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Biogeography and speciation of terrestrial fauna in the south-western Australian biodiversity hotspot

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ABSTRACT

The south-western land division of Western Australia (SWWA), bordering the temperate Southern and Indian Oceans, is the only global biodiversity hotspot recognised in Australia. Renowned for its extraordinary diversity of endemic plants, and for some of the largest and most botanically significant temperate heathlands and woodlands on Earth, SWWA has long fascinated biogeographers. Its flat, highly weathered topography and the apparent absence of major geographic factors usually implicated in biotic diversification have challenged attempts to explain patterns of biogeography and mechanisms of speciation in the region. Botanical studies have always been central to understanding the biodiversity values of SWWA, although surprisingly few quantitative botanical analyses have allowed for an understanding of historical biogeographic processes in both space and time. Faunistic studies, by contrast, have played little or no role in defining hotspot concepts, despite several decades of accumulating quantitative research on the phylogeny and phylogeography of multiple lineages. In this review we critically analyse datasets with explicit supporting phylogenetic data and estimates of the time since divergence for all available elements of the terrestrial fauna, and compare these datasets to those available for plants. *In situ* speciation has played more of a role in shaping the south-western Australian fauna than has long been supposed, and has occurred in numerous endemic lineages of freshwater fish, frogs, reptiles, snails and less-vagile arthropods. By contrast, relatively low levels of endemism are found in birds, mammals and highly dispersive insects, and *in situ* speciation has played a negligible role in generating local endemism in birds and mammals. Quantitative studies provide evidence for at least four mechanisms driving patterns of endemism in south-western Australian animals, including: (i) relictualism of ancient Gondwanan or Pangaeian taxa in the High Rainfall Province; (ii) vicariant isolation of lineages west of the Nullarbor divide; (iii) *in situ* speciation; and (iv) recent population subdivision. From dated quantitative studies we derive four testable models of historical biogeography for animal taxa in SWWA, each explicit in providing a spatial, temporal and topological perspective on patterns of speciation or divergence. For each model we also propose candidate lineages that may be worthy of further study, given what we know of their taxonomy, distributions or relationships. These models formalise four of the strongest patterns seen in many animal taxa from SWWA, although other models are clearly required to explain particular, idiosyncratic patterns. Generating numerous new datasets for suites of co-occurring lineages in SWWA will help refine our understanding of the historical biogeography of the region, highlight gaps in our knowledge, and allow us to derive general postulates

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from quantitative (rather than qualitative) results. For animals, this process has now begun in earnest, as has the process of taxonomically documenting many of the more diverse invertebrate lineages. The latter remains central to any attempt to appreciate holistically biogeographic patterns and processes in SWWA, and molecular phylogenetic studies should – where possible – also lead to tangible taxonomic outcomes.

Key words: systematics, conservation, evolution, Chordata, Arachnida, Insecta, Diplopoda, Decapoda, Mollusca, Onychophora.

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I. INTRODUCTION

Among the Earth's southern-temperate biomes, the south-western land division of Western Australia (SWWA), extending south-west of a line from Shark Bay to Israelite Bay (Fig. 1), is recognised globally as a hotspot of biodiversity (Myers *et al.*, 2000; see also Hopper & Gioia, 2004; Morgan, Roberts & Keogh, 2007). Also known as the 'South-western Australian Floristic Region' (SWAFR; Hopper & Gioia, 2004) or historically as the 'South-western Botanical Province' (Diels, 1906; Hopper, 1979; Beard, 1980) – in recognition of its extraordinarily rich and regionally endemic flora – SWWA is renowned for its island-like nature and unique biogeographic characteristics, occupying a temperate mesic zone surrounded by oceans and arid deserts (Hopper & Gioia, 2004). Landscapes throughout SWWA are ancient, flat and highly weathered, supporting little mountainous topography, no major river systems and largely nutrient-deficient soils underlain by continental granitic bedrock of Archaean age (Hopper *et al.*, 1996; Anand & Paine, 2002; Hopper & Gioia, 2004; Hopper, 2009). While largely geologically stable, repeated Quaternary sea-level fluctuations along the coastal margins have led to temporal dynamism of habitats and moderate levels of topographic complexity along the western and south-eastern coasts (Hearty & O'Leary, 2008; Lewis *et al.*, 2013). The region has a mediterranean-type climate and the annual rainfall is highly seasonal (and variable across the region), increasing from less than 300 mm in the east to more than 1000 mm in the extreme south-west (Fig. 1). This unique biological, geological and climatic setting supports a mosaic of largely transitional or xeric habitats (Fig. 2), with wetter mesic elements persisting only in the extreme south-west and southern sub-coastal zones.

Much has been written about the taxonomy, phylogeny, biogeography and evolution of the south-western Australian biota, not least because the region is so botanically distinctive and diverse, but also because authors have often struggled to understand or appreciate the origins of the biota. A central tenet of many south-western Australian studies remains 'Hooker's paradox' (stemming from observations first made by Hooker, 1860), i.e. how can such a seemingly deadly dull landscape generate and sustain such high levels of endemism and biodiversity? Certainly, the mechanisms that have generated plant and animal diversity in this region are not obvious, compared to many other biodiversity hotspots that are either complex tectonically or have obvious mechanisms/agents of vicariance, dispersal or continental drift implicated in the division and mixing of biotas across space and time. For example, in the Cape Floristic Province in Africa, species richness is higher in more mountainous, western areas (Forest *et al.*, 2007); in the Polynesia-Micronesia hotspot there exists a huge number of oceanic islands (Myers *et al.*, 2000); and in Wallacea, dispersal into newly formed land masses from adjacent biogeographic regions is a major source of diversity (Stelbrink *et al.*, 2012). In light of this paradox, and with the application in recent decades of

cladistic techniques (Nelson & Platnick, 1981) followed by molecular phylogenetic methods, a new understanding of historical biogeographic processes in SWWA has begun to emerge.

Systematic analyses and reviews in botany have played a central role in highlighting the biodiversity values of SWWA (e.g. Hopper, 1979; Hopper *et al.*, 1996; Myers *et al.*, 2000; Crisp *et al.*, 2001; Crisp, Cook & Steane, 2004; Hopper & Gioia, 2004; Orthia *et al.*, 2005; Byrne, 2007; Crisp & Cook, 2007; Byrne *et al.*, 2008; Hopper, 2009; Hopper *et al.*, 2009; Lambers *et al.*, 2010; Ladiges *et al.*, 2011) and these studies have contributed new data and biogeographic hypotheses for the diversification of the extremely rich south-western Australian flora. In a landmark review of floristic biogeographic patterns in SWWA, Hopper & Gioia (2004) noted the advances made over the last few decades in the discovery, collection and description of new flowering plant species in the region, and the concomitant progress made towards reaching a new 'phytogeographic understanding' of patterns of distribution and endemism in the region. Faunistic studies have generally lagged behind botanical studies in informing our understanding of south-western Australian biogeography, although several older works (e.g. Gentilli, 1949; Keast, 1958; Main, Lee & Littlejohn, 1958; Keast, 1961; Littlejohn, 1981; Hopper *et al.*, 1996) attempted to describe the origins and diversity of elements of the south-western Australian terrestrial fauna, greatly influencing subsequent studies on specific taxa (e.g. Maxson & Roberts, 1984; Morgan *et al.*, 2007). More recently, phylogenetic, population genetic and biogeographic studies have also begun to provide quantitative datasets for a number of key animal lineages (see Sections III and IV, below), including for less vagile invertebrate, fish and frog taxa with high levels of endemism in the region. Thus, while SWWA can still be described as something of a 'phytogeographic open-book' (Rix, Harvey & Roberts, 2010, p. 210) for numerous terrestrial metazoan lineages, three decades of accumulating systematic research on the fauna is beginning to complement and test hotspot concepts born out of botanical research.

As highlighted by Byrne *et al.* (2008, p. 4399), recent developments in the biological and earth sciences, combined with a revolution in phylogenetics and molecular ecology, have greatly assisted 'our capacity to unravel the histories of the Earth's biomes' and to test the mode, tempo and timing of evolutionary events. Crisp *et al.* (2004), in a comparative analysis of the evolution and diversity of the Australian flora, recognised the need for, and the importance of, rigorous, dated molecular phylogenetic studies to test questions of historical speciation and divergence in the complex biological and environmental context of the Australian continent ('dated' throughout this paper refers to molecular analyses with temporal estimates of time since divergence, inferred using molecular clocks, rates of nucleotide evolution or fossil calibrations). A central premise of the observations of both Crisp *et al.* (2004) and Byrne *et al.* (2008) was that quantitative data from phylogenetic and population genetic analyses

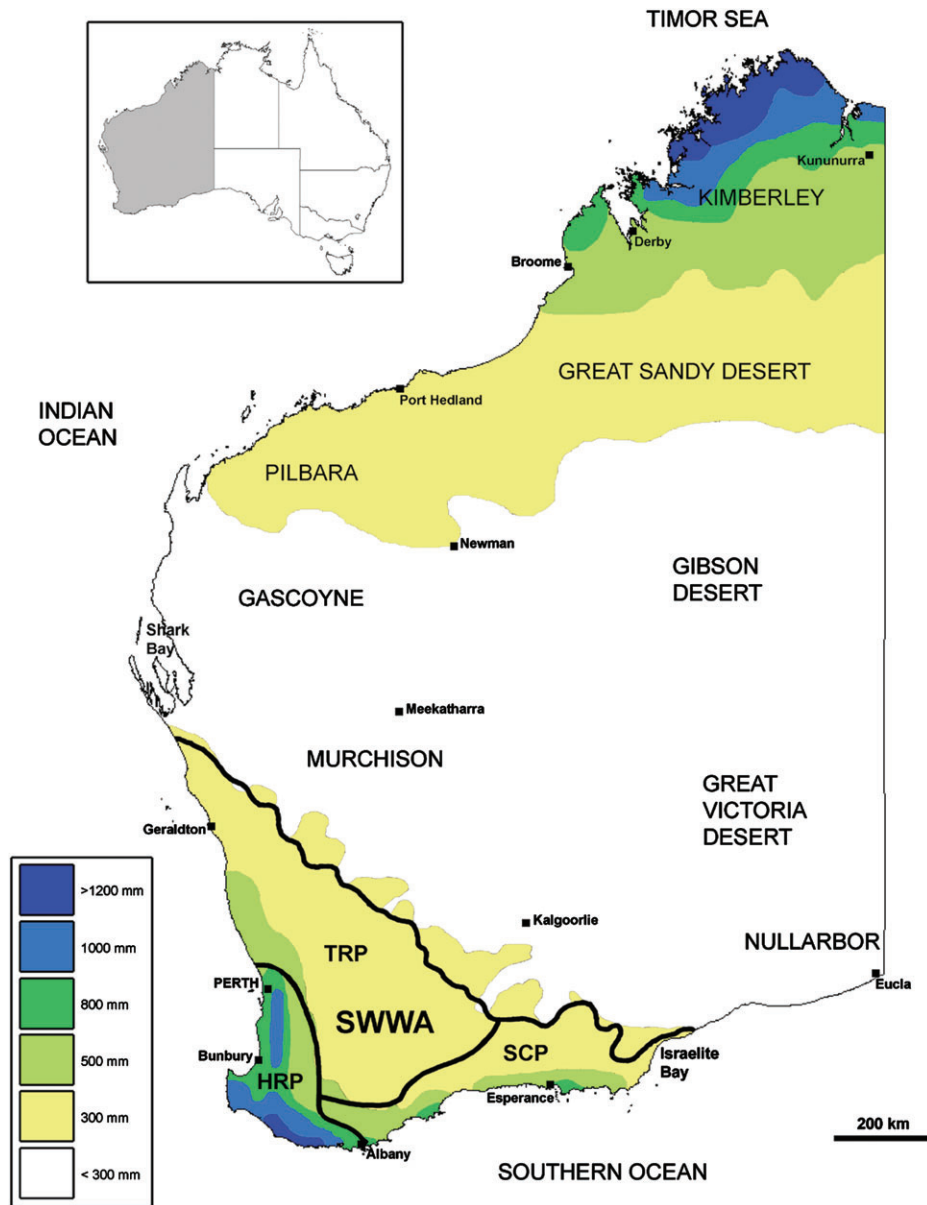


Fig. 1. Map of Western Australia, showing approximate annual rainfall zones, the extent of the south-western land division (SWWA) and the three inclusive biogeographic provinces of Hopper & Gioia (2004; HRP = High Rainfall Province; SCP = Southeast Coastal Province; TRP = Transitional Rainfall Province). Also shown are other major biogeographic regions within Western Australia and municipal landmarks. Rainfall data courtesy of the Australian Bureau of Meteorology, based on a standard 30-year climatology (1961–1990).

