the Interior Lowlands; the Lake Eyre, Bulloo-Bancannia and Murray-Darling divisions. No obvious physical barriers separate these catchments. However, ridge-lines (as minor as they may be in the arid lowlands of central Australia) are expected to be the driest parts of the landscape, and under the coldest and driest phases of the Pleistocene may have limited plant growth both in vegetation density and/or species composition. This would presumably have important consequences for the distribution of terrestrial taxa. An understanding of the ecology of organisms also may shed light on this intriguing pattern—beaked geckos predominantly shelter in spider holes in the ground (Wilson & Swan, 2017). Sand is transported away from basin margins, so there likely would have been more exposed bedrock along catchment boundaries, which would have strong implications for burrowing organisms. Along with the major drainages in the Interior Lowlands already mentioned, the major divides between the Pilbara-Gascoyne and southern South West Coast, the adjacent North Western Plateau and South Western Plateau, and the division between the former and the Tanami-Timor Sea Coast, as well as their nested catchments, remain to be tested. The broad and more simplified drainage divisions across the arid zone compared to the substantially more complex regions along the continental fringes of the north and east should facilitate testing this hypothesis. In addition, the relationship between effective precipitation and vegetation cover is affected by other environmental factors such as temperature and atmospheric carbon dioxide (see Hesse et al., 2004). As such, in parts of the arid zone such as the southeastern interior, the cold landscapes during peak glacial cycles appear to have been characterized by sparse vegetation and patchy, active sand dunes at the same time as experiencing enhanced hydrological conditions relative to today. The large fluvial and lacustrine systems still active during the LGM could have served to reinforce vicariant diversification instigated during wetter periods earlier in the Cenozoic. Molecular dating of terrestrial taxa that show biogeographical breaks across major river systems in the Murray-Darling Basin would shed light on this hypothesis.



3. *Do diversity patterns of substrate specialized taxa reflect contemporary ecological gradients or historical vicariance?* (see Desert Dunes & the Modern Physiography, above, and Figure 2e above);

The heterogeneous mosaic of different desert substrates (dunefields, stony desert, clay plains, dune-free regions) across the arid zone could have generated current patterns of diversity in a number of ways. It can be very difficult to distinguish historical from ecological factors in biogeography (Endler, 1982). However, four simple scenarios with predictions about the distribution of habitat specialists on a phylogeny could help to identify the possible processes leading to speciation.

Crisp and Cook (2013) discuss the role of soil mosaics and edaphic specialization in the speciation and diversification of the Australian flora, and Anderson et al. (2016) suggest substrate and ecological differentiation may be responsible for divergence in spinifex grasses in the Pilbara region. Pepper et al. (2006) and Pepper et al. (2013) also found substrate variation in the Pilbara matched the distribution of closely related gecko lineages, and spatial heterogeneity of soil types was found to be an important predictor of genetic divergence in five reptile species occupying the coastal sand-dune and sandplain habitats of southwestern Australia (Edwards et al., 2012). Adaptation to distinct habitats (Endler, 1982; Moritz et al., 2000) (i.e., sandplains, gibber pavement, or swelling-clay soils) should act to reduce gene flow between habitat types, resulting in greater genetic divergence between, rather than within, habitat types. Finding that sister lineages frequently occur in adjacent but distinct habitats would support this model (Scenario 1). Alternatively, a widespread species may show little or no genetic variation across multiple habitat types, indicative of a much more generalist ecology (Scenario 2). Phylogenetic patterns that indicate sister lineages are frequently found within the same habitat type suggests the influence of isolation and vicariant diversification (Scenario 3). Indeed, fluctuations in habitat boundaries or the dissection of a habitat into isolated patches is expected to lead to genetic divergence of continuously distributed populations. Following extraordinarily detailed ecological studies of almost 100 desert lizards, Pianka (1972) grouped species into biogeographical categories and identified common patterns based on geographical distribution and major habitat type. His intuitive hypothesis for enhanced speciation in the arid zone centred on the fluctuating configuration of sandridges (dunefields), sandplain-*Triodia* and shrub-*Acacia* habitats periodically breaking up or connecting the geographic ranges of highly habitat specialized taxa. There has so far been limited phylogenetic information available to examine the role of these habitat junctures in shaping genetic differentiation of habitat restricted desert lizards in the Australian arid zone (but see Chapple et al. [2004], Shoo et al. [2008] and Melville et al. [2016]). Substrate specificity promoting vicariance has been highlighted as an important evolutionary agent in *Pachydactylus* geckos in arid southern Africa (Bauer, 1999), with the same scenario invoked for scorpions and other stenotopic taxa in the same region (Prendini, 2001). The fragmentation of rocky habitats by the

