Evolutionary History

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Introduction

Australia is a vast continent with a range of environments broadly differentiated into three major biomes. The best studied of these, the mesic biome, is confined to the eastern coast and the southeast and southwest corners and has pockets of ever-wet rainforest along the east coast. The monsoon tropics biome occurs in the northern part of the continent including Cape York Peninsula in the east, and the arid-zone biome covers the vast central and western parts of the continent, generally west of the Great Dividing Range. The arid zone is Australia's largest biome, occupying approximately 70% of the entire continent (Fig. 1a) and broadly corresponding to the Eremaean and northern desert regions of the Australian Bioregionalisation Atlas (Ebach et al. 2015) (Fig. 1b). It covers a range of environments such as sandy

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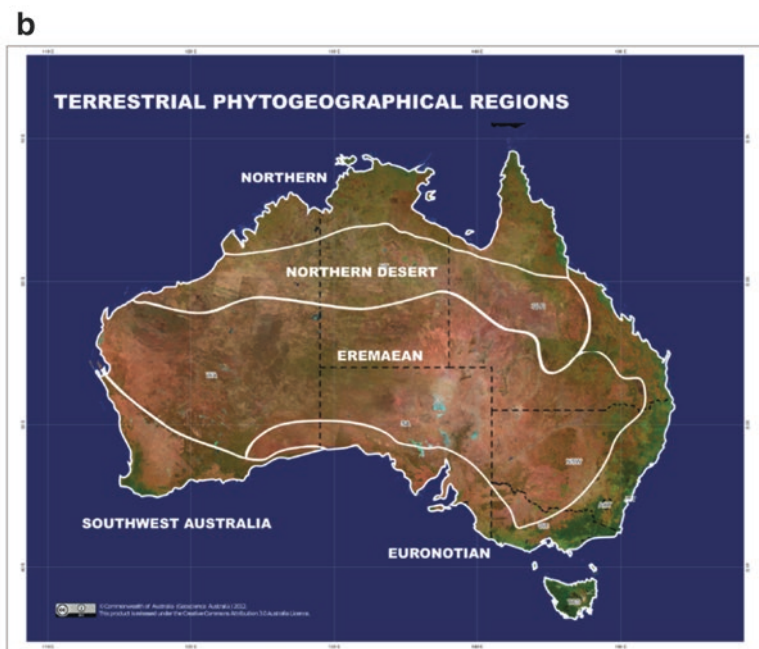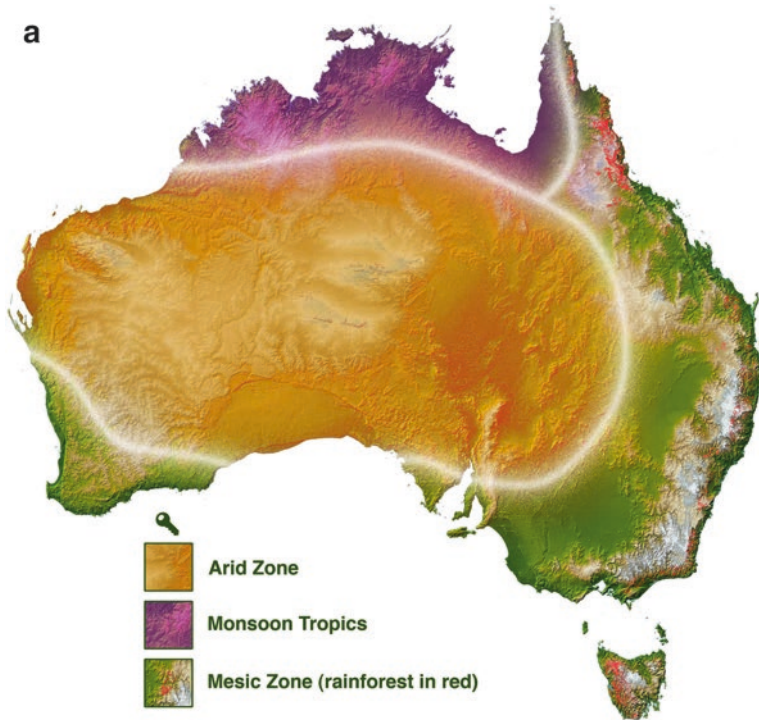Life and Environmental Sciences, University of California, Merced, CA, USA

Fig. 1 (**a**) Geomorphological map of Australia showing the three major biomes of Australia with the arid zone encompassing the central and western parts of the continent (Anne Hastings, CSIRO). (**b**) The arid zone broadly corresponds to the Eremaean and northern desert phytogeographical regions of Australia. (From Ebach et al. 2015)

deserts, gibber deserts and steppes, ranges and coastal plains and hosts a variety of vegetation types, shrub woodlands, acacia and mallee eucalypt shrublands, spinifex grasslands, tussock and hummock grasslands and chenopod shrublands. On average, the arid zone is only 300 m above sea level with low relief and a broad flat plain covering most of the central western area (Williams 1984; Pain et al. 2012; Pillans 2018).

Although the arid zone covers a vast area of often inhospitable environments, the diversity of plants, animals, birds, reptiles and invertebrates that make up the biota of this biome is reasonably well understood (Barker and Greenslade 1982; Cogger and Cameron 1984; Cracraft 1986, 1991; Dawson and Dawson 2006; Schodde 1982; Stafford Smith and Morton 1990). Assessments of species diversity have revealed greatest diversity in the reptiles and invertebrates; 43% of the continent's reptiles and a similar proportion of termites and ants inhabit arid environments (Byrne et al. 2008), the majority of Australia's 7500 ant species occurring in the arid zone (Andersen 2016). The diversity of other groups is less; only 15% of birds and 10% of plant species are endemic to the arid zone (Barker and Greenslade 1982; Schodde 1982, 2006). Analysis of turnover of species from six groups of vascular plants and three groups of non-vascular plants identified major change in vegetation communities within the arid zone and specified nine phytogeographical subregions, the western, central and eastern deserts, the Pilbara and Great Sandy Desert interzone, the Central Queensland area and the Nullarbor, Eyre Peninsula and Adelaide areas (Ebach et al. 2015).

The current arid zone is defined here as having a moisture index (mean annual rainfall divided by evaporation) of 0.4, annual rainfall that is generally below 250 mm and unpredictable, and little seasonality (Stafford Smith and Morton 1990). Byrne et al. (2008) provided a detailed summary of the environmental history of arid Australia, based on a review of evidence from plant macro- and microfossils, sedimentology, fossil faunal assemblages, palaeodrainage, geomorphology and isotope analyses. We provide a short contextual summary here and in Fig. 2.