are required to adequately inform and test biogeographic hypotheses. While these data are crucial to developing phylogenetic and temporal perspectives on diversification, an understanding of the origins of biodiversity requires several additional and complementary elements, including: (i) an understanding of spatial patterns of relatedness that might be used to infer mechanisms of speciation (e.g. see area cladograms in Figs 7 and 8); (ii) known data on geology (e.g. tectonic events, continental drift, sea-level changes, marine incursions etc.; see Fig. 3); and (iii) data on climatic history inferred from climate models, either alone or combined with

geological data (Fig. 3). For the south-western Australian biota, distributional data, ecological studies and population and community diversity measures have all featured heavily in historical attempts to describe biogeographic processes, although relatively few studies have given us an understanding of evolutionary mechanisms and models of divergence in both space and time. Excluding Australia-wide analyses of biotas or biomes (e.g. Harvey, 2002; Crisp *et al.*, 2004; Byrne *et al.*, 2008, 2011), floristic and faunistic studies of south-western Australian biogeography – whether focussed only on the region (e.g. Hopper, 1979; Main & Main, 1991;



Fig. 2. Examples of major habitats and landscapes of south-western Western Australia. (A–E) High Rainfall Province. (A) Jarrah-marri eucalypt forest, Greater Preston National Park; (B) wandoo eucalypt forest, Wandoo National Park; (C) tall karri-tingle eucalypt forest, ‘Valley of the Giants’, Walpole-Nornalup National Park; (D) tall karri eucalypt forest, Porongurup National Park; (E) banksia-jarrah woodland, Neerabup National Park. (F–K) Southeast Coastal Province. (F) Mallee woodland and temperate heathland, Stirling Range National Park; (G) temperate heathland near Barren Ranges, Fitzgerald River National Park; (H) coastal heathland on granite near Thistle Cove, Cape Le Grand National Park; (I) open temperate heathland, Cape Arid National Park; (J) flowering coastal heathland, Waychinicup National Park; (K) mallee woodland, Cape Arid National Park. (L–O) Transitional Rainfall Province. (L) Mallee woodland and heathland, Lesueur National Park; (M) sheoak woodland, Tutanning Nature Reserve; (N) Kwongan heathland, Drovers Cave National Park; (O) open escarpments and sandplains, Murchison Gorge, Kalbarri National Park. All images by M. Rix except F by M. Wojcieszek (used with permission) and K and N by D. Edwards.

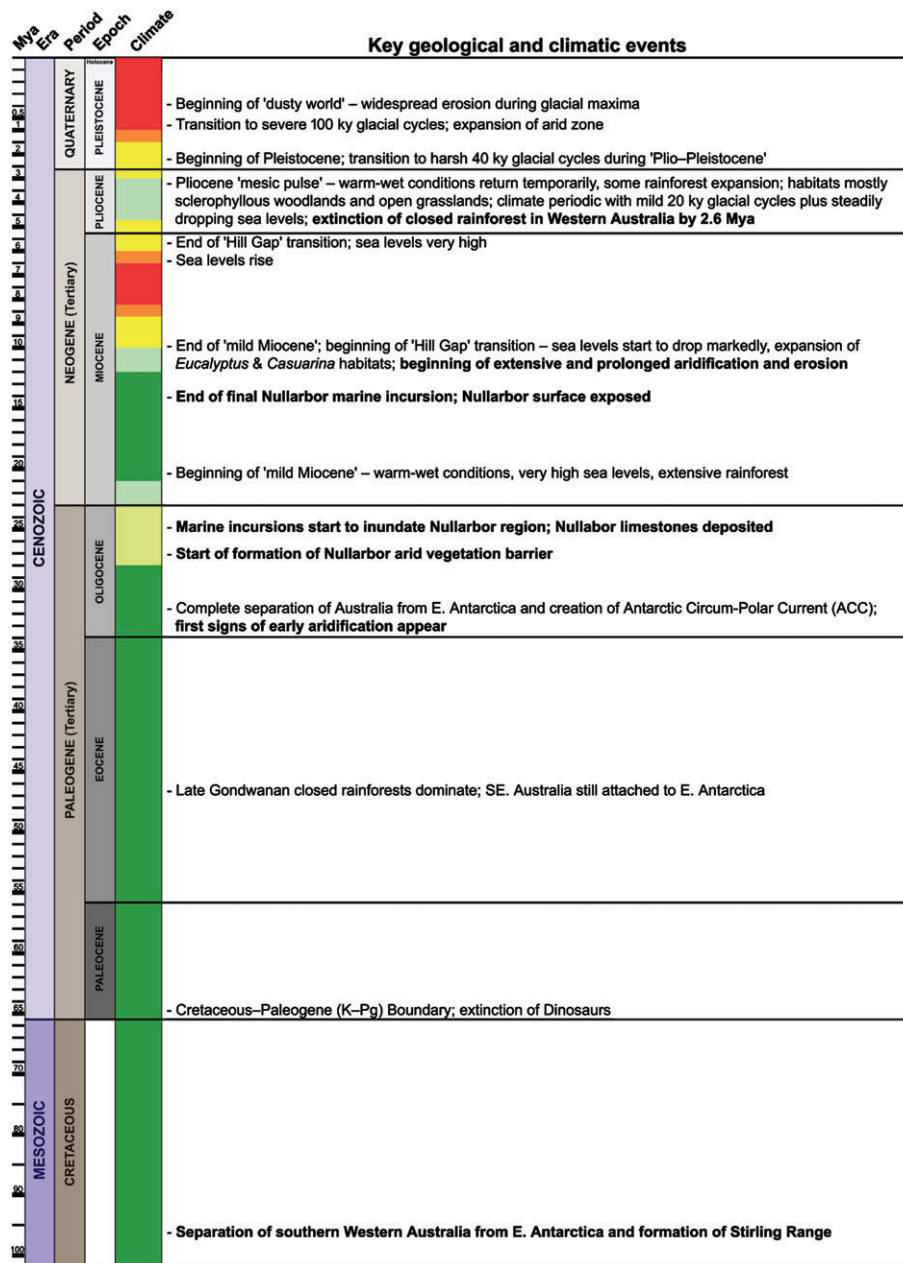


Fig. 3. Geological timeline showing key geological and climatic events in Australia and Western Australia from the late Cretaceous. Broadly prevailing climatic conditions in Australia generally are depicted with coloured bars – dark green for warm-wet (mesic) conditions, grading to yellow, orange and red for progressively more xeric climates. Events pertinent to the south-western land division of Western Australia (SWWA) are highlighted in bold. Note that the calibrated time-scale is not linear (0.5 Mya calibrations < 10 Mya; 0.1 Mya calibrations < 1 Mya). Mya/kya = millions/thousands of years ago. Derived from: McLoughlin (2001); Hopper & Gioia (2004); Byrne *et al.* (2008, 2011).

Hopper *et al.*, 1996; Hopper & Gioia, 2004) or in a broader continental context (e.g. Keast, 1961; Schodde, 2006; Slatyer, Rosauer & Lemckert, 2007) – have generally relied heavily (and usually unavoidably) on qualitative, comparative patterns to derive general postulates. This situation has clouded our understanding of faunistic biogeography in SWWA, and resulted in the widespread assumption that the region is a biodiversity hotspot for the entire biota.

The goal of this review is to analyse critically phylogenetic datasets – especially those with estimates of divergence times – for all available elements of the south-western Australian terrestrial fauna, and to compare these datasets to those available for plants. Our data necessarily generate an incomplete perspective on evolutionary mechanisms in a biodiversity-rich region, but will derive explicit, testable hypotheses stipulating what those mechanisms may have

been and how they may have operated in both space and time. Conservation priorities were central to the initial recognition of SWWA as a biodiversity hotspot (Myers *et al.*, 2000), and SWWA is certainly a heavily modified environment having had significant loss of vegetation, heavily modified ground water regimes and concomitantly severe impacts on soils, water quality and biodiversity (Hobbs, 1993, 2001; Wardell-Johnson & Horwitz, 1996; George, McFarlane & Nulsen, 1997; Gibson *et al.*, 2004; Keighery *et al.*, 2004; Pitman *et al.*, 2004; EPA, 2007; Burrows, 2008; George, Clarke & English, 2008). An additional aim of this study is to relate biogeographic patterns and historical processes to potential conservation outcomes and avenues for future research.

II. THE SOUTH-WESTERN AUSTRALIAN BIODIVERSITY HOTSPOT

(1) Recognition of SWWA as a biodiversity hotspot

The biota of SWWA has been the subject of continuous and generally increasing scientific interest since the late 18th century, after successive French and British voyages visited, surveyed and collected along the southern and south-western coastlines between 1791 and 1803 (Watts, Pomfret & Maberley, 1997; George, 1999; Hunt & Carter, 1999; Hopper, 2003, 2004; Brown, 2008). Although Dutch explorers were the first Europeans to visit Western Australia in the late 17th century (Playford, 1998), it was the celebrated, highly successful and politically competing voyages of discovery led by Matthew Flinders (on the *Investigator* expedition) and Nicolas Baudin (on the *Naturaliste* and *Géographe* expeditions) that had the greatest influence on early attempts to document and describe the natural history of SWWA (Serventy & Whittell, 1976). Since that time, the considerable botanical richness of SWWA, with its more than 7000 vascular plant species (Hopper, 1992; Hopper & Gioia, 2004), has played a central role in most attempts to characterise the biodiversity and biogeography of the region (summarised in: Brown, 1810; Hooker, 1860; Diels, 1906; Gardner, 1944; Seddon, 1972; Hopper, 1979, 2003, 2004, 2009; Crisp, Linder & Weston, 1995; Hopper *et al.*, 1996; Hopper & Gioia, 2004; Gibson, Yates & Dillon, 2010; Ebach, 2012; Ebach *et al.*, 2013; González-Orozco *et al.*, 2013).

The eventual 'formal' recognition of SWWA as a biodiversity hotspot by Myers *et al.* (2000) – the only such global hotspot to be recognised in Australia – was, in common with other biodiversity hotspots, based on: (i) a large number of endemic plant species (>0.5% of global plant species); and (ii) severe habitat loss (>70% of the primary vegetation). In south-western Australia, endemic plants account for at least 1.4% of the world's plant species, and the region has lost nearly 90% of its primary vegetation since European settlement (Myers *et al.*, 2000). Unsurprisingly, SWWA also includes 5 of 15 national biodiversity hotspots recognised by the Commonwealth of Australia (see: <http://www.environment.gov.au/biodiversity/hotspots/national-hotspots.html>) and was further recognised as a hotspot by the State of Western Australia (EPA, 2007). This formal recognition of the region has encouraged conservation measures at all administrative levels, and highlighted the significant ongoing threats to the biota by pathogens (e.g. *Phytophthora*: Shearer, Crane & Cochrane, 2004; Shearer *et al.*, 2009), weeds (Scott & Delfosse, 1992; Hobbs, 2001), feral animals (e.g. foxes, cats: Burbidge & McKenzie, 1989; May & Norton, 1996; Hobbs, 2001) and changing climate conditions (Hughes, 2003; Pitman *et al.*, 2004) (see also EPA, 2007).

(2) **Phytogeographic characterisation of SWWA**

Recognition and phytogeographic characterisation of SWWA has had a long history, dating at least from Hooker (1860). Numerous authors since Hooker have attempted to define and outline broad biogeographic floristic regions within SWWA (e.g. Diels, 1906; Gardner, 1944; Burbidge, 1960; Beard, 1975, 1980; Hopper, 1979; Hopper & Gioia, 2004), in most cases integrating vegetation and rainfall characteristics with surface geology and levels of floristic similarity. At its simplest, SWWA has been broken into three main provinces according to rainfall (Fig. 1) – the High Rainfall Province (HRP), the Southeast Coastal Province (SCP) and the Transitional Rainfall Province (TRP) (Hopper & Gioia, 2004), these concepts expanding on an earlier characterisation that saw SWWA broken into just two rainfall provinces (the HRP and TRP; Hopper, 1979; Hopper *et al.*, 1996), with the HRP also including a 'Southern Forest Region' (Hopper *et al.*, 1996).

(2) Phytogeographic characterisation of SWWA

The HRP of Hopper & Gioia (2004) (Fig. 1) is characterised by annual rainfall in excess of 600 mm and eucalypt-dominated open and tall-open forests (Fig. 2A–D). These habitats are especially evident along the Darling Escarpment and throughout the southern forests where annual rainfall is greater than 800 mm. In these wet or seasonally wet forests, there are a very few dominant eucalypt tree species: jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*) and wandoo (*E. wandoo*) in the northern forests from Perth to Albany (Fig. 2A, B); and karri (*E. diversicolor*), jarrah and red tingle (*E. jacksonii*; see Wardell-Johnson & Coates, 1996) in the southern forests from Margaret River to Denmark (with karri also extralimital in the Porongurup National Park) (Fig. 2C, D). Along the coastal margins of the Indian Ocean (i.e. throughout the Swan Coastal Plain), tall sclerophyll forests are replaced by eucalypt and *Banksia* woodlands or heathlands to the north of Bunbury (Fig. 2E), and more open tall forests of tuart (*E. gomphocephala*) and peppermint (*Agonis flexuosa*) between Cape Naturaliste and Bunbury. All areas of the HRP possess additional diverse assemblages of understorey plants, although modelling by Hopper & Gioia (2004) suggests that much of the HRP may be less diverse and exhibit less local endemism than parts of the TRP or SCP, with some notable exceptions (e.g. Phillips *et al.*, 2011).