eastern migration of the Kalahari sands in southern Africa also has been identified as a major driver of speciation within the flat lizards *Platysaurus* (Broadley, 1978).

The expansive dunefields across the Australian arid zone have fragmented the pre-existing hard and rocky substrates and sandplains. Figure 2e shows the distribution of dunefields is not continuous, and there are regions that are largely dune free. For example, in Western Australia the stony Gibson Desert disconnects the dunefields of the Great Sandy and the Great Victoria deserts, and in the east, Sturt Stony Desert separates the Strzelecki and Simpson Desert dunefields. While isolation of rocky substrates by sand accumulation may promote divergence, by the same token connectivity of habitats could facilitate gene-flow over large geographical areas. For example, a sand specialist may have a large distribution within a single habitat type, with little phylogeographical structure across that habitat (Scenario 4). Indeed, Laver et al. (2017) suggested the lack of diversity within the widespread arid zone phasmid gecko lineage may reflect long-term connectivity facilitated by a more continuous distribution of spinifex (commonly associated with sandplains and dunefields) in the arid biome. While the Tanami Desert in the northern arid zone is largely dune free (though some definitions of the Tanami include the adjacent Wiso dunefield), the landscape is formed by regolith/saprolite of the local geology and most of the region is covered by alluvial-colluvial sediments and aeolian sands (Wilford, 2003). As such we might expect continuous distributions of taxa across the adjacent Great Sandy Desert. In contrast, the Pilbara and Yilgarn are predominantly sand free (with the exception of the coastal sandplains). Here, the eastern boundary of the Pilbara and Yilgarn where the rocky hills and ranges meet the sands of the Great Sandy and Great Victoria deserts may constitute a biogeographical barrier to more saxicolous taxa.

Differences in substrate, topography and moisture among desert systems suggest some areas might have enhanced genetic diversity relative to others. For example, in the Great Sandy Desert, the interdunes are often sand free. This frequent exposure of low ridges, hills and ranges that occurs between the dunes creates a much more heterogeneous landscape than the desert dunefields in the lowland basins to the east (for example the Simpson Desert), which may imply more structured populations in this area. Few studies have sampled throughout this vast northwestern desert region, however, genetic work on *Liopholis striata* and *L. kinntorei* appear support this idea (Chapple et al., 2004; Dennison et al., 2015). The Mallee Desert in the far southeastern arid zone is largely separate from the dunefields of the neighbouring Strzelecki Desert, and also comprises a very different dune landscape. The Wiso and Barkly dunefields in the northern arid zone also are separated from the more extensive inland dunefields. Given the relative isolation of these sand deserts, they might be expected to harbour genetically distinctive taxa. The effect of substrate variation across the Australian arid zone on morphology of skin, feet and toes will no doubt provide additional fascinating insights into the adaptation and habitat specialization of terrestrial vertebrates (i.e., Lamb & Bauer, 2006; Riedel et al., 2019).