The arid zone is considered to be younger than the mesic zone. This is because the rainforest vegetation of the Australian continent in the Eocene (55–35 million years ago) reflects far more mesic conditions historically than currently (Hill 1994; Schodde 2006). Geomorphological evidence indicates that the whole of Australia was warm and wet in the Early to Mid-Miocene (23–20 million years ago) (Alley and Lindsay 1995; Martin 2006). Progressive aridification of the Australian environment occurred from the Mid-Miocene (~20 million years ago), the first signs of aridity evident in cessation of regular flows in western palaeodrainage channels (Bowler et al. 2006). Pockets of arid environments may have been present in the current arid zone in the Mid-Miocene, but the stony and sandy desert environments did not fully develop until the Pliocene (6–2.8 million years ago) and Mid-Pleistocene (~1 million years ago) respectively (Fujioka et al. 2009, 2005). The Nullarbor Plain, a large limestone plateau in the central southern region of Australia, was subject to marine inundation in the Mid-Miocene (~15 million years ago) (McGowran et al. 2004), effectively separating the mesic environments of the southwest and southeast
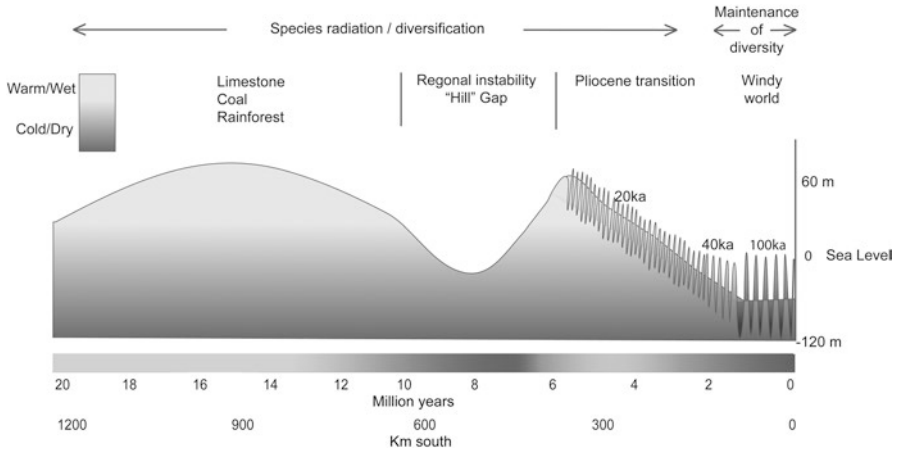
Fig. 2 Diagrammatic representation of the palaeoclimatic conditions of Australia during the evolution of the arid zone over the last 20 million years. Horizontal axes represent (i) time in the past and (ii) distance that the Australian continent was further south than present during the past. Vertical axis representing sea level is not to scale. Development of cycling of climatic conditions and sea level changes are evident through the Pliocene and Pleistocene. Shading indicates warm/wet vs. cold/dry climatic conditions. (From Byrne et al. 2008)

(Crisp and Cook 2007). At this time, the sea level fell around Southern Australia, and the ocean's incursions into the south-eastern marine basins retreated (Murray, Otway and Gippsland), leaving repeated shoreline ridges evident in the Murray Basin (Bowler et al. 2006).

As highlighted in an earlier review (Byrne et al. 2008), the environmental changes of the Late Miocene (10–6 million years ago) remain poorly understood. A major termination of the previous warm, wet environments and very high levels of erosion indicate destabilisation of vegetation cover. Fossil evidence shows that rainforest contracted, and sclerophyllous taxa like *Eucalyptus* and *Casuarina* expanded, as did dry, open woodlands and chenopod shrublands (Martin 2006). Conditions in the Pliocene (6–2.6 million years ago) showed a temporary return of warmer, wetter conditions than those of the Late Miocene, but not to the extent of the Early Miocene (Sniderman et al. 2016). Depositional activity in the Pliocene is indicative of drier conditions (Bowler et al. 2006), and the vegetation comprised sclerophyllous forest and woodlands and development of shrublands and grasslands (Martin 2006; Sniderman et al. 2007). Development of the first stony desert pavements in Central Australia occurred 3–2 million years ago at the end of the Pliocene (Fujioka et al. 2005).

The onset of the Pleistocene heralded the development of glacial and interglacial cycles of 20,000–40,000 years duration in the northern hemisphere (Williams et al. 1998). In Australia, these were manifest as arid-mesic cycles. These climatic oscillations became more intense, having major increases in amplitude and periodicity of 100,000 years from the Mid-Pleistocene, concomitant with the development of the sandy deserts (Fujioka et al. 2009). The last 400,000 years saw major change in hydrological conditions, such as drying of inland lakes and widespread erosion and

wind-blown dust (Bowler et al. 1998; Revel-Rolland et al. 2006). Conditions at the Last Glacial Maximum (~25–15,000 years ago) were extremely arid. Sea level was ~120 m lower than present, freshwater lakes dried out or became saline, streams showed large sand and gravel flows, mobile dune systems were activated, and large areas were treeless or devoid of vegetation (Williams 2000, 2001). Analysis of isotopes in emu eggshells shows evidence for a peak in aridity between 30,000 and 15,000 years ago (Miller et al. 2016).

The environmental changes throughout the Miocene, Pliocene and Pleistocene led to development of the current arid zone and contraction of mesic environments to the southwest and southeast, eastern seaboard and northern areas of Australia (Byrne et al. 2011). These environmental changes must have had significant impact on the plants and animals inhabiting these areas, and they led to the evolution of the current arid-zone biota. Modern approaches to understanding the evolutionary history of these plants and animals complement a rich, earlier literature built on morphological data. They are based on molecular genetic data and analysis of phylogenies and phylogeographic studies of the biota. Further, they are conducted in the context of historical climatic and geological events and so can reveal significant, novel insights into the response of the biota to changing environmental conditions. Byrne et al. (2008) reviewed the phylogenetic and phylogeographic evidence for the development of the arid-zone biota and found two broad phases of development. First, there is evidence for diversification and radiation of lineages through the Miocene and Pliocene when arid environments were forming throughout Central Australia. Second, there was a phase of maintenance of species diversity through the Pleistocene, when extreme aridity occurred through cyclic climatic conditions. Here, we assess molecular analyses published since 2008 to test and explore the generality of these conclusions.

Origins and Diversification of the Arid-Zone Biota

In their review of the origins of the arid-zone biota, Byrne et al. (2008) found evidence of both adaptive diversification in situ from ancestral forms present in Central Australia prior to the Miocene and for multiple independent divergences from mesic ancestors over time. Assessment of molecular phylogenies showed origin of arid lineages from mesic ancestors in plants and in animals (Fig. 3). A pattern of sister arid-mesic lineages showing divergence of arid lineages was present in plant phylogenies of *Tetratheca* (Crayn et al. 2006), *Calotis* (Watanabe et al. 2006), *Lepidium* (Mummenhoff et al. 2001) and *Halosarcia* (Shepherd et al. 2004) and in the agamid lizards (Hugall et al. 2008), the *Egernia whitii* complex of skinks (Chapple and Keogh 2004), diving beetles, amphipods (Cooper et al. 2007; Leys et al. 2003; Rix and Harvey 2012; Schmidt and Walter 2014) and *Artamus* woodswallows (Joseph et al. 2006). More recent studies have found further evidence for this, as phylogenetic analysis of the large plant family Goodeniaceae suggests a most likely south-western Australian origin, with the *Goodenia* clade diversifying
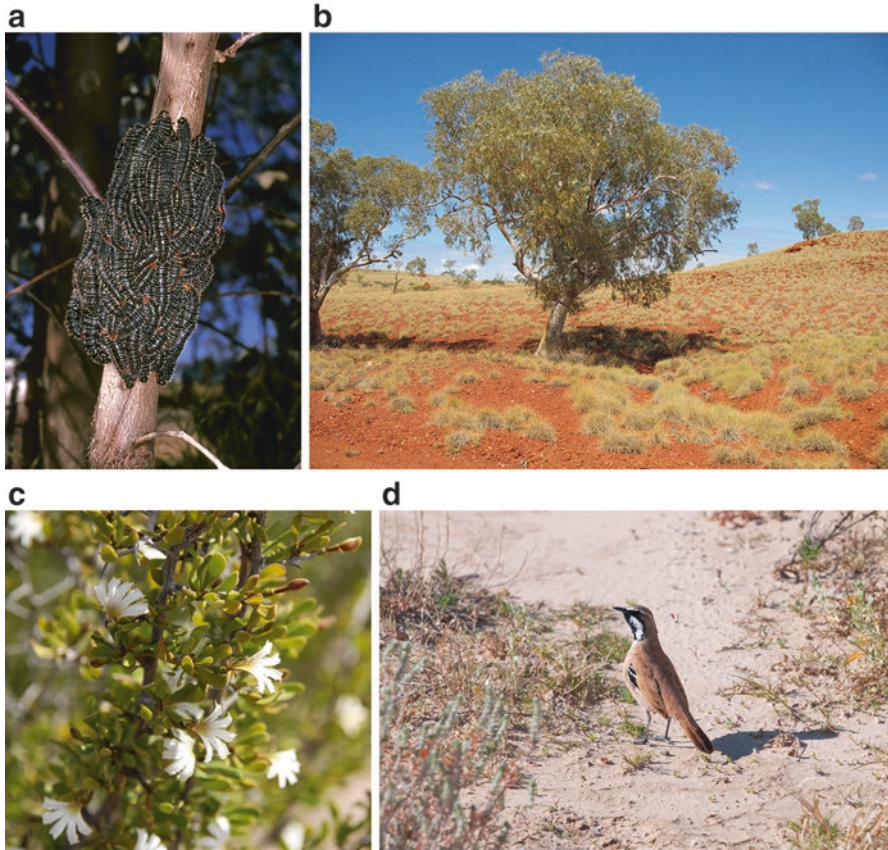
Fig. 3 Many arid-zone groups have diversified from mesic ancestors such as (**a**) sawflies. (Photo David Yeates), (**b**) eucalypts. (Photo Margaret Byrne), (**c**) *Scaevola.* (Photo Kelly Shepherd) and (**d**) quail-thrush. (Photo Chris Sanderson)