The SCP (Hopper & Gioia, 2004; Fig. 1) is largely characterised by more xeric, temperate communities dominated by sandy heathlands, mallee woodlands and shrublands (Fig. 2F–K). Annual rainfall is mostly 300–500 mm, although important pockets of higher rainfall exist around Bremer Bay, Cape Le Grand and in the Porongurup and Stirling Ranges. The vast TRP (Hopper & Gioia, 2004; Fig. 1) is similarly characterised by semi-arid woodlands, heathlands and shrublands (Fig. 2L–O), where annual rainfall is in the range 300–600 mm. In both the SCP and the TRP, open woodlands with a high diversity of mallee eucalypts are characteristic of inland areas (Fig. 2F, K, L), with lower sandy heathlands and shrublands (often referred to as ‘Kwongan’) dominant in more coastal areas (Fig. 2G–J, N). Throughout these more xeric inland and coastal areas (many of which have been extensively cleared for agriculture), species of Myrtaceae (eucalypts, mallees, myrtles), Proteaceae (banksias, dryandras, grevilleas), Mimosaceae (acacias), Fabaceae (peas), Asteraceae (daisies) and Orchidaceae (orchids) are both prevalent and highly diverse, with suites of other families creating vegetation communities that include some of the largest, most diverse and biologically significant temperate heathlands and woodlands on Earth. However, accumulating evidence suggests that SWWA is not a uniformly significant hotspot for plant diversity and endemism, and that certain highly localised regions are more important than others in terms of species richness and endemism. The Stirling Range (Fig. 2F), Fitzgerald River (Fig. 2G), Kalbarri (Fig. 2O) and Lesueur (Fig. 2L) regions have all been cited as outstanding local hotspots of floristic diversity (e.g. Crisp *et al.*, 2001; Hopper & Gioia, 2004), although the Ravensthorpe Range, Lake Muir, Darkan/Narrogin and Darling Range regions may also be significant (Hopper & Gioia, 2004, fig. 5; see also <http://www.environment.gov.au/biodiversity/hotspots/national-hotspots.html>).

(3) Faunistic diversity in SWWA

Like virtually every terrestrial ecosystem on Earth, the fauna of SWWA is composed of suites of taxa having varying levels of diversity and histories of taxonomic documentation. These terrestrial ecosystems include all ecotypes above the high-tide level, and for our purposes we include freshwater and other inland aquatic habitats. This fauna includes a diverse range of taxa (Fig. 4) belonging to at least nine phyla (i.e. Annelida, Arthropoda, Chordata, Mollusca, Nematoda, Onychophora, Platyhelminthes, Rotifera and Tardigrada), of which Arthropoda, Chordata and Mollusca are the most conspicuous. The vertebrates of the phylum Chordata (i.e. fish, amphibians, reptiles, birds and mammals; Fig. 4A–F) are by far the best documented and most intensely studied, however there have been significant, recent advances in the taxonomy of numerous terrestrial invertebrate groups.

Among vertebrates, there were approximately 500 species in SWWA at the time of European settlement, including eight freshwater (non-diadromous) fish, 32 frogs, 174 reptiles, 231 birds and 54 mammals. Of these, 113 species are endemic

to SWWA; we define ‘endemic’ species/taxa as those with a total distribution range wholly or largely restricted to SWWA (the latter having ranges that may extend slightly east of the 300 mm isohyet). This number equates to ~23% of the total diversity, and includes eight fish (100% endemism, defined as the ratio of endemic species to species known to occur in SWWA), 27 frogs (84% endemism), 54 reptiles (31% endemism), 14 birds (6% endemism) and 10 mammals (19% endemism). Of the total vertebrate fauna, there is evidence (phylogenetic and/or taxonomic) for only 21 genera having undergone *in situ* speciation in SWWA (i.e. one of seven fish genera recorded from the region; 6 of 12 frog genera; 12 of 54 reptile genera; 1 of 143 bird genera; and perhaps 1 of 33 mammal genera), and very few of these lineages have undergone significant species-level radiation (at least in comparison to plants). For example, the proportion of endemic vertebrate species in SWWA belonging to clades that have speciated *in situ* is approximately 65% of the total number of endemic species, and over 90% of these are frogs and reptiles.

The almost complete level of taxonomic documentation for vertebrates in SWWA has not been replicated for virtually any order of terrestrial invertebrates. As a result, it is not possible to compile accurate or reflective summaries of faunistic composition or relative levels of endemism for most invertebrate groups. This is especially so within the major arthropod orders of insects, arachnids and myriapods. However, recent monographic revisions of south-western Australian taxa allow us to highlight patterns of diversity for some taxa, and a suite of older revisionary and taxonomic works provide an entrée into the composition, diversity and biogeography of select lineages. For example, SWWA is clearly a region of high diversity and/or endemism for at least several taxa, including orthopteroid insects (e.g. Rentz, 1985, 1993, 2001; Fig. 4M), wasps (e.g. Burks *et al.*, 2012), mirid bugs (e.g. Schuh & Weirauch, 2010), mygalomorph spiders (e.g. Main, 1985, 1991; Raven, 1994; Fig. 4I; see also Fig. 8D), harvestmen (e.g. Giribet, 2003; Taylor, 2011), bothriembryontid snails (e.g. Iredale, 1939; Breure & Whisson, 2012; Fig. 4N), onychophorans (e.g. Reid, 2002; Murienne *et al.*, 2013; Fig. 4O), millipedes (e.g. Main, Harvey & Waldock, 2002; Moir & Harvey, 2008; Moir, Brennan & Harvey, 2009; Edward & Harvey, 2010; Fig. 4J, K) and parastacid decapods (e.g. Riek, 1969; Austin & Knott, 1996; Horwitz & Adams, 2000; Fig. 4G; see also Fig. 8B), among many others (e.g. Harvey, 1996, 1998, 2002; Hopper *et al.*, 1996; Main, 1996; Harvey *et al.*, 2000, 2004; Judd & Horwitz, 2003; Rix, 2006; Rix, Roberts & Harvey, 2009; Rix & Harvey, 2010; Crews & Harvey, 2011). However, short-range endemism within these groups is not unique to SWWA, and many of these taxa exhibit similar levels of high regional endemism across continental or global ranges. For example, the assassin spiders (family Archaeidae; Fig. 4H) are represented by six species in SWWA, all of which are short-range endemics (see Fig. 8C; Rix & Harvey, 2012*a,c*). The family is further represented in eastern Australia, southern Africa and Madagascar, where all 64 named species



Fig. 4. Examples of animal taxa endemic to south-western Western Australia. (A) Salamander fish, *Lepidogalaxias salamandroides* (Lepidogalaxiidae; image by G. Allen, W.A. Museum). (B) Nornalup frog, *Geocrinia lutea* (Myobatrachidae; image by B. Maryan). (C) Sunset frog, *Spicospina flammocaerulea* (Myobatrachidae; image by B. Maryan). (D) Keeled legless lizard, *Pletholax gracilis* (Pygopodidae; image by B. Maryan). (E) Carnaby's cockatoo, *Calyptorhynchus latirostris* (Cacatuidae; image by T. Kirkby, W.A. Museum). (F) Quokka, *Setonix brachyurus* (Macropodidae; image by M. Wojcieszek). (G) Freshwater crayfish, *Engaewa walpolea* (Parastacidae; image by Q. Burnham). (H) Talyuberlup assassin spider, *Zephyrarchaea barrettae* (Archaeidae; image by M. Rix). (I) Trapdoor spider, *Moggridgea* sp. (Migidae; image by M. Harvey). (J) Marri millipede, *Antichiropus variabilis* (Paradoxosomatidae; image by C. Car). (K) Tiger millipede, *Atelomastix tigrina* (Iulomorphidae; image by M. Rix). (L) Scorpionfly, *Austromerope poultoni* (Meropeidae; image by J. Taylor). (M) Green westwind katydid, *Windbalea viride* (Tettigoniidae; image by D. Rentz). (N) Land snail, *Bothriembryon* sp. (Bothriembryontidae; image by M. Harvey). (O) Velvet worm, *Kumbadjena* sp. (Peripatopsidae; image by M. Harvey). All images used with permission.

are also short-range endemics (see Lotz, 1996, 2003, 2006; Wood, Griswold & Spicer, 2007; Wood, 2008; Rix & Harvey, 2011, 2012*b*). Similar levels of local endemism occur in other terrestrial invertebrate lineages throughout Australia (as in SWWA), including within the well-studied Decapoda (e.g. Riek, 1969; Fig. 4G; see also Fig. 8B), and perhaps most spectacularly in the indigenous millipede fauna (Fig. 4J, K), where all orders (excluding Polyxenida) exhibit high levels of diversity and short-range endemism Australia-wide (e.g. see Humphreys & Shear, 1993; Mesibov, 2006, 2009, 2010; Car & Harvey, 2013). This propensity for short-range endemism may be correlated more with life-history characteristics than historical biogeography *per se* (Harvey, 2002; Harvey *et al.*, 2011).

Conversely, many other terrestrial invertebrate lineages in SWWA do not show high levels of regional endemism, a phenomenon that may also be explained by life-history characteristics including high vagility (e.g. dispersive juvenile stages and the ability to fly), ecological plasticity or xeric adaptation. This is exemplified in groups that are known or expected to be highly dispersive, e.g. dragonflies and damselflies (43% endemism; Theischinger & Endersby, 2009), butterflies (22% endemism; Braby, 2004), cicadas (53% endemism; Moulds, 1990), wolf spiders (13% endemism across five genera; Framenau & Vink, 2001; Framenau, 2002, 2007, 2010; Langlands & Framenau, 2010) and centipedes (36% endemism across 10 genera; Koch, 1982, 1983*a,b,c*, 1984*a,b*, 1985*a,b*; Waldock & Edgecombe, 2012), among many others.

Evidence for any terrestrial invertebrate lineage having undergone significant *in situ* radiation in SWWA (i.e. >20 congeneric endemic species) – at a scale comparable to many plant taxa (e.g. *Banksia*, genera of Fabaceae; Chandler, Bayer & Crisp, 2001; Mast, Jones & Havery, 2005; Orthia *et al.*, 2005; Cardillo & Pratt, 2013) – is extremely limited, although millipedes of the genus *Antichiropus* (Paradoxosomatidae; Fig. 4J) have clearly undergone a major endemic radiation throughout the region, with over 150 species known (C. Car & M. Harvey, unpublished data; see also Harvey, 2002; Wojcieszek, Harvey & Rix, 2011; Wojcieszek & Simmons, 2011, 2012; Car, Wojcieszek & Harvey, 2013). Species of the millipede genus *Atelomastix* (Iulomorphidae; Fig. 4K) have also experienced considerable *in situ* speciation in southern and far south-western habitats, albeit on a much smaller scale than *Antichiropus* (Edward & Harvey, 2010).

III. ORIGINS AND DIVERSITY OF THE TERRESTRIAL FAUNA

The accumulation of quantitative molecular and cladistic data over the last 30 years, for numerous lineages of south-western Australian plants and animals, has seen new perspectives emerge on the biogeography of the south-western Australian biota. While influential historically, qualitative taxonomically and ecologically derived postulates

regarding the origins, evolution and diversification of the south-western Australian biota do little to inform explicit biogeographic models of vicariance, speciation or population fragmentation in space and time. Several early cladistic studies on Western Australian animal taxa used morphological datasets to generate cladograms for exploring speciation or endemism (e.g. Gray, 1981, 1992; Cracraft, 1986, 1991; Harvey, 1995; Rix, 2006), although these studies were unable to test the temporal modes of cladogenesis that are so critical to better understanding potential mechanisms of divergence. The introduction of molecular methods, starting with albumin and allozyme studies in the 1980s and later DNA sequence analyses, plus the development of molecular clock theory (particularly as applied to phylogenetic analyses of nucleotide sequence data), enabled explicit testing of biogeographic models in both space and time. This process is ongoing with recent advances in coalescent theory, Bayesian analysis and next-generation sequencing. Numerous authors have commented on the importance of quantitative – especially dated – phylogenetic and phylogeographic datasets for better understanding the complex biogeographic history of the Australian continent (e.g. Crisp *et al.*, 2004; Byrne *et al.*, 2008, 2011), and all highlight the power of assessing congruence across well-sampled co-occurring taxa (see also Ladiges, Bayly & Nelson, 2012). Here, we summarise the available, quantitative, dated datasets for fauna from south-western Australia (Figs 5–8), and we highlight four mechanisms driving patterns of endemism among co-occurring taxa, and compare them with patterns identified in plant datasets. In all instances where divergence estimates are reported between higher taxa or clades, stem ages are used.