4. Do ecologically related taxa have synchronous population divergence and expansion histories? (see Vegetation & bioregions above, and Figure 2F)

Figure 2aF shows the distributions of the three major vegetation types across the arid zone. Spinifex grasses are clearly the predominant vegetation in the northwestern and central arid zone, *Acacia* shrublands or mulga tends to have a more southerly distribution, and the northeast arid zone is dominated by tussock grasslands. Phylogenetic information from plant groups can shed light on the timing and patterns of diversification of organisms adapted to them. Inferred molecular dates from recent studies indicate the spinifex genus *Triodia* began to diversify rapidly in the mid-late Miocene (Anderson et al., 2019; Toon et al., 2015), while the widespread arid zone *T. basedowii* complex began to radiate in the early Pleistocene (Anderson et al., 2019). Divergence dating in the Australian lineages of *Acacia* also suggest the major diversifications were coincident with Miocene aridification, with age estimates for taxa within the arid *A. victoriae* and *A. pyrifolia* clade inferred to be less than 7 Ma (Miller et al., 2013). A prediction for taxa strongly associated with a particular vegetation type is that diversification might have occurred simultaneously. Indeed, the crown radiation for the spinifex-specialised phasmid geckos in the mid-Miocene broadly overlaps with the inferred age of the spinifex radiation (Laver et al., 2017; Skipwith, et al., 2019). Recent work on Australian nasute termites inferred a transition from wood to grass and litter feeding in one major group occurred in the mid-Miocene, with the switch to exclusive grass feeding in two sister-pairs (including the spinifex termite *Nasutitermes triodea*) inferred to have occurred ~ 5–6 Mya (Arab, et al., 2017). Alternatively, as vegetation types would have expanded and contracted their distributions with climatic cycles, taxa may have diverged after the emergence of an associated vegetation formation, but during these contraction phases.

5. Do the eastern deserts (including the Simpson, Strzelecki and Mallee deserts, as well as the channel country and Darling-Paroo region) harbor greater phylogenetic diversity than the western deserts (including the Great Sandy, Gibson, Great Victoria, Tanami, Wiso, Barkly and Eyre deserts as well as the Pilbara and Yilgarn regions) due to vast differences in historical water availability? (see Geological Setting and Palaeolandscapes above);

Of fundamental importance for organisms living in the broad center of the Australian continent, the extensive watercourses that traversed the Western Plateau for much of the Cenozoic ceased flowing in the late Miocene (Quilty, 1994), while palaeochannels in the eastern arid zone indicate the large volume of water that continued to drain from the Monsoonal Tropics during wet periods. Indeed, the modern riparian systems and floodplains of eastern Australia are the largest on the continent, and palaeo evidence suggests they were up to four times wider during the last interglacial (reviewed in Smith 2013). These systems are associated

with the largest expanse of the moisture-retaining vertisol soils which are extensive in the channel country and Cooper Creek drainage catchment. Increased moisture availability following the late Miocene in the eastern arid zone suggests phylogenetic diversity within taxa may be higher in this region compared to the west, where arid landscapes may have remained too cold and dry to sustain populations during glacial periods of the Quaternary. Persistence in the eastern deserts and therefore higher effective population sizes over long periods of time is expected to leave a signature of high nucleotide diversity within populations and species, with relatively constant diversification rates and an overall even topology. In contrast, higher rates of extinction in the western deserts may be reflected in long branches on a phylogeny, with relatively low effective population sizes and consequently lower levels of nucleotide diversity within populations and species. Duckett and Stow (2013) sampled nearly 750 geckos from populations of *Geyhra variegata* in the central and eastern arid zone and found increased genetic diversity in the channel country was likely associated with higher mean annual run-off in this region. In addition, they found genetic diversity declined significantly with increasing distance from water sources in the Simpson Desert. Nylinder et al. (2014) compared nucleotide diversity between the eastern and western arid zone populations of a number of species in the genus *Centipeda*, a group of small herbs often found in proximity to ephemeral sources of water and moisture. Higher diversity was found in the east, which in concert with inferred ancestral ranges as well as timing of speciation events led the authors to infer recent dispersal of a small number of individuals from east to west, with western populations subject to founder effects. However, they also recommended more rigorous tests with additional data to explore alternative explanations for the greater nucleotide diversity in the eastern arid zone. Study systems such as this, where water availability is more obviously a limiting factor would provide a logical choice for testing this hypothesis.