within the arid zone as it developed and the *Dampiera/Lechenaultia* clade diversifying mainly in the southwest (Jabaily et al. 2014). Eucalypts diversified from the Early Miocene with south-western Australia resolving as the most ancestral area (Ladiges et al. 2011a). Area phylogenetic analysis in the plant genus *Nicotiana* shows older taxa in peripheral mesic areas and derived taxa in arid inland areas (Ladiges et al. 2011b). Biogeographic and phylogenetic analysis of the *Hakea* shows multiple biome shifts, but the majority of arid diversification arises from mesic biomes, particularly south-western Australia (Cardillo et al. 2017), and arid-adapted species of *Callitris* have diversified from mesic ancestors (Larter et al. 2017). Similar patterns have been observed in sawflies (Schmidt and Walter 2014), flightless weevils (Toussaint et al. 2015b), *Delma* geckoes (Brennan et al. 2016) and several birds such as the nectarivorous lorikeets and budgerigar (Schweizer et al. 2015; Wright et al. 2008), platycercine parrots (Schweizer et al. 2012), honeyeaters (Joseph et al. 2014), *Cinclosoma* quail-thrush (Toon et al. 2012),

whipbirds and wedgebills (Toon et al. 2013) and malurid fairy wrens (Driskell et al. 2011; Lee et al. 2012). Among marsupials, Mitchell et al. (2014) found a pattern of mesic-adapted lineages evolving to use more arid and open habitats that is broadly consistent with regional climate and environmental change. Additionally, several mammal groups, including Dasyuromorphia, Vombatiformes, Trichosurini and Peramelemorphia, appear to have made the transition to open environments prior to the onset of widespread Miocene aridification, possibly reflecting lineages that survived from drier periods in the Oligocene (34–23 million years ago) when limited open forest habitats may have been available (Kear et al. 2016; Travouillon et al. 2009). Phylogenies show multiple radiations into the arid zone during the Miocene in the *Pauropsalta* complex of cicadas (Owen et al. 2017), the spiny trapdoor spiders (Rix et al. 2017) and the *Melophorus* ants (Heterick et al. 2017). Phylogeny of the truffle-like fungi also shows radiation of arid-zone species from mesic ancestors (Sheedy et al. 2016). Evidence from multiple stygobiont invertebrates suggests that microallopatric speciation within individual calcretes is significant and that the fauna may total to almost 3,000 species (Guzik et al. 2009, 2011a, b). In contrast, some amphipods, isopods and copepods appear to have entered the underground environments through separate colonisation events (Bradford et al. 2010; Finston et al. 2009; Javidkar et al. 2016; Karanovic and Cooper 2012; King et al. 2012).

While many arid lineages are derived from mesic ancestors (e.g. Pepper and Keogh 2014), there is also evidence of divergence from tropical ancestors in the plant genera *Gossypium* (Liu et al. 2001; Seelanan et al. 1999) and *Flindersia* (Scott et al. 2000). More recent studies have identified similar divergence from tropical ancestors in the plant genus *Atriplex* (Kadereit et al. 2010); in the frog genera *Uperoleia* (Catullo et al. 2011, 2014; Catullo and Keogh 2014), *Platyplectrum* and *Litoria* (Pyron and Wiens 2011) (Fig. 4); and in the *Heteronotia*, *Diplodactylus*, *Oedura* and *Strophurus* geckoes (Fujita et al. 2010; Oliver et al. 2016; Oliver and McDonald 2016; Laver et al. 2017).

Broad estimates of the relative timing of divergence events can be determined through molecular dating of phylogenies. In their review Byrne et al. (2008) found that in general, lineages that diversified in situ tended to occur at the genus and subgenus level and showed older diversification times during the Mid- to Late Miocene, e.g. *Gossypium* (Liu et al. 2001; Seelanan et al. 1999), *Ctenophorus* lizards (Melville et al. 2001) and elapid snakes (Sanders et al. 2008). Similar patterns have been found more recently in the plant genera *Triodia* (Toon et al. 2015), *Atriplex* (Kadereit et al. 2010), and *Eucalyptus* (Ladiges et al. 2011a) and the chenopods (Kadereit and Freitag 2011), in *Uperoleia* frogs (Catullo et al. 2011, 2014; Catullo and Keogh 2014) and in *Diporiphora* agamids (Edwards and Melville 2011; Smith et al. 2011) and *Oedura* geckoes (Oliver et al. 2014). While most arid species of *Oedura* geckoes diverged in the last 5 million years, an early diverging lineage over 10 million years was also recently identified (Oliver and McDonald 2016). The vacronini Tenebrionidae beetles of arid Australia have closest relatives in North America, originated in the Early Cretaceous (~145 million years ago), and may have inhabited coastal dune systems before the Australian arid biome developed (Kergoat et al. 2014; Matthews 2000). *Warramaba* grasshoppers diverged in the
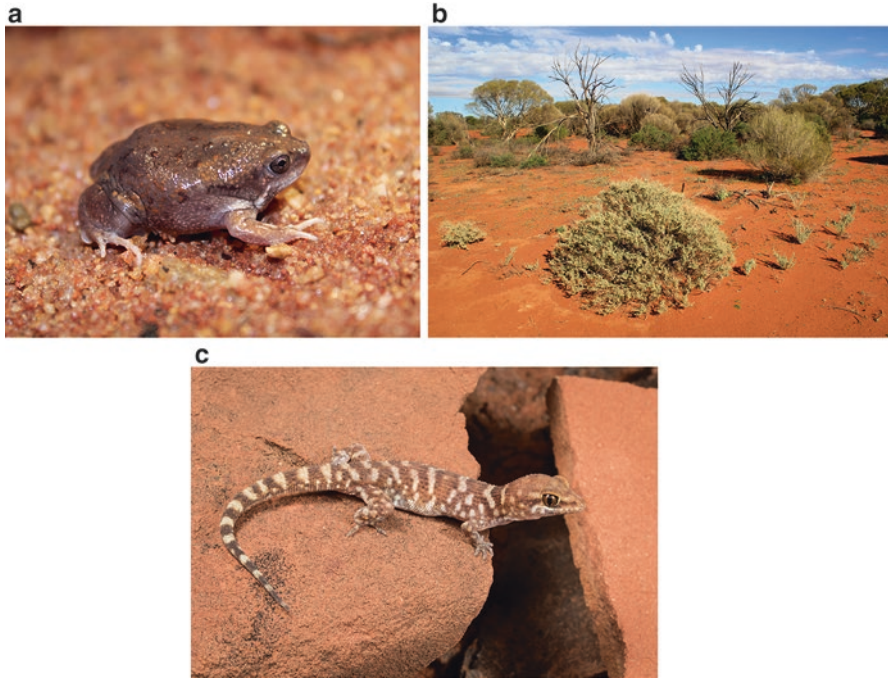
Fig. 4 Some arid-zone groups have diversified from tropical ancestors such as (**a**) *Uperoleia* toadlets. (Photo Renee Catullo), (**b**) *Atriplex.* (Photo Kelly Shepherd), (**c**) *Heteronotia* gecko. (Photo Stephen Zozaya)

Pliocene; northern sexual lineages persisted in local refugia in the Pleistocene, but parthenogenetic lineages expanded in the Pleistocene, suggesting that habitats became unsuitable in the north (Kearney and Blacket 2008).