(1) Ancient relicts?

The south-western Australian fauna has been proposed to consist of a complex assemblage of older relictual taxa and younger, more recently arrived or more recently evolved species, the latter of which may also belong to clades that are themselves relatively ancient (Hopper *et al.*, 1996). However, the biota also includes numerous higher taxa (genera mostly, plus several families) which are endemic to SWWA. Clearly, for many such taxa, determining how ‘endemic’ or ‘relict’ they are on the basis of taxonomy alone is difficult, given (i) the possible ‘inflationary’ effect different (especially paraphyletic) taxonomies may have on generic relationships and estimates of phylogenetic endemism, and (ii) the importance of both topology and time since divergence for determining when and from what a particular taxon evolved.

(a) Ancient clades

For the south-western Australian fauna, dated phylogenetic datasets are available for only a handful of endemic higher taxa (Fig. 5, left panel), although these few studies – which importantly include estimates of both topology and time since divergence – provide tantalising clues to the origins of at least some of south-western Australia’s most iconic animal lineages. These studies highlight three important

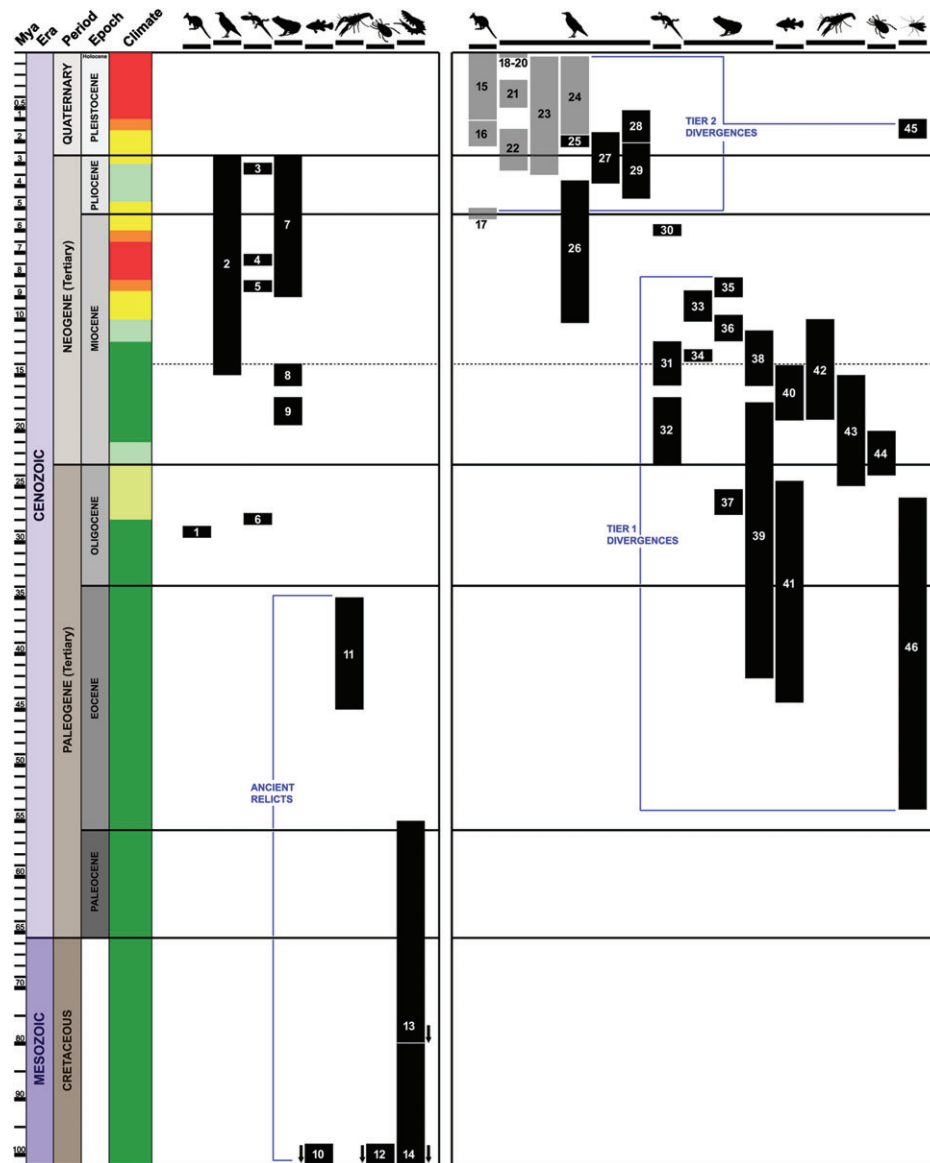


Fig. 5. Geological timeline from the mid-Cretaceous to the present (see Fig. 3), overlaid with fauna ‘taxon boxes’ highlighting: (left) divergence events for south-western Australian endemic higher taxa (i.e. genera and families); and (right) divergence events between congeneric sister lineages, species or populations in south-western versus south-eastern Australia. Each box covers a range of divergence dates inferred from a dated, published molecular dataset. The mid-Miocene is denoted by a thin dotted line, with intraspecific divergences in mammals and birds shown by paler grey boxes. Taxa and references are as follows: ¹*Tarsipes* (Bininda-Emonds *et al.*, 2007); ²*Purpureicephalus* (Schweizer *et al.*, 2011, 2012); ³*Paroplocephalus* (Sanders *et al.*, 2008); ⁴*Elapognathus* (Sanders *et al.*, 2008); ⁵*Neelaps (calonotus)* (Sanders *et al.*, 2008); ⁶*Pletholax* (Jennings *et al.*, 2003); ⁷*Myobatrachus/Arenophryne* (Maxson & Roberts, 1985; Roberts & Maxson, 1989); ⁸*Metacrinia* (Roberts & Maxson, 1989); ⁹*Metacrinia-Myobatrachus-Arenophryne (MMA)* clade (Maxson & Roberts, 1985; Roberts & Maxson, 1989); ¹⁰*Lepidogalaxias* (Near *et al.*, 2012); ¹¹*Engaewa* (Schultz *et al.*, 2009); ¹²*Karripurcellia* (Giribet *et al.*, 2009, 2012); ¹³*Kumbadjena/Occiperipatoides* (Murienne *et al.*, 2013); ¹⁴W.A. Onychophora clade (Murienne *et al.*, 2013); ¹⁵*Petrogale lateralis* (Potter *et al.*, 2012); ¹⁶*Pseudomys shortridgei* (Salinas *et al.*, 2009); ¹⁷*Phascogale tapoatafa* (Spencer *et al.*, 2001); ¹⁸*Gymnorhina tibicen* (Toon *et al.*, 2007); ¹⁹*Anas gracilis/A. castanea-1* (Joseph *et al.*, 2009); ²⁰*Biziura lobata* (Guay *et al.*, 2010); ²¹*Amytornis textilis* (Austin *et al.*, 2013); ²²*Stipiturus malachurus* (Donnellan *et al.*, 2009); ²³various bird species (Dolman & Joseph, 2012); ²⁴*Anas gracilis/A. castanea-2* (Dhami *et al.*, 2013); ²⁵*Pezoporus* (Murphy *et al.*, 2011); ²⁶*Acanthorhynchus* (Joseph *et al.*, 2014); ²⁷*Malurus* (McLean *et al.*, 2012); ²⁸*Calyptorhynchus* (White *et al.*, 2011); ²⁹*Melithreptus* (Toon *et al.*, 2010); ³⁰*Lerista (L. viduata/L. bougainvillii)* (Lee *et al.*, 2013); ³¹*Delma* (Jennings *et al.*, 2003); ³²*Aprasia* (Jennings *et al.*, 2003); ³³*Pseudophryne* (Roberts & Maxson, 1985, 1989); ³⁴*Limnodynastes* (Roberts & Maxson, 1985, 1986); ³⁵*Litoria-1* (Roberts & Maxson, 1985); ³⁶*Litoria-2* (Burns & Crayn, 2006); ³⁷*Geocrinia* (Roberts & Maxson, 1985); ³⁸*Crinia* (Barendse, 1984; Roberts & Maxson, 1985); ³⁹*Heleioporus* (Morgan *et al.*, 2007); ⁴⁰*Nannoperca* (Unmack *et al.*, 2011); ⁴¹*Galaxiella* (Unmack *et al.*, 2012); ⁴²*Cherax-1* (Munasinghe *et al.*, 2004); ⁴³*Cherax-2* (Schultz *et al.*, 2009); ⁴⁴*Zephyrarchaea* (Rix & Harvey, 2012c); ⁴⁵*Antiporus* (Hawlitschek *et al.*, 2011); ⁴⁶*Stictocladus* (Krosch & Cranston, 2013). See text for details.