6. Alternative to hypothesis 5, do the western deserts harbor greater phylogenetic diversity than the eastern deserts due to increased topographic complexity and proximity to major uplands? (see The Evolution of Biodiversity above and Figure 2A)

The Western Plateau, on which the Great Sandy, Gibson, Great Victoria, Tanami, Wiso, Barkly and Eyre deserts are developed, is characterized by substantially more variable surface geology and topography than the Interior Lowlands that house the eastern Simpson, Strzelecki and Mallee deserts. Indeed, the Pilbara, Yilgarn, Central Australian ranges and the Flinders Ranges comprise the largest rocky uplands within the boundaries of the modern arid zone, and all are associated with the division of the Western Plateau (Figure 2A & B). These uplands are likely to have maintained less xeric and more heterogeneous conditions during arid periods (Byrne et al., 2008), and unsurprisingly are ranked among the most significant biological refugia in Australian drylands (Morton, et al, 1995; summarized in Smith, 2013). More specifically these refugia include the Pilbara



(Hamersley and Chichester Gorges and Ranges) and the Cape Range caves and gorges, those in the southern Kimberley (Bungle Bungles, caves of the Oscar and Napier Ranges, Edgar Ranges) and the Nullarbor Caves in Western Australia, with a number of others in Central Australia/the Northern Territory (Western MacDonnell Ranges, Eastern MacDonnell Ranges, George Gill Range, Davenport and Murchison Ranges, Dulcie Ranges) as well as the Carpentaria Sandstone in the far north. In South Australia the most significant refugia identified are the Northern Flinders Ranges and the Gawler Ranges, while in Queensland they include Lawn Hill Gorge, the Selwyn Range and the Northern Grey Range (Morton et al., 1995). The authors suggest the disproportionately small number of potential refugia in arid and semi-arid Queensland compared to the rest of the arid zone may be an artifact relating to the general lack of knowledge of the evolutionary history of biota in this region. Given the arid and semi-arid zone is thought to have extended almost to the continental margin of Queensland during the LGM, the loosely connected uplands along the Great Dividing Range, particularly those in Queensland's central highlands and the Gregory Range in the north would likely have constituted important refugia despite falling outside the boundaries of the modern arid zone. These and other uplands at the present arid/mesic interface are expected to have been particularly important refugia for arid zone biota by providing environments much less arid than those deeper in the arid core. Such peripheral areas have been reviewed by Byrne et al., (2008) in southern Australia, who concluded biota often comprised highly divergent, geographically structured intra-specific lineages indicative of major early-mid Pleistocene refugia, with multiple, more localised patterns of persistence in areas of environmental heterogeneity shaping idiosyncratic responses in the late Pleistocene. Klein, Wilson, Watts, Stein, Berry et al. (2009) used gross primary productivity calculated from high-resolution satellite data from 2000-2005 to identify ecological refugia across the arid and semi-arid zones. While many of the areas depicted are unsurprising based on associated topographic complexity, the Gibson Desert in particular stands out as having high productivity during drought conditions. This highlights the strong influence of even minor topographic hills and ranges on moisture availability, and suggests the Gibson Desert may be an additional important refugium in the central arid zone.

Significantly, there are no major uplands in the vast area of the Interior Lowlands. The Simpson and Strzelecki deserts in this region are the driest areas of the modern arid zone, and were significantly drier during the LGM and other glacial periods prior. Comparing levels of diversity between the Simpson-Strzelecki deserts as well as stony deserts in Queensland's channel country to the Great Sandy-Little Sandy-Gibson-Victoria deserts in the west would reveal whether taxa in the eastern arid zone were able to persist during the cold and arid Pleistocene glacial cycles, and where diversity is centered in these major arid zone regions. If aridification during the Plio-Pleistocene resulted in high rates of extinction across taxonomic groups in the eastern deserts, phylogenies should exhibit long branches, with significantly lower species richness and little nucleotide diversity within populations and species. Importantly, all of

the sandy deserts also contain small range systems, with rockholes, gorges and run-on areas that provide focal points for human use of the region (Smith, 2013), and their locations can be inferred using the primary productivity map of Klein et al. (2009). The location and effects of these more localized putative refugia within the eastern and western arid zone also could be tested by inferring areas of habitat stability through environmental niche modelling, and coupling these results with phylogeographic and demographic inferences.