While many phylogenies show patterns of divergence of major lineages as discussed above, Byrne et al. (2008) also found a second pattern of individual arid species or lineages present throughout phylogenies indicating multiple origins of arid species in the large plant genus *Acacia* (Ariati et al. 2006; Murphy et al. 2003), dasyurid marsupials (Crowther and Blacket 2003; Krajewski et al. 2000), the sphenomorphine skinks (Rabosky et al. 2007) and *Neobatrachus* frogs (Mable and Roberts 1997). This pattern has also been found more recently in the plant genera *Dampiera* and *Lechenaultia* (Jabaily et al. 2014), and *Hakea* and *Grevillea* (Mast et al. 2015; Cardillo et al. 2017), as well as in pseudoscorpions (Harrison et al. 2014) and the *Pauropsalta* complex of cicadas (Owen et al. 2017). Among birds, the radiation of the iconic Australo-Pacific family of honeyeaters, Meliphagidae, neatly illustrates the independent evolution of several arid-zone genera in the Mid- to Late Miocene (20–6 million years ago). These include a number of monotypic genera of the arid and semiarid zones (*Sugomel*, *Purnella*, *Certhionyx*, *Acanthagenys*, *Epthianura*, *Ashbyia*, *Grantiella*, *Plectorhyncha*) (Joseph et al. 2014). In general, most groups show diversification of species or lineages in the Late Miocene to
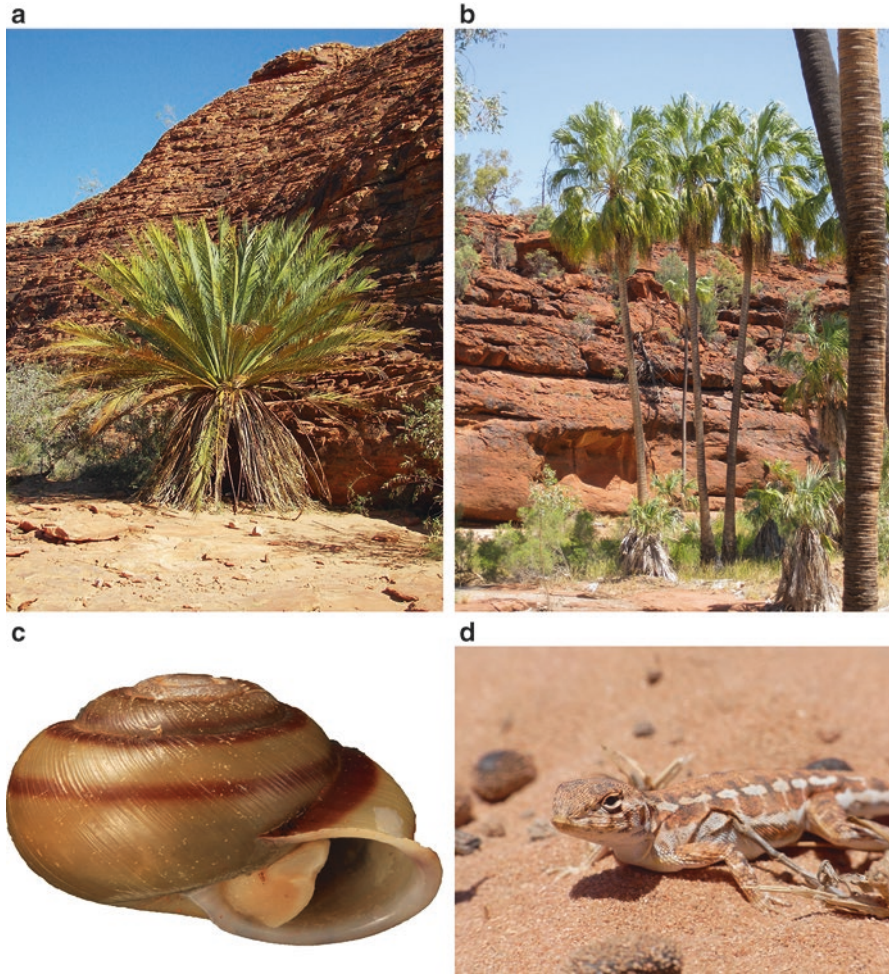
Fig. 5 While most diversification of arid-zone biota occurred in the Miocene and Pliocene, some groups diversified in the Pleistocene: (**a**) *Macrozamia macdonnellii.* (Image James Ingham), (**b**) *Livistona.* (Photo Mike Crisp), (**c**) *Granulomelon* land snails. (Photo Francesco Criscione), (**d**) *Ctenophorus maculatus.* (Photo Dan Edwards)

Pliocene, e.g. *Acacia* (Ariati et al. 2006; Murphy et al. 2003), *Hakea* (Cardillo et al. 2017) and the dasyurid marsupials (Krajewski et al. 2000), and there is less evidence for species divergence in the Pleistocene. Byrne et al. (2008) only found three cases of Pleistocene speciation that had been documented, Australian species of *Lepidium* (Mummenhoff et al. 2004); the geographically restricted shrub, *Acacia sciophanes* (Byrne et al. 2001); and a number of gall-forming *Kladothrips* species associated with *Acacia* (McLeish et al. 2007). More recent studies have revealed more cases of Pleistocene speciation (Fig. 5). Ingham et al. (2013) found that *Macrozamia macdonnellii*, the only species in the arid zone among 41 *Macrozamia*

species, diverged approximately 1.08 million years ago, much later than the divergence of the south-western and south-eastern mesic species of the genus; and divergence of two arid-zone species of *Livistona* from monsoon tropical congeners occurred in the Late Pleistocene (Crisp et al. 2010). Divergence among species in *Nicotiana* section *Suaveolentes* began 6 million years ago but accelerated in the Pleistocene from 2.6 million years ago (Clarkson et al. 2017). Two species of *Granulomen* land snails are widespread in the arid zone and diverged in the Mid-Pleistocene (Criscione and Köhler 2016), and there is evidence of in situ speciation between river systems in the Pilbara Craton and the Gascoyne drainages in *Uperoleia* frogs (Catullo and Keogh 2014). Species within the *Ctenophorus maculatus* species complex further show rapid divergence throughout the Pleistocene, coincident with the diversification of sand plain and dune habitats (Edwards et al. 2015); similar sand habitat diversification has likely been involved in the diversification of other species-rich arid clades (e.g. *Lerista* (Lee et al. 2013)). Diversification of lineages of golden perch in upland basins from coastal areas is believed to represent speciation during the Upper to Middle Pleistocene (Beheregaray et al. 2017).

The above examples illustrate diversification of arid lineages and species from mesic and tropical ancestors. So it is interesting to see that more recent work has revealed the converse of diversification of some species or lineages into mesic and tropical biomes from ancestral arid groups. Phylogenetic analysis of *Triodia* indicates that the arid zone is ancestral in this group, with multiple shifts and range expansion of species into the tropical savannah and into the southern mesic biomes during the Mid–Late Miocene and Pliocene (Toon et al. 2015). Similarly, diversification of mesic species is evident within the mainly arid plant genera *Scaevola* and *Goodenia* (Jabaily et al. 2014) and in the paper daisies *Leucochrysum* (Schmidt-Lebuhn and Smith 2016). Derived mesic species from arid ancestors are evident within *Ctenophorus* lizards (McLean et al. 2013, 2014) and *Strophurus* geckoes (Nielsen et al. 2016). Analysis of pygopodoid geckoes shows diversification of arid species along with some transition of species back to mesic biomes (Brennan and Oliver 2017). Area phylogenetic analysis led Ladiges et al. (2011b) to propose that *Nicotiana* section *Suaveolentes* had a widespread ancestral distribution with diversification in the arid zone as aridification progressed from the Mid-Miocene, along with persistence in peripheral mesic areas. Nyari and Joseph (2012) identified instances in the acanthizid bird genus *Gerygone*, where ancestry of tropical mangrove endemics may have involved arid-zone ancestors. In marsupials, some instances of lineages reverting from drier to more mesic habitats are apparent in several clades and individual species of Macropodidae and Dasyuridae (Mitchell et al. 2014). Several reptile groups confirm complex dynamic patterns between mesic, tropical and arid biomes, whereby all groups likely had a tropical or mesic ancestor, followed by derived arid lineages and then repeated recolonisation of mesic and tropical environments, including the lygosomine (Skinner et al. 2011) and *Lerista* (Lee et al. 2013; Skinner and Lee 2009) skinks; carphodactyline (Oliver and Bauer 2011), diplodactine (Oliver et al. 2009, 2010) and gekkotan (Sistrom et al. 2009, 2014) geckoes; and *Tympanocryptis* (Shoo et al. 2008), *Ctenophorus* (Edwards et al. 2015; Melville

et al. 2016) and *Lophognathus/Amphibolurus* (Melville et al. 2011) agamids. Mesic species of *Pseudophryne* frogs appear to have been derived from an arid lineage (Donnellan et al. 2012).