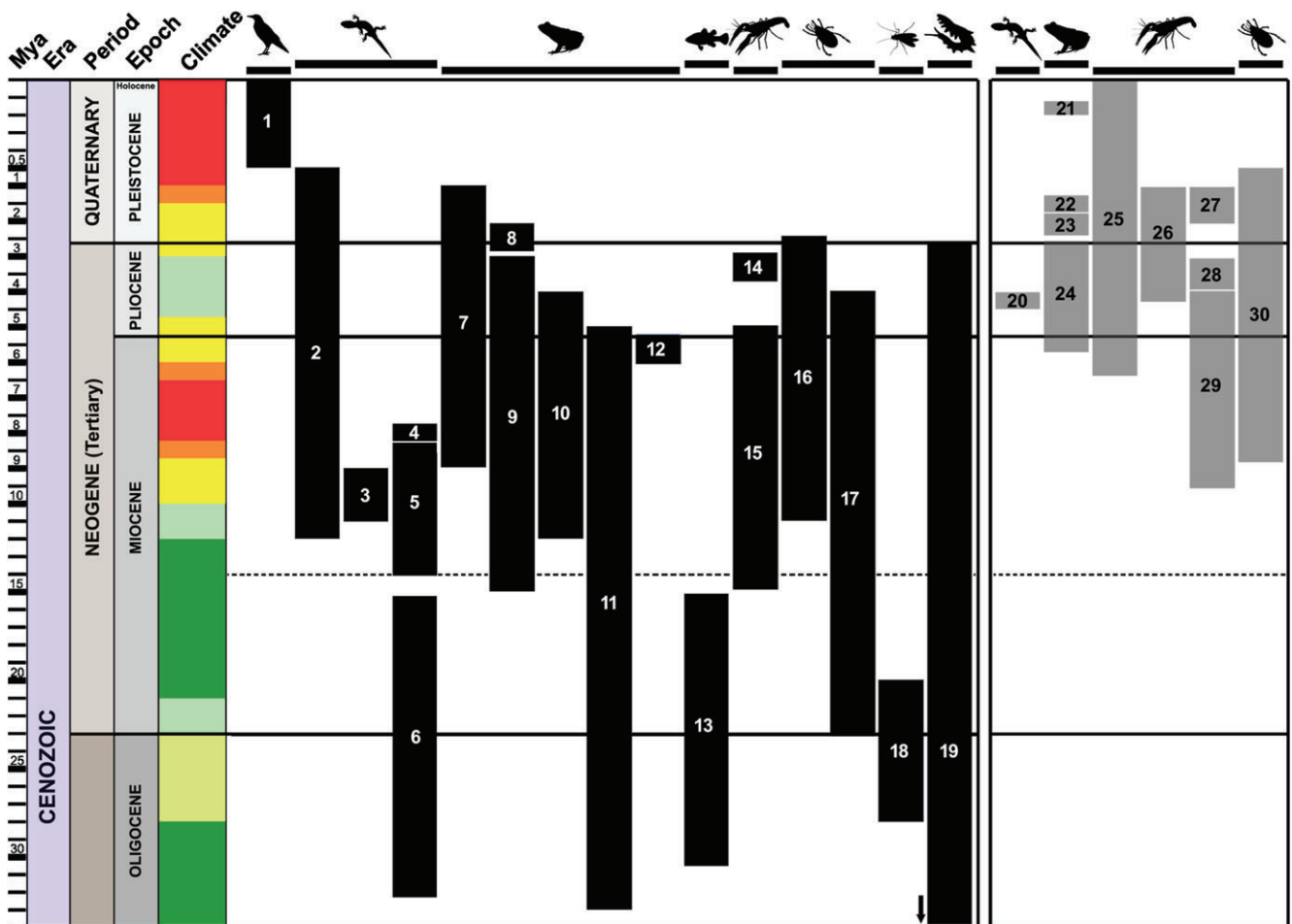


Fig. 6. Geological timeline from the Oligocene to the present (see Fig. 3), overlaid with fauna ‘taxon boxes’ highlighting: (left) *in situ* speciation events for congeneric south-western Australian taxa; and (right) intraspecific population-level (phylogeographic) divergences in south-western Australian species. Each box covers a range of divergence dates inferred from a dated, published molecular dataset. The mid-Miocene (14 Mya) is denoted by a thin dotted line. Taxa and references are as follows: ¹*Calyptorhynchus baudinii*/*C. latirostris* (White *et al.*, 2011); ²*Lerista* spp. (Lee *et al.*, 2013); ³*Diplodactylus ornatus*/*D. polyophthalmus* (Oliver *et al.*, 2009); ⁴*Delma fraseri*/*D. grayii* (Jennings *et al.*, 2003); ⁵*Aprasia* spp. (Jennings *et al.*, 2003); ⁶*Crenadactylus ocellatus* spp. complex (Oliver *et al.*, 2010); ⁷*Neobatrachus* spp. (Roberts *et al.*, 1996); ⁸*Pseudophryne guentheri*/*P. occidentalis* (Roberts & Maxson, 1989); ⁹*Crinia* spp. (Barendse, 1984); ¹⁰*Heleioporus* spp.-1 (Maxson & Roberts, 1984); ¹¹*Heleioporus* spp.-2 (Morgan *et al.*, 2007); ¹²*Arenophryne rotunda*/*A. xiphorhyncha* (Edwards, 2007); ¹³*Galaxiella munda*/*G. nigrostriata* (Unmack *et al.*, 2012); ¹⁴*Amphisopus* spp. (Gouws & Stewart, 2013); ¹⁵*Cherax* spp. (Schultz *et al.*, 2009); ¹⁶*Moggridgea* spp. (Cooper *et al.*, 2011); ¹⁷*Zephyrarchaea* spp. (Rix & Harvey, 2012c); ¹⁸*Archaeochlus brundini* spp. complex (Martin *et al.*, 2002); ¹⁹*Kumbadjena* spp. (Murienne *et al.*, 2013); ²⁰*Ctenophorus ornatus* (Levy *et al.*, 2012); ²¹*Spicospina flammocaerulea* (Edwards & Roberts, 2011); ²²*Crinia georgiana* (Edwards *et al.*, 2007); ²³*Arenophryne xiphorhyncha* (Edwards, 2007); ²⁴*Metacrinia nichollsi* (Edwards *et al.*, 2008); ²⁵*Branchinella longirostris* (Zofkova & Timms, 2009); ²⁶*Paramphisopus palustris* (Gouws & Stewart, 2007); ²⁷*Cherax preissii*-1 (Gouws *et al.*, 2006); ²⁸*Cherax preissii*-2 (Gouws *et al.*, 2006); ²⁹*Cherax quinquecarinatus*/*C. preissii*-3 (Gouws *et al.*, 2010); ³⁰*Moggridgea tingle*/*M.* sp. (Cooper *et al.*, 2011). See text for details.

biogeographic patterns that may be characteristic of endemic higher taxa in SWWA more generally. Firstly, the mite harvestman genus *Karripurcellia* and the onychophoran genera *Kumbadjena* and *Occiperipatoides* provide evidence that SWWA is home to at least some very ancient relictual (Mesozoic) lineages, which are restricted to mesic, temperate habitats in the HRP, and (in the case of *Karripurcellia*) whose surviving closest relatives may not be in Australia (see Giribet *et al.*, 2009, 2012; Murienne *et al.*, 2013). Similarly, the lepidogalaxiid fish *Lepidogalaxias salamandroides*

(Fig. 4A) – which is restricted to creeks and ephemeral pools between Margaret River and Walpole in the southern HRP (Morgan, Gill & Potter, 1998) – has been shown to be sister to all other euteleost fishes, diverging in the Triassic (Near *et al.*, 2012). Based on additional (undated) phylogenetic datasets, other lineages that may be ancient relicts include the Western Swamp Tortoise *Pseudemydura* (Shaffer, Meylan & McKnight, 1997; Georges *et al.*, 1998; but see also Archer, 1996), the mygalomorph spider genus *Moggridgea* (Griswold & Ledford, 2001; Cooper *et al.*, 2011) and the bombycoid

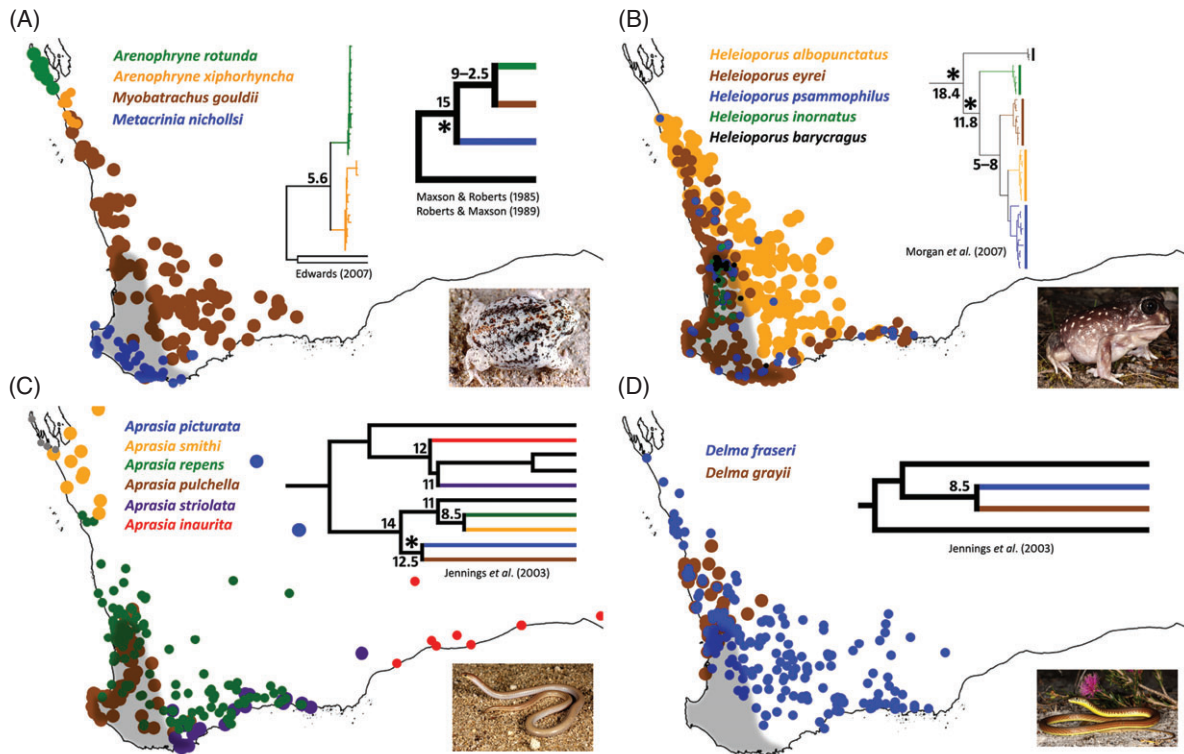


Fig. 7. Example area cladograms showing *in situ* speciation within lineages characteristic of the more xeric Transitional Rainfall Province (TRP) and Southeast Coastal Province (SCP) of south-western Australia. Numbers on nodes denote mean divergence estimates inferred from dated molecular datasets, with coloured dots showing the distributions of different species in the south-western land division of Western Australia (SWWA). The High Rainfall Province (HRP) of Hopper & Gioia (2004) is shaded grey. Area cladograms show: (A) myobatrachid frogs of the *Metacrinia*–*Myobatrachus*–*Arenophryne* (MMA) clade (Maxson & Roberts, 1985; Roberts & Maxson, 1989; Edwards, 2007); (B) myobatrachid frogs of the genus *Heleioporus* (Morgan *et al.*, 2007); (C) pygopodid lizards of the genus *Aprasia* (Jennings *et al.*, 2003); (D) pygopodid lizards of the genus *Delma* (Jennings *et al.*, 2003). Note the highlighted (*) divergence of taxa restricted to the HRP. Distribution maps generated by the Atlas of Living Australia (ALA) website (<http://www.ala.org.au/>), reproduced under a Creative Commons Attribution 3.0 Australia Licence. Images by B. Maryan, used with permission.

moth genus *Carthaea* (Zwick *et al.*, 2011), along with several taxa for which only qualitative data exist (see Section IV.1). Of the latter, one of the most remarkable insects in SWWA is the meropeid scorpionfly *Austromerope poultoni* (Fig. 4L), found in forested habitats in the HRP (see Abbott, Burbidge & Wills, 2007). The Meropeidae are known from only three extant species: *Merope tuber* from eastern North America; *A. poultoni* endemic to SWWA; and the recently discovered *A. brasiliensis* from Espírito Santo, Brazil (Machado, Kawada & Rafael, 2013). Given this distribution, and given additional fossil evidence and morphology, it has been proposed that modern Meropeidae are now highly disjunct Pangaean relicts (Machado *et al.*, 2013), although this hypothesis remains to be tested phylogenetically.

(b) ‘Late Gondwanan’ clades

Divergence of the freshwater crayfish lineage *Engaewa* (Fig. 4G) in the late Eocene (Schultz *et al.*, 2009) suggests that a second suite of ancient relictual clades from the climatically buffered HRP may have later Gondwanan origins, having been isolated in SWWA before the final rifting

of south-eastern Australia from Antarctica in the late Eocene. In this instance, determining additional ‘late Gondwanan’ lineages based on topology alone is difficult, given the inability to separate older Paleogene divergences from younger, Miocene nodes. Furthermore, in the case of genera like *Karripurcellia*, *Lepidogalaxias* and *Engaewa*, their relative antiquity and the likely extinction of closely related taxa (e.g. see Archer, 1996) may cloud our ability to reconcile broad divergence estimates with geological or climatic correlates.

(c) Late Tertiary clades

Divergence of the red-capped parrot *Purpureicephalus spurius* (Schweizer, Seehausen & Hertwig, 2011; Schweizer, Güntert & Hertwig, 2012), the elapid snake genera *Elapognathus*, *Neelaps* and *Paroplocephalus* (Sanders *et al.*, 2008) and the monophyletic *Metacrinia*–*Myobatrachus*–*Arenophryne* (MMA) frog clade in the Miocene and Pliocene (Maxson & Roberts, 1985; Roberts & Maxson, 1989), along with earlier divergences inferred for the honey possum *Tarsipes rostratus* (Bininda-Emonds *et al.*, 2007) and the keeled legless lizard *Pletholax gracilis* (Jennings, Pianka & Donnellan, 2003) in the