While topography is generally uniform across the Interior Lowlands, the Flinders Ranges extend some 600 km inland from the South Australian coast to the edge of the Lake Eyre Basin, and include uplands between 300 m to more than 1100 m in elevation. In addition, unlike many other regions of high topographic relief in Australia that are likely to be ancient (Twidale & Campbell, 1995), the Flinders Ranges are thought to have developed much more recently in response to tectonism and uplift during the Plio-Quaternary (C  l  rier, et al, 2005; Quigley, et al, 2007). The combination of proximity to the Interior Lowlands as well as recent dynamic geologic activity in the Flinders Ranges suggests they may be highly significant for both the generation and persistence of diversity of arid taxa. Indeed, using bioclimatic modelling of 20 vascular plant species, Guerin & Lowe (2013) identified shared patterns between individuals with similar characteristics and inferred putative refugia in the southern Mount Lofty Ranges as well as the northern Flinders Ranges. Further assessment of these South Australian refugia using additional independent taxonomic groups is warranted.

7. Do desert margins harbor greater phylogenetic diversity compared to areas deeper within the arid core? (see Palaeoclimatic History above, and Figure 2aB).

The semi-arid zone attained its maximum extent during the Last Glacial Maximum and would have been repeatedly reduced in area during moist periods of the Late Pliocene and Pleistocene interglacials. These areas were therefore highly variable, fluctuating between sand dunes and forest in the last 1 Mya, whereas the landscapes further inland would have remained more typically arid. In addition, topography is greater in the uplands of the Monsoon Tropics and also along the Great Dividing Range down the eastern Australian coast. As such, as well as having periodic shifts in latitude/longitude, taxa persisting at the desert margins also would have had the opportunity to shift their geographic ranges altitudinally. These fluctuating environments at the desert margins would repeatedly have expanded and fractured the distributions of both taxa adapted to arid environments and those with a preference for mesic habitats, depending on whether glacial or interglacial conditions prevailed. As such, we would expect these marginal areas at the interface of the semi-arid and mesic zones to harbor higher species diversity and exhibit greater phylogeographic structure. Indeed, recent genetic studies of a burrowing toadlet and an agamid lizard suggest the geographic region between the northern arid zone and the adjacent Monsoon Tropics is emerging as a center of endemism in its own right (Catullo et al., 2014; Smith et al., 2011). A signature of

increased species richness in marginal areas may not necessarily be visible in phylogenetic tree shape due to the possibility of increased extinction in these highly variable habitats. However, we might expect the range sizes of species or populations living in the proximity to the semi-arid/mesic transition zone to be smaller than for populations in the preferred/primary habitat, be that arid or mesic. Finding a large number of short-range endemics or geographically isolated populations within species at the exterior margins of the semi-arid zone would support this hypothesis.

8. *Did the recent expansion of sand deserts drive species sympatry via secondary contact?* (see Evolution of Arid Zone Diversity above)