Analysis in the plant *Nicotiana* section *Suaveolentes* shows marked radiation into arid environments (Clarkson et al. 2017), and species differentiated into the northern desert before they did in the central desert, suggesting that aridification occurred earlier in the northern desert than in the central western and eastern deserts (Ladiges et al. 2011b). Biogeographical analysis of *Acacia* also indicates a break in species turnover between the northern and southern regions of the arid zone, corresponding with the summer-winter rainfall divide (Gonzalez-Orozco et al. 2013; Foster 2017).

Although rigorous analysis of diversification rate is not possible for most studies, evaluation of phylogenies shows diversification rates can be relatively constant such as in the salt lake-adapted tiger beetles over the past 4 Ma (Pons et al. 2006), or rates can differ by mediation through different ecological contexts. Comparison of diversification rates between arid lineages and their mesic sister lineages shows some cases of similar diversification rates, such as in the *Egernia whitii* group (Chapple and Keogh 2004), in the *Pauropsalta* complex of cicadas (Owen et al. 2017) and in gall thrips (*Kladothrips*) that specialise on arid species of *Acacia* section *Juliflorae* (McLeish et al. 2007), but increased diversification in arid lineages compared with mesic lineages in the plant genus *Tetratheca* (Crayn et al. 2006) and *Nicotiana* section *Suaveolentes* (Clarkson et al. 2017) and in the sphenomorphine skinks (Rabosky et al. 2007) and the pygopodoid geckoes (Brennan et al. 2016; Brennan and Oliver 2017). In contrast, a slower rate of diversification is evident in the arid lineage of *Gossypium* compared with its tropical sister lineage (Liu et al. 2001; Seelanan et al. 1999). More recent analysis has found similar variation in rates and diversification in arid lineages having increased compared with mesic lineages in the plant genus *Ptilotus* (Hammer et al. 2015) and in the arid lineages of *Strophurus* geckoes compared to tropical sister lineages (Laver et al. 2017), but a slower rate in arid lineages of *Scaevola* compared with mesic lineages (Jabaily et al. 2014). Onstein et al. (2017) found a higher rate of diversification in open vegetation compared to the ancestral state of closed vegetation in Proteaceae, and Goldie et al. (2010) tested mutation rate in the internal transcribed spacer in mesic-arid pairs of woody species and found higher substitution rates in the majority (76%) of mesic species. Lineage through time plots of the arid genus *Triodia* shows progressive increase in diversification rate from the Mid-Miocene, consistent with rapidly intensifying aridification, and then decreasing diversification in the Pliocene (Toon et al. 2015). Surface and subsurface sister lineages of diving beetles show declining and variable diversification rates, respectively, related to the availability and distribution of their epigean and hypogean habitats (Toussaint et al. 2015a). Mesic lineages of allodapine bees experienced acceleration radiation during the Hill Gap (10–6 mya), but xeric groups did not (Chenoweth and Schwarz 2011). The genus *Pseudotetracha* of nocturnal tiger beetles also appears from molecular data to have undergone speciation and divergence among individual

lakes or palaeodrainage basins in response to their isolation in turn produced by aridification of Australia (López-López et al. 2016), consistent with the findings of Pons et al. (2006) on *Rivacindela* tiger beetles.

Adaptation to Aridity

The question of whether adaptation occurred in conjunction with aridification or whether lineages were preadapted to arid conditions is difficult to answer. The divergence of lineage radiations during the Mid- to Late Miocene when the arid zone was emerging suggests preadaptation may have enabled rapid colonisation of arid environments by some plant and animal groups. Early dispersal into Australia from arid and semiarid areas facilitated large radiation of the *Maireana*/*Sclerolaena* tribe during the Pliocene (Cabrera et al. 2011) (Fig. 6). The development of aridification was not constant and was punctuated by development of more arid conditions during the "Hill Gap" (10–6 million years ago), followed by more mesic conditions before a return to arid conditions in the Pliocene and Pleistocene. So, this early development of aridity may have enabled evolution of adaptive traits that facilitated life under the arid conditions of the Pliocene and Pleistocene (Fig. 7). Phylogenetic clustering seen as lower levels of phylogenetic diversity in Australian angiosperms in arid regions compared to mesic and tropical biomes has been interpreted as indications of fewer clades having adaptation to arid conditions (Thornhill et al. 2016). In a study of community structure across six arid lineages of squamates and marsupials, Lanier et al. (2013) showed that each group displayed distinct patterns of phylogenetic structure suggesting that neither current climate nor historical habitat stability resulted in a uniform response by arid assemblages, and that taxon-specific history is important in determining patterns of phylogenetic community relatedness.
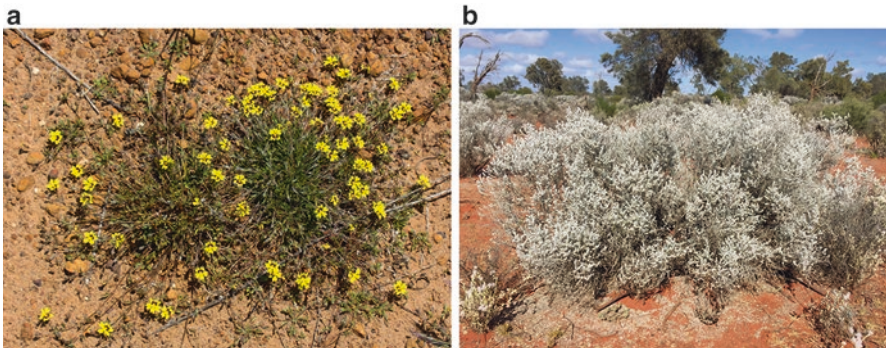