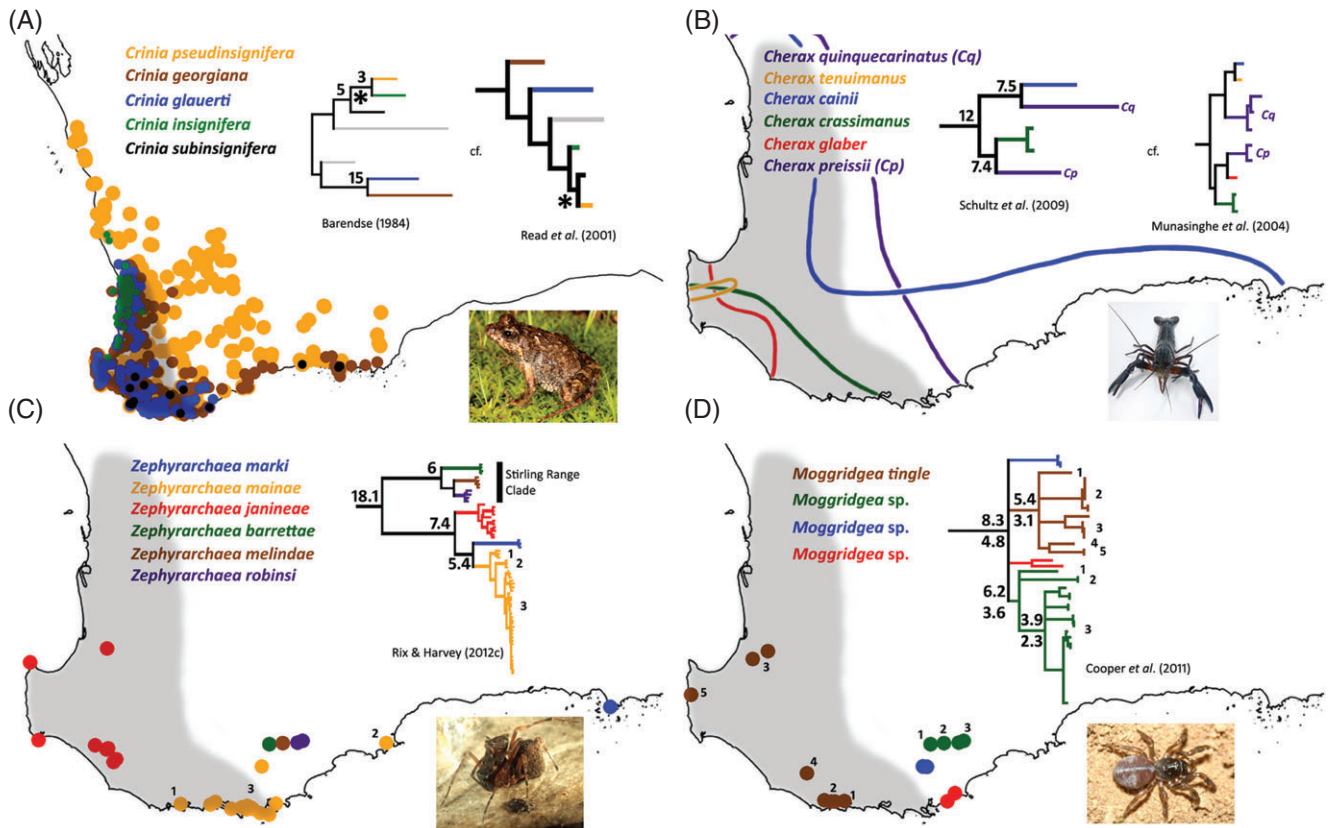


Fig. 8. Example area cladograms showing *in situ* speciation within lineages characteristic of the south-western Australian mesic zone. Numbers on nodes denote mean divergence estimates inferred from dated molecular datasets, with coloured dots (or range boundaries) showing the distributions of different species in the south-western land division of Western Australia (SWWA). The High Rainfall Province (HRP) of Hopper & Gioia (2004) is shaded grey. Area cladograms show: (A) myobatrachid frogs of the genus *Crinia* (Barendse, 1984; see also Read *et al.*, 2001); (B) parastacid crayfish of the genus *Cherax* (Schultz *et al.*, 2009; see also Munasinghe *et al.*, 2004); (C) archaeid spiders of the genus *Zephyrarchaea* (Rix & Harvey, 2012c); (D) midgid spiders of the genus *Moggridgea* (Cooper *et al.*, 2011). Note the highlighted (*) divergence of *Crinia pseudinsignifera* in (A), which is distributed throughout more xeric inland regions of SWWA, and the two divergence estimates for each node in (D), highlighting different values inferred according to different rate calibrations. Distribution map for (A) and map outlines for (B–D) generated by the Atlas of Living Australia (ALA) website (<http://www.ala.org.au/>), reproduced under a Creative Commons Attribution 3.0 Australia Licence. Distributional boundaries for (B) from SERCUL Brochure (2013). Images: (A) by B. Maryan; (B) by Q. Burnham; (C) by M. Rix; (D) by M. Harvey; all used with permission.

mid-Oligocene, provide evidence for a third tier of endemic higher taxa in SWWA. These lineages appear to follow a more classical pattern of isolation/vicariance in SWWA with subsequent adaptation (+/– *in situ* speciation or extralimital extinction) during the major climatic upheavals of the Oligocene and Miocene (see Sections III.2 and III.3). These taxa cannot really be considered ‘ancient relicts’ since at this evolutionary scale different classification schemes not only inflate perceived levels of higher phylogenetic endemism, but may also imply reciprocal monophyly among groups being compared (depending on the degree of autapomorphy or the levels of diversity within a particular lineage). This is well illustrated by the long recognition of the plant genus *Dryandra* as separate to, and by implication sister to, *Banksia*, when molecular data convincingly show that *Banksia* is in fact rendered paraphyletic by *Dryandra* (Mast *et al.*, 2005; Mast & Thiele, 2007; Cardillo & Pratt, 2013). The same

is true of the *MMA* frog clade (see above): one could reasonably argue that all four species in this clade are in fact unusual or highly specialised species of *Pseudophryne* (as both *Pseudophryne sen. str.* and the *MMA* clade are reciprocally monophyletic sister-taxa; Roberts & Maxson, 1989; Read *et al.*, 2001). Such a situation would significantly reduce the perceived levels of higher phylogenetic endemism within south-western Australian Myobatrachidae. It is well recognised that taxonomic estimates of higher phylogenetic endemism (i.e. β estimates) can be heavily influenced (and inflated) by nomenclatural considerations. This highlights the need for temporal data to distinguish older relicts (e.g. *Lepidogalaxias*) from more recently evolved genera arising from *in situ* speciation or radiation (e.g. *MMA* clade), and the use of techniques that ignore taxonomic designation in favour of branch-length-based metrics (e.g. Rosauer *et al.*, 2009).

(2) South-western vicariance and the Nullarbor divide

We here refer to the ‘Nullarbor divide’ as comprising the Nullarbor Plain and its fringing xeric habitats. The Nullarbor Plain itself formed during the late Oligocene and Miocene by successive marine incursions associated with large climate shifts (summarised in Crisp & Cook, 2007; Byrne *et al.*, 2008). As so defined the Nullarbor divide extends from north-east of Israelite Bay in Western Australia (Fig. 1) to the Eyre Peninsula in South Australia. It is the largest and most significant climatic and edaphic biogeographic barrier in southern Australia, and the only major expanse of the arid zone to intersect Australia’s temperate mesic biome (Crisp & Cook, 2007; Byrne *et al.*, 2008, 2011; Dolman & Joseph, 2012). The Nullarbor divide is today a vast arid expanse separating more mesic or transitional temperate zones. Classical patterns of east–west endemism either side of the Nullarbor divide, in south-western and south-eastern Australia, have been proposed for numerous plant and animal taxa, although the timing of vicariance events, the mechanisms of separation and the potential role of dispersal have all influenced attempts to explain and test patterns of reciprocal east–west endemism (see summaries in Maxson & Roberts, 1984; Roberts & Maxson, 1985; Crisp & Cook, 2007; Morgan *et al.*, 2007; Dolman & Joseph, 2012). Clearly, determining the temporal scale of divergence and the nature of intra- *versus* interspecific variation is critical to adequately testing alternative models of vicariance and dispersal, and congruence approaches are powerful in helping to determine likely mechanisms (e.g. Crisp & Cook, 2007).

For the southern Australian fauna, dated molecular datasets are available for at least 28 genera distributed across south-western and south-eastern Australia, including mammals (Spencer, Rhind & Eldridge, 2001; Salinas *et al.*, 2009; Potter *et al.*, 2012), birds (Toon *et al.*, 2007; Donnellan *et al.*, 2009; Joseph *et al.*, 2009, 2014; Guay *et al.*, 2010; Toon, Hughes & Joseph, 2010; Murphy *et al.*, 2011; White *et al.*, 2011; Dolman & Joseph, 2012; McLean *et al.*, 2012; Austin *et al.*, 2013; Dhami *et al.*, 2013), reptiles (Jennings *et al.*, 2003; Lee, Skinner & Camacho, 2013), frogs (Barendse, 1984; Roberts & Maxson, 1985, 1986, 1989; Burns & Crayn, 2006; Morgan *et al.*, 2007), fish (Unmack *et al.*, 2011, 2012), freshwater crayfish (Munasinghe, Burridge & Austin, 2004; Schultz *et al.*, 2009), spiders (Rix & Harvey, 2012c), beetles (Hawltischek *et al.*, 2011) and flies (Krosch & Cranston, 2013) (Fig. 5, right panel). These data provide compelling evidence for two main pulses of east–west lineage separation in south-western and south-eastern Australia. The first tier of divergence dates cluster within the first half of the Miocene, between the late Oligocene and ~10–12 Mya (Fig. 5, right panel, ‘Tier 1 divergences’), although a few outlier divergence estimates extend back to or beyond the early Oligocene, or up to the later Miocene. These datasets with first-tier divergences include invertebrates, fish, frogs and lizards. A second tier of divergence dates in the Plio–Pleistocene comprises birds,

mammals, snakes and diving beetles (Fig. 5, right panel, ‘Tier 2 divergences’). Of these, most provide evidence of recent phylogeographic intraspecific subdivision either side of the Nullarbor divide (e.g. Toon *et al.*, 2007; Donnellan *et al.*, 2009; Salinas *et al.*, 2009; Potter *et al.*, 2012), although slightly older speciation in SWWA during the mid-Pliocene to early Pleistocene has been documented in several bird taxa (e.g. Toon *et al.*, 2010; Murphy *et al.*, 2011; McLean *et al.*, 2012), snakes (Sanders *et al.*, 2008) and in beetles (Hawltischek *et al.*, 2011). Two additional datasets – one for honeyeaters of the genus *Acanthorhynchus* and one for lizards of the genus *Lerista* – straddle the late-Miocene divide between first and second tier divergences (Fig. 5, right panel).

These dated datasets highlight the importance of both the early-mid Miocene and the later Plio–Pleistocene in generating differential patterns of east–west endemism across southern Australia. For many small, less vagile freshwater or mesic-adapted animal taxa, the inundation, uplift and eventual aridification of the Nullarbor divide during the first half of the Miocene was almost certainly a major isolating process that eventually resulted in speciation within multiple southern Australian lineages. This pattern is comparable to that detected in lineages of southern Australian plants (for a comprehensive summary see Crisp & Cook, 2007), which showed a cluster of east–west divergence events around 13–14 Mya. However, these data tell a complex story, and suggest that: (i) for both animals and plants the process of isolation in the early Miocene may not necessarily have been especially abrupt for all taxa; and (ii) that phases of east–west migration or at least partial gene flow may still have occurred in some first-tier lineages up until the mid-late Miocene (e.g. see Unmack *et al.*, 2011). Interestingly, two of the latest inferred (first-tier) animal divergences (in the range of 8–10 Mya) are for frogs in the genus *Pseudophryne* (Roberts & Maxson, 1985, 1989) and two of three endemic snake genera with sister-lineages in eastern Australia (Sanders *et al.*, 2008; see Section III.1). These taxa represent more xeric-adapted organisms that currently occupy both semi-arid and arid habitats, and which may have more easily crossed through or around a less arid Nullarbor divide in the mid-Miocene. Similarly, a very late (~6 Mya) inferred divergence for sister-species of lizards in the genus *Lerista* (i.e. *L. viduata* *versus* *L. bougainvillii*) may be explained by the marked xeric adaptations characteristic of this genus (see Skinner, Lee & Hutchinson, 2008; Skinner, 2010; Lee *et al.*, 2013). By contrast, some rather early Eocene and/or Oligocene divergence estimates have been inferred for strongly mesic-adapted fish (Unmack *et al.*, 2012), frogs (Roberts & Maxson, 1985) and chironomid flies (Krosch & Cranston, 2013), along with several plants (Crisp & Cook, 2007), suggesting that for another set of taxa a vicariant barrier may have been established relatively early, by or even well before the early Miocene. However, for many large vertebrates or more vagile taxa, the formation of an exposed, calcareous Nullarbor Plain by the mid-Miocene was probably a far less significant barrier to gene flow compared

to the pulses of more severe aridification and climate change that occurred during the Pliocene and Pleistocene. For example, a flying insect, several bird species and numerous populations of birds and mammals show clear evidence of relatively recent separation from their sister-species or conspecifics in south-eastern Australia (Fig. 5, right panel, ‘Tier 2 divergences’). The same is true for several plant taxa which are more ecologically tolerant to aridity or to the calcareous soils characteristic of the Nullarbor Plain (Crisp & Cook, 2007).

(3) *In situ* speciation

For plants, one of the most striking characteristics of the south-western Australian biota is the very high proportion of endemic species (perhaps up to 80% of the vascular flora; Hopper & Gioia, 2004), many of which also belong to endemic (and often highly diverse) clades. It has been hypothesised that this species richness was driven by *in situ* speciation (Hopper, 1992; Hopper & Gioia, 2004) and phylogenies with largely south-western Australian groups do provide evidence for numerous, speciose south-western endemic clades (e.g. Mast, 1998; Chandler *et al.*, 2001; Mast & Givnish, 2002; Crisp & Cook, 2003a; Steane, Wilson & Hill, 2003; Hopper, Chase & Fay, 2006; Rosauer *et al.*, 2009; Cardillo & Pratt, 2013). This is challenging given the region’s subdued topography and apparently simple palaeo-climatic profile (Hopper & Gioia, 2004; Hopper, 2009), since evolutionary models often invoke complex topography as a driver of speciation (e.g. Stebbins & Major, 1965; Linder, 2003; Forest *et al.*, 2007). Recent evaluation of fossil plant diversity in the early Pleistocene in eastern Australia revealed high diversity on a scale similar to that in SWWA, indicating that lack of extinction may have also been a significant driver of plant species richness in SWWA (Sniderman, Jordan & Cowling, 2013; but see also Archer, 1996). For animals, numerous lines of taxonomic and phylogenetic evidence suggest that *in situ* speciation within SWWA has played at most a moderate role in the generation of local diversity (at least within certain lineages; see Section II.3), although in many cases the biogeographic mechanisms involved remain to be fully elucidated. Plio–Pleistocene extinction, at least in some animal lineages (e.g. vertebrates), has also been significant (Archer, 1996).