Closely related taxa tend to have non-overlapping ranges, an ecogeographical pattern dubbed Jordan's rule (Jordan, 1905; Fitzpatrick & Turelli, 2006, but see Jordan [1892] for his other ecogeographical rule on the "Law of Vertebrae"), whereas range overlap is more likely between deeper clades (Barraclough & Vogler, 2000). A phylogenetic study of the fat-tailed gecko *Diplodactylus conspicillatus* and close relatives revealed broad geographic sympatry across the entire central arid zone of two close relatives (*D. conspicillatus* and *D. laevis*), with further sympatry at the eastern and northern arid zone margins with two other, largely mesic, taxa (Oliver, Couper et al., 2014). This uncommon pattern of sympatry among sister taxa also was found in two sister pairs of arid zone pygopodid lizards (Jennings et al., 2003). In one of the sister-pairs (*D. borea* & *D. tincta*) the sympatry occurs largely at the margins of the arid zone, however a second sister-pair (*Delma butleri* & *D. nasuta*) have areas of sympatry in the central arid zone. Chapple et al. (2004) also showed cf. *Liopholis striata* and cf. *Liopholis kintorei* are sister species, and while they only used a single representative of the endangered cf. *Liopholis kintorei*, the two taxa are known to have sympatric distributions across the sand deserts of western and central Australia. The ages of the pygopodid sister pairs were inferred to be pre-Pleistocene, with molecular dates suggesting ages of between 5–10 Mya (Jennings et al., 2003). Age ranges for the origins of the sympatric fat-tailed gecko taxa also fall into the same time period (Oliver, Couper et al., 2014). Jennings et al. (2003) suggested the sympatric pygopodid pairs could have formed via allopatric speciation if one of each pair or taxa had undergone recent range expansions, however they were unable to test this using their data. Demographic analyses of the fat-tailed gecko taxa found significant signatures of population size expansion for *D. laevis*, lending support for this hypothesis. The lizard taxa in each of these four sympatric sister pairs have close ecological associations with sandy substrates and spinifex grass. Dating analyses for the widespread arid zone spinifex *Triodia basedowii* complex suggests diversity arose from a crown radiation that began approximately 1.9–2.7 Ma (Anderson et al., 2019), and continued through the climatic transition ~ 1 Ma that led to the formation and expansion of sandy dunefields. Identifying additional sympatric sister pairs that diverged prior to the expansion of *Triodia* would be the first step in testing this hypothesis. If population size increase is visible in one or

both of the taxa, and this pattern is found across many sister-pairs, it is plausible that the radiation and geographic expansion of spinifex enabled the concurrent expansion of formerly allopatric lineages. In their detailed study of Australian squamate assemblages in the Great Victoria Desert, Rabosky, et al. (2011) found closely related species pairs in skinks, agamids and gecko lizards were exceptionally divergent in patterns of habitat use, suggesting both historical divergence in species' habitat preference and contemporary species interactions play an important role in the distribution of individual within particular habitat types. Detailed ecological studies are needed to determine whether each member of the sister pairs mentioned above is found in syntopy with its sister, or if they are ecomorphologically divergent from each other (Jennings et al., 2003; Cardillo & Warren, 2016).

7 | CONCLUSIONS AND FUTURE DIRECTIONS

The Australian arid zone harbours a unique biota, with the distributions of taxa historically intertwined with changing climates, landscape physiology and geological history. Collectively, the patterns exhibited by arid zone taxa—persistence in localized refugia, recent and rapid population expansions, increasing rates of diversification and phenotypic evolution—complement the geological records preserved in dried up river channels, ephemeral salt lakes and ancient dunes, and together paint a picture of the tumultuous transition to aridity that began in the late Miocene. While there seems to be consensus in the biogeographic literature that big diversification events across many Australian taxa occurred 10–15 Mya around the inferred timing of the "onset of arid conditions", simultaneously there also appears to be broad misconceptions regarding what the landscapes might have looked like during this time (notwithstanding the great uncertainty regarding interpretation of the often sparse geomorphological and palaeontological records!). The Australian arid zone is a surprisingly heterogeneous biome. Since the initiation of drier conditions in the late Miocene, the landscapes have been spatially and temporally variable. The magnitude and nature of aridity in Australia was not uniform, and thus "aridity" across the arid zone also has been spatially and temporally variable (Hesse et al., 2004). For much of Australia's biota living in the broad centre of the continent, their deeper history was shaped by an environment characterized by vast fluvial systems, feeding enormous volumes of water into permanent mega-lakes and transporting large quantities of sand across the landscape. In Western Australia, this extensive surface water dried out first, and elsewhere fluvial systems switched to an ephemeral state and progressively became saline. But wet pulses in history would have reactivated these inland rivers from time to time as precipitation waxed and waned with glacial cycles (even during the LGM in southeastern Australia there were large rivers and enhanced run-off from the highlands [Hesse et al., 2004]). When they were dry, their sand filled valleys could be blown