Fig. 6 Early dispersal into Australia of arid-zone adapted groups facilitated diversification within the arid zone as it developed. (**a**) *Goodenia*/*Scaevola* lineages diversified during the Miocene. (Photo Kelly Shepherd). (**b**) *Maireana*/*Sclerolaena* lineages diversified during the Pliocene. (Photo Margaret Byrne)
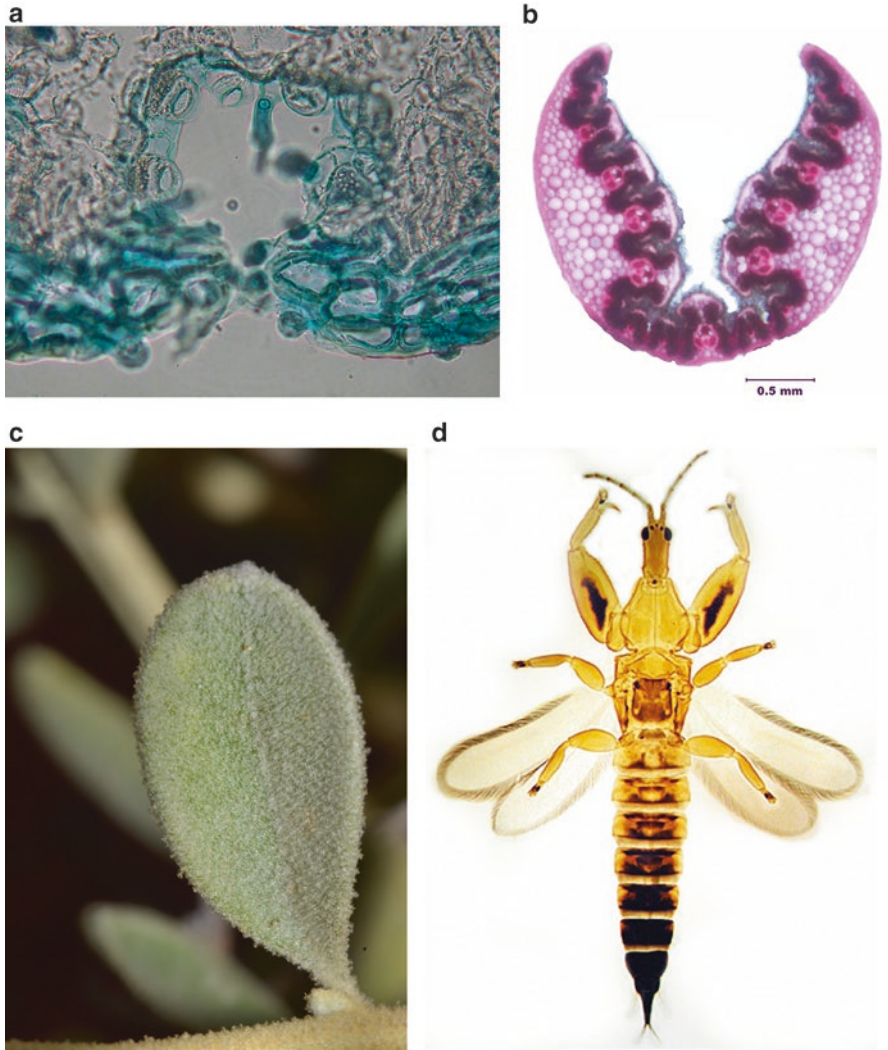
Fig. 7 Many arid-zone groups possess adaptations to aridity, such as (**a**) encrypted stomata in Proteaceae. (Photo Greg Jordan), (**b**) loss of abaxial stomata in *Triodia*. (Photo Harshi Gamage), (**c**) dense indumentum in *Ptilotus*. (Photo Tim Hammer), (**d**) a gall thrip, *Lichanothrips pastinus*, which produces domiciles by glueing phyllodes of *Acacia harpophylla*. (Photo Laurence Mound)

Evidence of adaptations to aridity in plants is considered to have occurred in the evolution of deeply encrypted stomata that has occurred 11 times in species of Proteaceae in arid environments compared to other stomatal features that have evolved in species present in both arid and wet environments (Jordan et al. 2008) but may contribute to effective gas exchange rather than reducing transpiration (Hassiotou et al. 2009; Roth-Nebelsick et al. 2009). Adaptations to low-nutrient

environments are found in many sclerophyllous plant groups (Hill 1994), dense indumentum on stems and leaves in *Ptilotus* (Hammer et al. 2015) are thought to increase reflectance and reduces heat load, and the salinity tolerance of cheno-pods enabled them to colonise saline habitats (Cabrera et al. 2011). Evolution of embolism resistance in xylem hydraulic function facilitated the diversification of the *Callitris* into arid environments (Larter et al. 2017), and increased leaf thickness and leaf venation in eucalypts are considered to be an adaptation in arid environ-ments (de Boer et al. 2017). Similarly, the low metabolic requirements and toler-ance to heat and desiccation of many reptiles can be considered preadaptations to aridity. The presence of specialised groups in specific environments within the arid zone suggests specific adaptations to changing conditions, for example, the diversi-fication of halophytic chenopods appears related to the emergence of saline water bodies through arid regions during the Late Pliocene (Shepherd et al. 2004), and the divergence of hydrobiid snails is related to development of freshwater springs in the Great Artesian Basin (Perez et al. 2005). Similarly, the transition from primarily surface-dwelling organisms to groundwater dwelling in diving beetles, amphipods and isopods between 11 and 3 Ma appears to be correlated with a reduction in per-manent surface water (Cooper et al. 2007, 2008; Leys et al. 2003; Toussaint et al. 2015a). In contrast, more recently, Toon et al. (2015) considered the loss of abaxial stomata in the largely arid zone genus *Triodia* to represent an adaptation that devel-oped after radiation into the arid zone rather than a trait conferring preadaptation to arid conditions. The domiciles of arid-zone gall thrips protect against desiccation (Gilbert 2014), and these gall thrips diversify through drift in allopatry due to the paucity of host species, in contrast to mesic-zone species that diversify ecologically in sympatry through host shifting (McLeish 2011; McLeish et al. 2011). The heleine Tenebrionidae lack the physiological adaptations to reduce water loss that charac-terise day-active desert tenebrionid beetle species, so they have become nocturnal (Duncan and Dickman 2009), and adaptations to phragmotic burrow-plugging have evolved multiple times in arid taxa of spiny trapdoor spiders (Rix et al. 2017). Physiological adaptation to heat stress and evaporative water loss along with transi-tion to nocturnality are considered to be preadaptations to aridity facilitating diver-sification (Brennan and Oliver 2017). In birds, the ancestor of the familiar budgerigar may well have been preadapted morphologically and in social structure to life in the arid zone. The budgerigar is the sister group to lorikeets (Joseph et al. 2011), which have a streamlined morphology for rapid and sustained flight required to search for food resources that are patchily distributed in space and time. Genomic approaches to understanding adaptation to aridity in birds are exemplified by two recent studies in birds. McElroy et al. (2018) found strong evidence for purifying selection across all codons in the mitogenome of the mulga parrot *Psephotellus varius*, a species widespread across the arid zone. Lamb et al. (2018) studied mitochondrial DNA variation in 17 oscine passerines (songbirds) and found that climate was a signifi-cant predictor of mitochondrial variation in 8 species.

Ancestral polyploidy and hybridisation in *Nicotiana* section *Suaveolentes* may have facilitated adaptation to arid environments, because polyploids are considered to be well adapted to aridity (Winterfeld et al. 2009), and other Australian plant

genera that are common in the arid zone are polyploid (e.g. *Cassia*, *Eremophila*, *Senna*) (Barlow 1981). Two tetraploid frogs are common in the arid zone (Anstis 2013; Mahony and Robinson 1980), but many other arid-zone frogs are diploid, and polyploid species also occur widely in mesic areas (Roberts and Edwards 2018), suggesting ploidy levels have not provided additional advantage in arid environments. Within the *Ctenophorus maculatus* species complex, rapid (0.3–1.5 million years) adaptive diversification in both ecomorphological and social signalling traits suggests complex interactions between adaptation and species interactions may have driven speciation in response to dynamic shifts in arid habitats (Edwards et al. 2015). Traits that reduce water loss in frogs, such as waterproof cocoons and burrowing, may enable persistence of frogs in the arid zone, but these traits are not exclusive to arid-zone frogs (Roberts and Edwards 2018).

Species Persistence and Intraspecific Divergence

The previous review of the arid-zone biota (Byrne et al. 2008) found two key points concerning intraspecific divergences. First, most arid-zone lineages and species had radiated within the biome by the end of the Pliocene, and, second, the Pleistocene was a time of maintenance of lineages and phylogeographic structuring in response to environmental changes. The dramatic climatic oscillations of the Pleistocene have led to major redistribution of species throughout the world (Hewitt 2001, 2004), particularly leading to major contraction and expansion of species in temperate biomes. Byrne et al. (2008) found evidence of intraspecific diversification in many arid lineages with three main patterns of genetic structure, reflecting multiple localised refugia, broad expansion and hybridisation or contraction and persistence of mesic relicts.