Dated molecular datasets from which *in situ* speciation in SWWA can be inferred provide compelling evidence for the primacy of the late Miocene and also the Pliocene (i.e. 15 to ~3 Mya) in driving the species-level diversification of animals within south-western Australia. This pattern is evident in frogs and reptiles and several invertebrates (Fig. 6, left panel). However, two datasets also highlight much more recent Pleistocene-age speciation in cockatoos (White *et al.*, 2011) and xeric-adapted lizards (Lee *et al.*, 2013), and at least five datasets also provide fragmentary evidence for another pulse of much earlier *in situ* speciation in the late Oligocene or early Miocene, two of which may be associated with mesic-adapted taxa isolated in more inland areas of the TRP and SCP (Martin *et al.*, 2002; Rix & Harvey, 2012c) (Fig. 6, left panel). Interestingly, there

is little phylogenetic or taxonomic evidence to suggest that *in situ* speciation has played more than a minor role in the generation of local diversity or endemism in either birds or mammals. This is perhaps unsurprising given the potentially late (i.e. Plio–Pleistocene) isolation of most south-western clades, and the relevance of these groups to macro- rather than micro-habitats. The dated datasets available suggest that climate change and increasingly severe aridification during the late Miocene and Pliocene were integral to *in situ* speciation processes and diversification within SWWA. Further, they suggest that these processes largely operated on animal taxa that were already allopatrically isolated west of the Nullarbor divide by the mid-Miocene (see Section III.2). However, teasing apart the mechanisms of diversification in different regions – and determining the relative roles of parapatric or allopatric speciation, local adaptation, extinction, refugial contraction or range expansion (e.g. into or out of the arid zone) – remains a challenging prospect, especially for sister-taxa with broadly overlapping distributions. Nonetheless, a comparison of dated area cladograms (Figs 7 and 8) and additional quantitative datasets reveals several common themes that highlight potential key processes, which are further elucidated in Section IV.

(a) Divergence of ‘basal’ mesic taxa

Firstly, among those clades with species in both the HRP and more xeric inland Provinces (i.e. SCP, TRP), ‘basal’ and early-diverging nodes invariably separate HRP taxa from those found in more xeric regions, with subsequent speciation within more arid-adapted lineages usually occurring during the later Miocene and Pliocene (Figs 7A–C and 8A). This general pattern can be found in both frogs (Barendse, 1984; Maxson & Roberts, 1985; Roberts & Maxson, 1989; Morgan *et al.*, 2007) and multiple lizard families (Jennings *et al.*, 2003; Oliver *et al.*, 2009), suggesting that increasingly severe climatic gradients may have been driving xeric lineage adaptation and/or expansion on the one hand, and mesic sister-lineage contraction on the other, relatively soon after the period 16–14 Mya. By the time many south-western lineages were separated from eastern Australian congeners around the mid-Miocene, the process of aridification was well underway, and south-western animal populations either adapted to the changing conditions or endured range contraction, isolation and/or extinction.

(b) Speciation and distribution of taxa outside the High Rainfall Province

Amongst those taxa with more than one species in the TRP and SCP, dated datasets for frogs (Barendse, 1984; Maxson & Roberts, 1984, 1985; Roberts & Maxson, 1989; Roberts, Maxson & Plummer, 1996; Edwards, 2007; Morgan *et al.*, 2007) and lizards (Jennings *et al.*, 2003; Oliver, Adams & Doughty, 2010; Lee *et al.*, 2013) highlight that speciation in these groups also occurred throughout the later Miocene, Pliocene and even into the Pleistocene, presumably in response to the increased

aridification experienced throughout much of SWWA during these periods (Figs 3 and 6). Inland species from the TRP are often very widespread (e.g. *Aprasia repens*, *Delma fraseri*, *Heleioporus albopunctatus* and *Myobatrachus gouldii*), with strong evidence for relatively recent coastal or sub-coastal speciation in other, more restricted taxa (e.g. *Arenophryne*, *Aprasia*, *Ctenophorus*, *Lerista*) (Figs 6 and 7). Additional quantitative (undated) studies on both reptiles (Rabosky *et al.*, 2004; Melville, Shoo & Doughty, 2008; Edwards, Keogh & Knowles, 2012; Kay & Keogh, 2012) and spiders (Rix *et al.*, 2010) hint at very similar patterns, especially within the coastal and sub-coastal sandplain bioregions south of Shark Bay and west of Israelite Bay. In those regions, extremely diverse faunistic assemblages have clearly experienced a complex mix of climatic (e.g. temperature and precipitation; see online Figs S1 and S2), sea-level and habitat changes since the mid-Miocene (Edwards *et al.*, 2012).

Reptile datasets further suggest that the TRP and SCP may have been important ancestral areas for other more widely distributed Australian clades, which diverged in the Pliocene and Pleistocene (Lee *et al.*, 2013) or even earlier in the Oligocene (Oliver *et al.*, 2010), and subsequently expanded into the arid zone. Other groups like frogs of the genus *Neobatrachus* exhibit broadly overlapping inland distributions, and show further evidence for relatively recent speciation (possibly driven in part by cytogenetic shifts from diploidy to tetraploidy; Mahony, Donnellan & Roberts, 1996; Roberts *et al.*, 1996; Mable & Roberts, 1997; Roberts, 1997*a,b*). By contrast, another suite of taxa have multiple species still mostly restricted to the HRP, having only one or a very few terminal species lineages adapted to more xeric inland regions. These include frogs of the genus *Crinia* (e.g. *C. pseudinsignifera*; Barendse, 1984; Read *et al.*, 2001) (Fig. 8A), lizards within the *Ctenotus labillardieri* species complex (Kay & Keogh, 2012) and spiders of the genus *Raveniella* (e.g. *R. cirrata*; Rix *et al.*, 2010).

(c) Speciation of mesic-adapted taxa

Among more mesic-adapted taxa, many of which are wholly or largely restricted to the HRP, dated divergences reconciled with area cladograms imply a complex history of speciation. Datasets for trapdoor spiders (Cooper *et al.*, 2011), assassin spiders (Rix & Harvey, 2012*c*) and non-biting midges (Martin *et al.*, 2002) suggest that allopatric speciation, *via* Miocene and Pliocene fragmentation and contraction of populations into mesic refugia, has generated multiple short-range endemic species. This is especially so throughout southern and south-eastern coastal or upland regions currently separated by more xeric inter-zones (e.g. Cooper *et al.*, 2011; Rix & Harvey, 2012*c*). The second major pattern seen among more relictual, mesic taxa in SWWA is a series of mostly allopatric, short-range endemic species (usually sister-species) restricted to the southern forested region (i.e. the 'Warren' bioregion; Fig. 9, Model 4), between the Leeuwin-Naturaliste ridge and Albany. This well-documented pattern of the southern Karri forests is characteristic of certain frogs (Wardell-Johnson & Roberts, 1993; Read *et al.*,

2001; Driscoll & Roberts, 2007), freshwater crustaceans (Horwitz & Adams, 2000; Burnham, Koenders & Horwitz, 2012; Gouws & Stewart, 2013), spiders (Rix & Harvey, 2012*c*) and Onychophora (Reid, 2002; Murienne *et al.*, 2013), among others, and relevant divergences can be dated from three independent datasets to either the late Miocene/Pliocene (Rix & Harvey, 2012*c*; Gouws & Stewart, 2013) (Figs 6 and 8C) or throughout the Tertiary (Murienne *et al.*, 2013). Broadly congruent patterns of endemism among freshwater and terrestrial vertebrates and invertebrates suggest a congruence of mechanisms that may be both climatic and edaphic in origin (Wardell-Johnson & Roberts, 1993; Driscoll & Roberts, 2007). However, a third and less tangible pattern characteristic of several lineages (in both the HRP and TRP/SCP) is the presence of multiple, related south-western endemic species, each with largely overlapping distributions. Within the HRP this phylogenetic pattern is characteristic of certain fish (Unmack *et al.*, 2012), frogs (Barendse, 1984; Fig. 8A), freshwater crayfish (Schultz *et al.*, 2009; Fig. 8B) and spiders (Gray, 1981), among others, and dated datasets for *Crinia* and *Cherax* also suggest a late Miocene or Pliocene timeframe for speciation (Fig. 8A, B).

(4) Phylogeographic structure

Phylogeographic studies of intraspecific population structure have revolutionised our understanding of the historical demographic and evolutionary processes that have operated on populations of extant species; each study increasingly sheds more light on recent biogeographic history. For the south-western Australian fauna, dated molecular datasets exploring phylogeographic structure are available for frogs (Edwards, 2007; Edwards, Roberts & Keogh, 2007, 2008; Edwards & Roberts, 2011), reptiles (Levy *et al.*, 2012), crustaceans (Gouws, Stewart & Daniels, 2006, 2010; Gouws & Stewart, 2007; Zofkova & Timms, 2009) and spiders (Cooper *et al.*, 2011). Other dated datasets are available for more widespread southern Australian birds and mammals (Spencer *et al.*, 2001; Toon *et al.*, 2007; Donnellan *et al.*, 2009; Joseph *et al.*, 2009; Salinas *et al.*, 2009; Guay *et al.*, 2010; Dolman & Joseph, 2012; Potter *et al.*, 2012; Austin *et al.*, 2013). In addition to these dated datasets, other quantitative population genetic studies are available for mammals (Neaves *et al.*, 2009), birds (Christidis *et al.*, 2011; Toon, Joseph & Burbidge, 2013; Andersen *et al.*, 2014), reptiles (Levy *et al.*, 2010; Edwards *et al.*, 2012; Kay & Keogh, 2012), frogs (Driscoll, Wardell-Johnson & Roberts, 1994; Driscoll, 1997, 1998*a,b*; Davis & Roberts, 2005), freshwater crayfish (Austin & Ryan, 2002; Nguyen *et al.*, 2002), spiders (Rix *et al.*, 2010), orthopteroid insects (Dadour & Johnson, 1983) and snails (Hill, Johnson & Merrifield, 1983).

Dated phylogeographic studies of south-western Australian taxa (see Fig. 6, right panel; see also Fig. 5, right panel) tell a compelling story of mostly recent, late Pliocene- or Quaternary-age population subdivisions for vertebrates and most invertebrate animal taxa studied. The major progression and intensification of aridification during the Pliocene and Pleistocene, plus the concomitant expansion of