out by wind, forming extensive sandplains across the continent that would have been stabilized by a vegetation progressively shifting to dry woodlands, and open shrublands and grasslands. Geochronological evidence suggests that the formation of dune-fields began in the mid-Pleistocene, accelerating as the climate became increasingly arid in later glacial cycles (Hesse, 2010). These dunes reflect episodic accumulation, and patchy, rather than widespread, activity. With this in mind, it becomes more apparent how biota could have persisted and diversified in the arid zone despite the enormous and turbulent climatic changes of the Pleistocene. Indeed, human populations were faced with the same severe climatic conditions, and likely responded in a similar way. From renowned Australian archaeologist Mike Smith: *"... if we take the desert as a whole, the archaeological evidence is more consistent with a pattern of widespread 'cryptic' refugia than with a geographic division into refuges, corridors and barriers. People appear to have survived across much of the desert, but as scattered occurrences and at low densities—in effect, in pockets of microhabitat. Some regions may have been abandoned, including some areas of sandy desert and parts of the Pleistocene coast, but direct evidence for abandonment of large parts of the interior is more limited than once thought. 'Each desert has its own barriers, corridors and refuges,' says Cane, 'and one should look to this inner variability in order to understand the true nature of desert colonization and settlement' (1995:49)".*

In this synthesis our emphasis has centred on geological and landscape variation across the arid zone lowlands. While a review of this scale across such a vast area cannot be comprehensive, in doing so we hope to provide another base onto which fine-scale genetic studies can build to further our understanding of biotic diversification in this biome. We also acknowledge that we have been purposely restrictive in our coverage of taxonomic groups, notwithstanding significant work on a diverse array of organisms (subterranean invertebrates, fish, mammals, birds, plants) that has greatly contributed to our comprehension of arid zone biogeography. Collecting data to quantify edaphic complexity across the arid zone, widespread genetic sampling from disparate taxonomic groups, and a more detailed understanding of species ecology and life history will greatly improve our understanding of the ecological and historical drivers of diversity gradients in the Australian deserts. In order to capture genetic turnover across fine scale geomorphological divisions, mtDNA (or chloroplast DNA) screening that incorporates widespread and detailed geographical sampling will remain an important first step. However, the development of comparative genomic approaches have opened the toolbox to resolve more complex questions relating to the nature and timing of divergence and speciation across assemblages of nonmodel species. The addition of large numbers of nuclear loci using next generation sequencing has dramatically improved the performance of coalescent-based analytical methods, and enables statistical testing of substantially more complicated phylogeographical scenarios (Brito & Edwards, 2009). For example, through improved estimation of demographic inference, dating of divergence events, and estimation of population connectivity and gene-flow, sophisticated comparative phylogeographical