Many phylogeographic studies of arid-zone species have shown a common pattern of high diversity, but deep divergences among geographically structured intraspecific lineages (Byrne et al. 2008), and the divergence most commonly traced to the Mid-Pleistocene, which correlates with increased aridity and development of sandy deserts (Fujioka et al. 2009). The high diversity, but divergent lineages, suggests persistence of species during the climatic changes of the Pleistocene through localised contraction and expansion and presence of multiple localised refugia throughout the distribution of species (Fig. 8). Retention of localised refugia throughout species distributions would facilitate rapid colonisation of habitat under suitable climatic conditions. Application of Approximate Bayesian Computation methods to bird populations from a range of species supported a model of most of the populations showing a signal of a single co-expansion in the period just prior to the LGM when aridity was at a peak (Chan et al. 2014) indicating similar responses to environmental conditions. In further work, Dolman and Joseph (2012, 2015, 2016) explored the number of divergence events that have shaped present-day phylogeographic structure in Australian birds, especially those of the arid zone, and linked phylogeographic patterns to the birds' natural history and ecological diversity. The
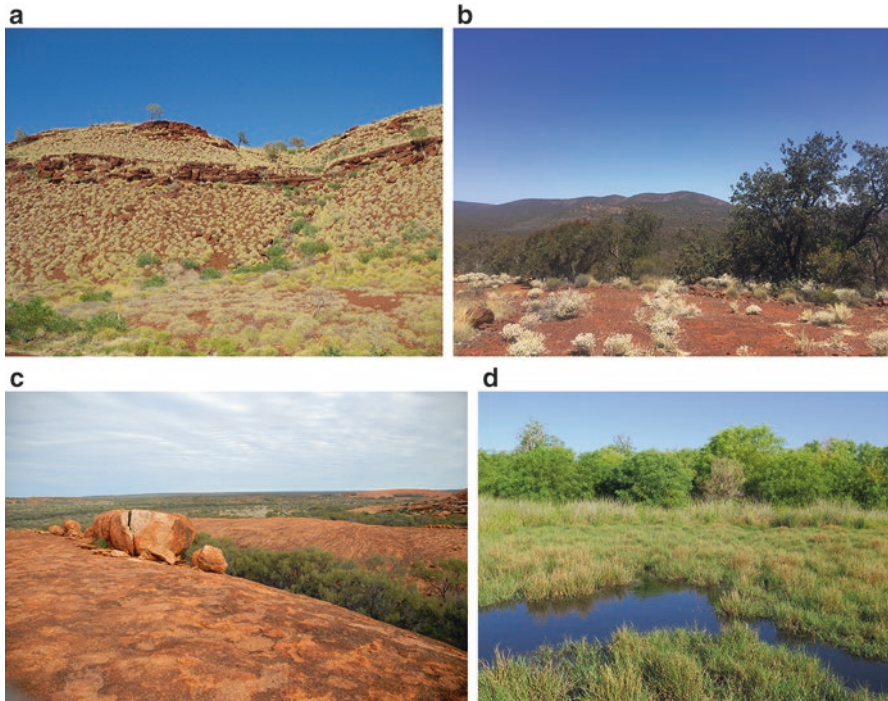
Fig. 8 Features of the arid zone providing heterogeneous environments that act as refugia (**a**) Hamersley Range. (Photo Margaret Byrne), (**b**) banded ironstone ranges. (Photo Margaret Byrne), (**c**) granite outcrops, (**d**) mound springs. (Photo Val English)

earliest event identified by Dolman and Joseph (2012), from the Middle to the Early Pleistocene explains the divergence of mesic populations of two species groups in south-eastern and south-western Australia, consistent with the increased aridification identified by McLaren and Wallace (2010). Conversely, the most recent divergence of semiarid south-eastern and south-western population pairs had its upper limit at the Mid-Pleistocene, but including the Last Glacial Maximum, and may be related to changes in plants with palatable leaves and fleshy fruits that were present in the Nullarbor Region between 180,000 and 400,000 years ago but now are found in remnant stands on the fringes of the Nullarbor Plain (Prideaux et al. 2007). Similarly, Hocknull et al. (2007) noted extinction of mesic fauna in central eastern Australia within this timeframe. Phylogeographic analysis of southern hairy-nosed wombat identified six lineages across the southern arid region (Alpers et al. 2016).

In contrast to the majority pattern of diverse but divergent lineages, there is evidence for a second pattern of widespread, low-diversity lineages in more vagile species (e.g. birds, snakes, lizards, freshwater fish, crayfish) (Bostock et al. 2006; Byrne et al. 2003; Joseph and Wilke 2006, 2007; Joseph et al. 2002, 2006; Kearns et al. 2008; Kuch et al. 2005; Nguyen et al. 2004; Strasburg and Kearney 2005; Toon et al. 2007), and this was also found more recently in pied butcherbirds (Kearns

et al. 2010), variegated fairy-wren (McLean et al. 2017) and clam shrimps (Schwentner et al. 2012). This pattern is indicative of widespread recent expansions across all or part of the arid zone, a characteristic being little phylogenetic structuring and little evidence of specific refugia. Several lineages were identified in blacksnakes using multilocus nuclear genes (Maddock et al. 2017) where no mitochondrial diversity was previously identified (Kuch et al. 2005), indicating several expansion events. Evidence for refugia was noted for some birds in inland southeastern Australia (Joseph and Wilke 2006; Kearns et al. 2008) and in northern and western regions (e.g. the galah, *Eolophus roseicapilla*) (Engelhard et al. 2015). Phylogeographic data from the galah (Engelhard et al. 2015) may well be consistent with the idea advanced in Byrne et al. (2008) that refugia for some species may have been linear, that is, in riparian woodland. In some species, rapid expansion of lineages has occurred following hybridisation, parthenogenesis and polyploidisation, as these processes produce instant reproductive isolation (Coyne and Orr 2004). This has resulted in diverse and widespread lineages of *Neobatrachus* frogs (Mahony et al. 1996), *Heteronotia* and *Menetia* lizards (Adams et al. 2003; Fujita et al. 2010; Moritz 1993), insects (*Sipyloidea*, *Warramaba*) and plants (*Acacia aneura*, *Senna artemisiodes*, *Cassia* sp.) (Andrew et al. 2003; Holman and Playford 2000; Randell 1970). Subspecies in the polyploid *Atriplex nummularia* are proposed to have multiple origins through hybridisation (Sampson and Byrne 2012). The expansion of the lineages in all these species is a result of evolutionary processes, rather than the contraction and expansion of species due to glacial cycles in temperate regions of the northern hemisphere.

An interesting pattern to have emerged in one species group of birds runs counter to the general pattern of reduction to refugia during the Pleistocene and particularly in response to the Last Glacial Maximum (LGM). Kearns et al. (2014) integrated palaeomodelling of the Last Glacial Maximum (~25–15,000 years ago) distributions and multilocus phylogenetic and phylogeographic analyses to argue that the grey butcherbird, *Cracticus torquatus*, expanded its range in arid, inland Australia at the Last Glacial Maximum. This led to introgressive hybridisation with a northern, tropical non-sister species, the silver-backed butcherbird, *C. argenteus*, and so explains an otherwise anomalous pattern of mtDNA diversity in these birds. Similarly, the use of past species distribution models shows vast increases in coastal sand plain habitats in reptile-plant arid hotspot on the mid-western Australian coast in a range of endemic reptile species (Edwards et al. 2012). Using explicit habitat-demographic models shows that shifts in suitable habitat explain intraspecific divergence (He et al. 2013).