methods can be used to test simultaneous divergence times (Leaché et al., 2007; Leache et al., 2020; Oaks, 2019), test for shared biogeographical barriers (Carnaval et al., 2009), estimate temporal synchronicity in expansion times across taxa (Burbink et al., 2016; Xue & Hickerson, 2015) and infer the location of origin of range expansions (Peter & Slatkin, 2013). Questions relating to the evolution of Australia's arid taxa include; did taxa endemic to the uplands of the Pilbara diverge from their closest non-Pilbara relatives at a similar time? For saxicolous endemics, are divergence times simultaneous between populations in the Pilbara and other rocky uplands such as the Kimberley and the central Australian ranges? Do desert taxa typically exhibit signatures of population expansion? And is there synchronicity in expansion times across taxa within particular regions? Integrating this genetic information with Environmental Niche Models (ENM) to infer the locations of historical persistence within the deserts (Moussalli et al., 2009; Portik, Leache et al., 2017), and evolutionary models that can estimate ancestral locations for speciation events (Nylinder et al., 2014) or distinguish between processes underlying lineage diversification (Quintero & Landis, 2020) will provide additional avenues for exploring and understanding the evolutionary history of arid biota. From our review of arid zone landscapes, it is clear that incorporating variables such as ground moisture availability and substrate type would improve the predictive power of species distribution models (Cianfrani et al., 2019). It also will be important to incorporate the locations of arid zone palaeochannels into divergence models. And of course reconstructing the historical distributions of arid zone taxa is only as good as the geological and palynological fossil records allow. More accurate dating estimates of dune fields, including for the vast areas that are as yet unsampled, as well as additional multiproxy datasets (palaeobiological, geochemical and geophysical) for palaeo-environmental reconstruction, and more detailed continent-wide maps of regolith and surface geology would greatly improve our understanding of the major diversification processes in arid Australia.

Increasing our knowledge of the evolution of arid zone diversity using the sorts of methods outlined above also will provide a crucial framework for management planning and conservation. Indeed, knowing how arid zone organisms evolved and responded to changing climates in the past is key to understanding their resilience and ability to adapt to environments in the future. Conserving biodiversity in the Australian arid zone presents a particularly significant challenge in the face of global warming. This biome is predicted to experience the greatest increase in temperature in Australia as well as decreased species richness over the next 50 years (Dunlop, 2012). Likewise, rainfall variability is already extremely high (Morton et al., 2011) and global climate models such as CSIRO-Mk3 predict a significant decrease in winter rainfall in the southern arid zone by 2090 (CSIRO & Bureau of Meteorology, 2015). The subdued topography over most of the deserts means species will be unable to shift to higher elevations as the climate warms up, and the disturbance and exploitation of ancient palaeovalley aquifers by human activities threatens to disrupt these significant groundwater resources for arid zone vegetation, stygofauna and associated ecosystems

(Magee & Geoscience Australia, 2009). It has long been recognized in studies of biogeography that species richness is significantly influenced by habitat heterogeneity (MacArthur & Wilson, 1967). If geophysical diversity promotes and maintains species diversity, then conserving habitats that encompasses geophysical variation will be an important strategy for long-term conservation success across the arid zone. This is in essence what bioregionalization frameworks such as IBRA aim to do, however, at present there is simply not available genetic information for species-level taxonomies and associated distributional data for many arid zone taxa. Having an understanding of the mechanistic niche of an organism (i.e., the species specific ways physiological and behavioural processes interact with different environmental factors in an organism's habitat to affect its growth, survival and reproduction) (see Kearney, 2006), and knowing species' physiological limits will be an important conservation tactic, to ascertain whether species have the ability to adapt or if they will have to migrate or change their behaviour to cope with rising temperatures, or whether extinction is more likely.

Finally, with improved sampling across the vast and remote regions of Australia's deserts, an obvious consequence will be the discovery of previously unrecognized lineages. Indeed, recent genetic assessments of widespread arid zone species have revealed substantial cryptic diversity (e.g., Hutchinson et al., 2014; Marin, Donnellan, Hedges, Puillandre, et al., 2013; Melville et al., 2019; Oliver et al., 2010; Oliver, Couper, et al., 2014; Pepper, Doughty, et al., 2011; Pepper et al., 2006; Rabosky et al., 2009). These data will continue to challenge study design and analysis in the short-term (i.e., a study that started out with detailed sampling for a single species might end up being one of few samples for multiple diverged lineages), but will ultimately allow us to better understand the evolutionary processes at species boundaries. We hope that our review and the hypotheses outlined here stimulate further studies of arid zone biogeography. In particular, we look forward to the ways in which future biological collections will open the vast "dead heart" of the continent, to further our understanding of how life has been able to persist and flourish amidst the formation of the largest desert in the Southern Hemisphere.

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No original data were used in this review.

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