While the majority of species show high diversity of divergent lineages, and some show widespread distribution of low-diversity lineages, there are some species that appear to represent species restricted to mesic habitat within the arid zone. More mesic environments, such as the springs of the Great Artesian Basin and granite outcrops, are areas where mesic relicts occur. An early study showed high genetic divergence in species of hydrobiid snails (*Jardinella* sp.) that are restricted to different groups of springs (Perez et al. 2005). More recent studies have revealed a suite of invertebrate species, including Crustaceae, molluscs and insects, which are

restricted to these desert springs and diverged well before the deserts developed, indicating they diverged in these tiny mesic refugia in isolation (Guzik et al. 2012; Murphy et al. 2012, 2015). In contrast, the frog *Limnodynastes tasmaniensis*, which also occurs in these spring systems, is broadly distributed through the Flinders Ranges and across most of eastern Australia in both mesic and arid systems. The arid-adapted fish species, *Chlamydogobius*, shows little differentiation among Lake Eyre waters, indicating periodic connectivity (Mossop et al. 2015). Many species of the arid plant genus *Goodenia* are annuals and are confined to mesic environments in the arid zone (Jabaily et al. 2014). Granite outcrops often harbour more mesic habitats within the arid zone and have been hypothesised to have acted as mesic refugia during extreme aridity (Byrne 2008; Byrne and Hopper 2008). The relictual species, *Acacia lobulata*, has no close relatives and is now restricted to mesic south-facing slopes on two granite outcrops (Byrne et al. 2001). In contrast, *Eucalyptus caesia*, which is also restricted to granite outcrops, shows high divergence but appears to be adapted to the specific granite rock habitat and does not show evidence of repeated cycles of population expansion and contraction (Byrne and Hopper 2008). More recent analysis of two very widespread plant species restricted to granite outcrops in both arid and mesic environments showed similar levels of high haplotype diversity with divergence among populations, with less diversity in more arid populations than in mesic populations (Tapper et al. 2014a, b).

Recent work has also focused on the Banded Ironstone Formation ranges of the Yilgarn and Pilbara cratons that are also areas that harbour more mesic environments. Analysis of species diversity in the western area of the arid zone shows the ranges to have higher species diversity than the surrounding lowland areas, and those on the arid-zone boundary have higher beta diversity and greater endemism and diversity than those further inland (Gibson et al. 2012). Recent studies have shown mixed patterns of phylogeographic diversity and structure. Some more restricted species, a *Grevillea* and a millipede, show patterns of persistence and divergence between isolated formations (Nistelberger et al. 2014, 2015a), while in other plant species, a combination of moderate diversity with persistence of ancestral haplotypes suggests maintenance of larger populations with some isolation (Binks et al. 2015; Millar et al. 2017; Nistelberger et al. 2015b). In contrast, a rare species of *Acacia* restricted to a localised group of formations shows evidence of local connectivity (Millar et al. 2013), as do two other regionally distributed plant species, having common haplotypes shared among populations (Millar et al. 2016). The arid lineages of the conifer *Callitris columellaris*, which are restricted to ranges, granite rocks and inselbergs, show evidence of strong bottlenecks and range contraction over multiple Pleistocene climatic cycles, indicating contraction to mesic refugia, in contrast to signals of population expansion in the mesic lineages in southern temperate areas (Sakaguchi et al. 2013). The arid-zone outliers of the mesic species of the *Egernia whitii* complex of skinks have been interpreted as relicts of a broader range now contracted to southern mesic areas (Chapple and Keogh 2004).

Ranges in the arid zone were predicted by Byrne et al. (2008) to be refugia for species. In a series of studies on reptiles, Pepper et al. (2008, 2011a, b, 2013a, b) explored the lineage divergence and the evolutionary consequences of relatively

recent development of widespread sand deserts between these arid-zone ranges. Pepper et al. (2011a) used multilocus phylogenetic analyses to show that among rock-dwelling *Heteronotia* geckoes, each range harbours a divergent lineage; substantial intraspecific diversity is likely due to topographic complexity in these areas. Old divergences (~4 Ma) among lineages predate the formation of the geologically young sand deserts (<1 Ma), suggesting that Pliocene climate shifts fractured the distributions of biota long before the spread of the deserts. In further analyses of multiple mitochondrial DNA datasets from four species complexes of Australian geckoes from three genera (*Heteronotia*, *Lucasium*, *Rhynchoedura*), Pepper et al. (2011b) found that topographically complex mountain regions harbour high nucleotide diversity, up to 18 times greater than that of the surrounding desert lowlands. Taxa in topographically complex areas have older coalescent histories than those in the geologically younger deserts and that both ancient and more recent aridification events have contributed to these patterns. In a later analysis, Pepper et al. (2013a) reviewed patterns of diversity in one region of inland ranges, the Pilbara, more extensively. While noting some repeated phylogeographic patterns, they also highlighted the importance of species-specific ecological differences in shaping idiosyncratic elements of these patterns of diversification. Similar high divergence between lineages in ranges and presence of two highly divergent lineages in the Central Ranges was observed in *Oedura* geckoes (Oliver and McDonald 2016). The plant *Triodia basedowii* complex occurs across the Pilbara and central arid zone, and diversification has been identified within the Pilbara compared with that in the deserts (Anderson et al. 2016). In addition, similar to reptiles, substrate was hypothesised to be important in diversification within the plant *Triodia basedowii* complex (Anderson et al. 2016). Substrate was also identified as an important feature explaining the genetic diversity of reptile communities along the Western Australian coast (Edwards et al. 2012). In *Uperoleia* froglets, species boundaries appear correlated with geological and substrate boundaries as well as major drainages between the Pilbara and Gascoyne (Catullo et al. 2011)

Phylogeographic analysis of plant species revealed high diversity in Pilbara ranges and lower diversity in the surrounding areas for *Eucalyptus leucophloia*, consistent with the ranges being refugia (Byrne et al. 2017). Although this pattern was not evident in either a widespread *Acacia* or its restricted congener that showed differing patterns, with high diversity throughout the distribution in the widespread species, and low diversity in the species restricted to the ranges, and there was evidence for greater genetic connectivity in populations of the widespread species in the ranges, suggesting maintenance of larger effective populations size (Levy et al. 2016).

New Insights

Our evaluation of molecular phylogenetic and phylogeographic studies conducted since the review of Byrne et al. (2008) has revealed further support for the main hypotheses identified there, particularly divergence and diversification of arid-zone

species and lineages derived from both mesic and tropical ancestors, and variation in diversification rates. Interestingly, more recent studies have also found evidence of mesic and tropical species being derived from ancestral arid groups and also some transition back to arid lineages. In addition, while few cases of speciation in the Pleistocene were previously noted, more recent studies have identified more cases in plants, land snails, frogs and fish. Distinct patterns of phylogenetic structure in mammals and squamates also suggest that neither current climate nor historical habitat stability resulted in a uniform response by arid assemblages highlighting that idiosyncratic historical and biogeographical aspects of community composition are important and that studies of individual taxa are necessary to fully understand the responses of species to aridity. Further evidence of adaptation to aridity was found in plants and reptiles.

More recent phylogeographic studies have found similar evidence of the two broad patterns of diverse but highly differentiated lineages, and widespread low-diversity lineages. Further investigations support the hypothesis that mesic habitats, such as salt lakes, desert springs, granite outcrops, banded ironstone ranges and Pilbara ranges, provide refugia enabling species to persist within the arid zone with high diversity and differentiation in these mesic arid-zone habitats. Evidence of range expansion after the LGM remains limited but has been identified in a study on butcherbirds.

Opportunities and Challenges

The ready availability of molecular tools has seen a huge growth in the number and scale of studies investigating evolutionary history in arid-zone species, with over three times as many studies available now compared to 2008. These studies highlight the complexity in patterns and processes of the evolutionary history of the arid-zone biota and demonstrate the diversity of responses to aridification across the vast Australian environment.

While the large number of studies on arid-zone species has shown commonality in a range of patterns, there is much still to learn about specific responses of the biota to arid environments. Patterns of refugia within arid environments remain enigmatic, beyond the obvious mesic habitats of ranges, inselbergs and mound springs, although the concept of linear corridors of habitats being refugia for birds appears validated in the galah. Despite sandy habitats dominating arid environments, there is a great deal we don't know about the evolution of species specific to sand habitats, particularly in reptiles, where there are many species with unique adaptations to sandy habitats and evidence that substrate has a role in generating intra- and interspecific divergences.

The revolution in molecular technology has facilitated major advances in our knowledge of evolutionary history, yet there is now much opportunity to integrate molecular techniques with advances in other fields. We are only just beginning to see the incorporation of other powerful tools like ecological modelling, hypothesis

testing frameworks, biogeographic model testing and morphological and behavioural analyses, with molecular studies in an integrative approach. We envisage that such integrative studies will have much more to reveal about the intricacies of the evolutionary history of the arid-zone biota in the years to come.

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