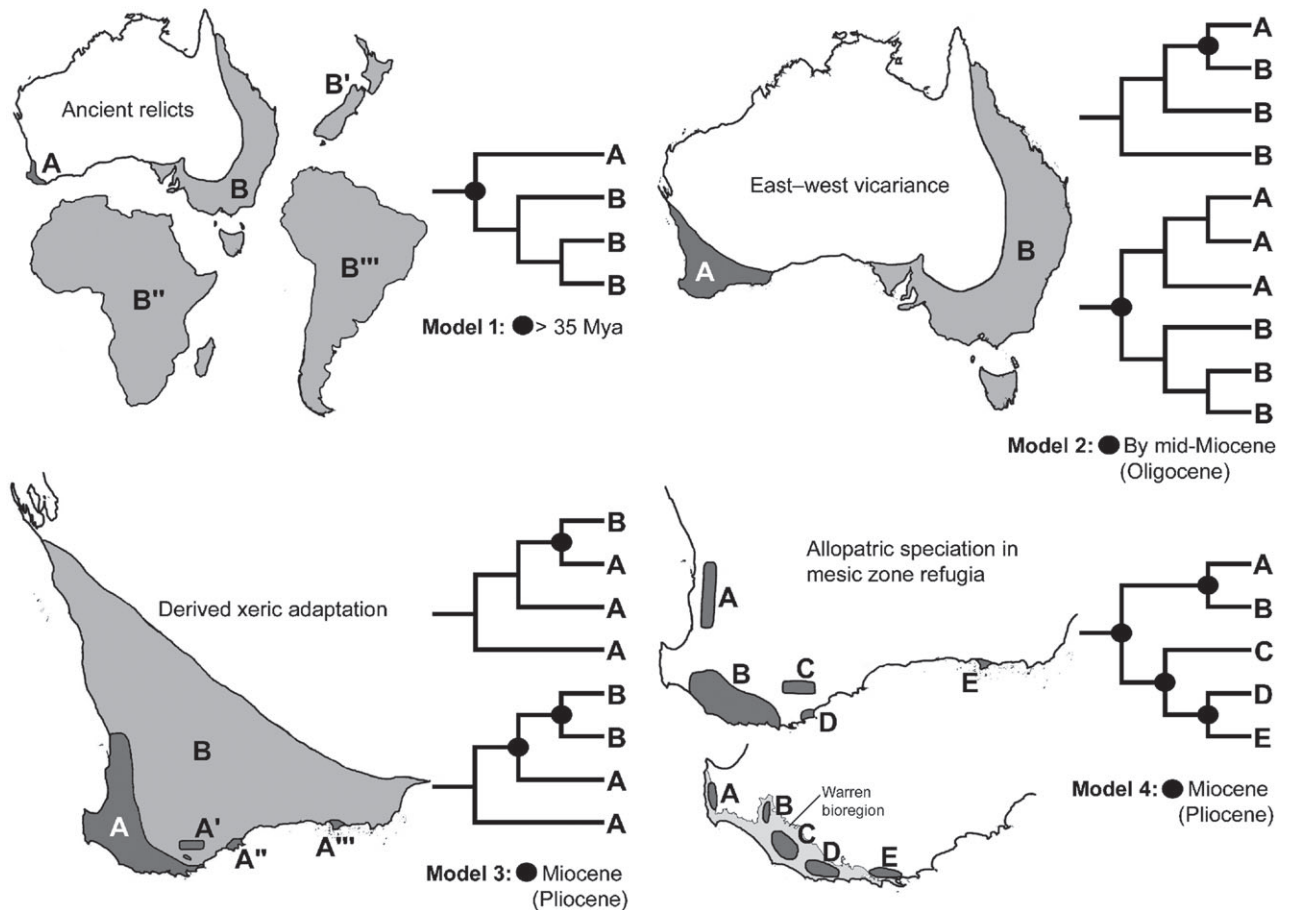


Fig. 9. Schematic dated area cladograms outlining the four testable models of historical biogeography proposed in this study (see Section IV for details). Note that taxon distributions and topologies are hypothetical in each instance. Bracketed geological time periods denote extremes of temporal divergence for Models 2–4. Base map templates and Warren bioregion outline for Model 4 generated by the Atlas of Living Australia (ALA) website (<http://www.ala.org.au/>), reproduced under a Creative Commons Attribution 3.0 Australia Licence.

the arid zone combined with fluctuating glacial cycles and sea levels, have been implicated in phylogeographic divergences in numerous vertebrates, invertebrates and plants throughout Australia (see Byrne, 2007; Byrne *et al.*, 2008, 2011). Many of these intraspecific divergence patterns mirror patterns of *in situ* speciation seen in other lineages (e.g. see Dadour & Johnson, 1983; Hill *et al.*, 1983; Edwards *et al.*, 2008; Cooper *et al.*, 2011), implying a common, underlying geographic and/or climatic (rather than temporal) influence. In other species, especially those that are more vagile or better adapted to xeric habitats, there is a lack of consistent cladogenic pattern across taxa (e.g. Edwards *et al.*, 2012). Correlation of population and species divergences with environmental variation suggest that ecological diversification may underlie recent radiations in xeric-adapted south-western Australian reptiles (Edwards *et al.*, 2012), and such incongruence of patterns may indicate a very important role for ecology in the historical diversification of other south-western Australian taxa. Further research is required to understand these complex processes better.

Finally, several other animal taxa for which molecular data are available show little evidence of significant phylogeographic subdivision throughout their ranges in SWWA, including the mammals *Cercartetus concinnus* (Pestell *et al.*, 2008), *Setonix brachyurus* (Sinclair, 2001), *Smithopsis crassicaudata* (Cooper, Adams & Labridis, 2000) and *Tarsipes rostratus* (Clancy, 2012); the birds *Barnardius zonarius* (Joseph & Wilke, 2006), *Biziura lobata* (Guay *et al.*, 2010), *Gavicalis virescens* (Joseph & Wilke, 2007) and *Malurus splendens* (Kearns *et al.*, 2009); and the spiders *Raveniella cirrata* and *R. peckorum* (Rix *et al.*, 2010). These taxa are significant in that they provide a useful point of comparison against those species with more pronounced phylogeographic structuring, and further highlight key characteristics (e.g. flight, larger size or increased vagility) that may preclude deep population subdivision in SWWA.

(5) Plant data

Although we know much about patterns of plant species richness and endemism in SWWA, we know less about

phylogenetic history (with some notable exceptions, e.g. Chandler *et al.*, 2001; Hopper *et al.*, 2006, 2009; Rosauer *et al.*, 2009; Cardillo & Pratt, 2013). Most plant phylogenetic studies have been designed to test broad patterns of plant evolution and distribution at continental or inter-continental scales, rather than to investigate patterns of species relatedness within SWWA. These data show that the major sclerophyllous families and genera in the south-western Australian flora are representatives of old groups that evolved during the Eocene, Oligocene and Miocene (Hopper & Gioia, 2004), the fossil record indicating that south-western Australian floras may have been more resilient to Pleistocene climatic shifts than those in south-eastern Australia (Dodson, 2001; Sniderman *et al.*, 2013), and that sclerophyllous communities co-occurred with rainforest taxa in SWWA during much of the Tertiary (McLoughlin & Hill, 1996; Byrne *et al.*, 2011). Old relicts of rainforest lineages, now restricted to the HRP, include the Emu Berry (*Podocarpus drouynianus*) and the Albany Pitcher plant (*Cephalotus follicularis*) (Hopper & Gioia, 2004). In Hydatellaceae, a basal family in the angiosperms related to water lilies, five of the 12 species (*Trithuria* syn. *Hydatella*) occur in SWWA (Saarela *et al.*, 2007; Iles *et al.*, 2012).

Dated phylogenetic species-level datasets are available for only a limited number of plant taxa, including eight genera of Haemodoraceae (Hopper *et al.*, 2009), one genus of Droseraceae (Yesson & Culham, 2006), two genera of Chenopodiaceae (Cabrera, Jacobs & Kadereit, 2011), one genus of Fabaceae (Byrne *et al.*, 2001; Byrne, Macdonald & Coates, 2002; Byrne, 2007), one genus of Apiaceae (Kadereit *et al.*, 2008), one genus of Santalaceae (Harbaugh & Baldwin, 2007), one genus of Proteaceae (Cardillo & Pratt, 2013), and a series of co-occurring taxa in six families analysed in Crisp & Cook (2007) (Table 1). However, these datasets do tell a consistent story, with many clades isolated in SWWA by the mid-Miocene, and ongoing speciation thereafter up to and including the Quaternary. Analysis of species divergences in groups with taxa either side of the Nullarbor divide (i.e. *Allocasuarina*, *Banksia*, Mirbeliaceae, Bossiaceae, Restionaceae, *Scaevola*, *Wurmbea*, *Xanthorrhoea*) showed a clustering of divergence dates around 13–14 Mya, consistent with isolation by the Nullarbor Plain – a strong edaphic barrier to plant communities (Crisp & Cook, 2007). A few genera (e.g. *Aotus*, *Chorizema*, *Scaevola*) showed more recent divergences either side of the Nullarbor divide at approximately 2–4 Mya, indicating that they maintained some connection across or around the Nullarbor up until the Plio–Pleistocene (Crisp & Cook, 2007). By contrast, two south-western Australian species of *Santalum* showed evidence for an early divergence from eastern congeners around 32 Mya (Harbaugh & Baldwin, 2007). These results closely mirror patterns seen in animals (see Section III.2; Fig. 5, right panel), highlighting concordant biotic responses during both the mid-Miocene and the Plio–Pleistocene.

In comparison to rainforest lineages that are generally species-poor, most sclerophyllous genera are species-rich (Byrne *et al.*, 2011) and include diverse clades distributed

throughout transitional, semi-arid and arid habitats of Australia, including SWWA. Speciation within these sclerophyllous lineages mostly occurred during the last 15 million years, with available datasets providing evidence of both steady speciation (e.g. Cardillo & Pratt, 2013) and punctuated radiations (e.g. Hopper *et al.*, 2006). For south-western Australian taxa, phylogenies show major endemic speciation events in the *Dryandra* lineage of *Banksia* (Mast, 1998; Mast & Givnish, 2002; Cardillo & Pratt, 2013), *Allocasuarina* (Steane *et al.*, 2003), *Conostylis* (Hopper *et al.*, 2006) and Mirbeliaceae and Bossiaceae (Crisp & Cook, 2003b; Orthia *et al.*, 2005). Hopper *et al.* (2009) argued for periods of accelerated diversification in the Haemodoraceae and Conostyloideae in the mid-Miocene and Plio–Pleistocene, while Byrne (2007) highlighted recent Pleistocene speciation in several *Acacia*. Evidence for such recent *in situ* plant speciation is in stark contrast to most (but not all) animal data, the latter of which generally fail to infer Quaternary speciation (Fig. 6, left panel). This discrepancy may be important in understanding and testing differential patterns of plant *versus* animal diversity in SWWA, although recent studies suggest that a lack of extinction during Pleistocene climatic cycles may be a primary explanation for the maintenance of plant species richness in SWWA (Sniderman *et al.*, 2013).

Phylogeographies for south-western Australian plant species show significant intraspecific sub-structuring and complex patterns of haplotype diversity, indicative of localised persistence throughout their ranges (Byrne, 2008). Dated phylogeographies are available for species in at least five families of plants (see Table 1), and many studies on widespread species have identified divergent lineages that separated during the mid-Pleistocene, e.g. *Eucalyptus loxophleba* (Byrne & Hines, 2004), *Acacia acuminata* (Byrne *et al.*, 2002), *Santalum spicatum* (Byrne, Macdonald & Brand, 2003) and *Calothamnus quadrifidus* (Nistelberger *et al.*, 2014). Older intraspecific divergences in the late Pliocene have also been noted in the widespread *E. marginata* (Wheeler & Byrne, 2006) and the restricted and disjunct *Lambertia orbifolia* (Byrne, Macdonald & Coates, 1999). The timings of intraspecific divergence events in plants are roughly concordant with the Plio–Pleistocene dates inferred for animals (Fig. 6, right panel; see also Byrne *et al.*, 2008, 2011), although most plant taxa exhibit a shallower history of population subdivision relative to less vagile reptiles, frogs and invertebrates.

IV. TESTABLE MODELS OF HISTORICAL BIOGEOGRAPHY IN SOUTH-WESTERN AUSTRALIA

A primary aim of this paper is to compile dated and otherwise quantitative phylogenetic or population genetic datasets to generate testable models of historical biogeography for the south-western Australian fauna. Our comparison of temporally and/or spatially congruent divergences among multiple co-distributed taxa (Figs 5–8) provides a framework

Table 1. Summary of dated datasets and a selection of other quantitative (undated) studies relevant to south-western Australian plant taxa. Inter-specific phylogenies (i.e. ‘species’) are distinguished from intra-specific phylogeographies (i.e. ‘populations’), and dated studies with estimates of time since divergence are separated from undated studies. Biogeographic patterns are ordered and refer to those outlined in Section II

Taxa		Analysis	Biogeographic pattern/s	References
Dated studies				
Apiaceae	Tribe Saniculeae	Species	E–W lineages	Kadereit <i>et al.</i> (2008)
Casuarinaceae	<i>Allocasuarina</i>	Species	E–W lineages	Crisp & Cook (2007); see also Steane <i>et al.</i> (2003)
Colchicaceae	<i>Wurmbea</i>	Species	E–W lineages	Crisp & Cook (2007); see also Vinnersten & Reeves (2003)
Fabaceae	Mirbelieae/Bossiaeeae	Species	E–W lineages	Crisp & Cook (2007); see also Crisp & Cook (2003 <i>b</i>) and Orthia <i>et al.</i> (2005)
Goodeniaceae	<i>Scaevola</i>	Species	E–W lineages	Crisp & Cook (2007); see also Howarth <i>et al.</i> (2003)
Restionaceae	SWWA Restionaceae	Species	E–W lineages	Crisp & Cook (2007); see also Briggs <i>et al.</i> (2000)
Xanthorrhoeaceae	<i>Xanthorrhoea</i>	Species	E–W lineages	Crisp & Cook (2007); see also Givnish <i>et al.</i> (2005)
Droseraceae	<i>Drosera</i>	Species	E–W lineages/ <i>in situ</i> speciation	Yesson & Culham (2006)
Haemodoraceae	SWWA Haemodoraceae	Species	E–W lineages/ <i>in situ</i> speciation	Hopper <i>et al.</i> (2006, 2009)
Proteaceae	<i>Banksia</i>	Species	E–W lineages/ <i>in situ</i> speciation	Crisp & Cook (2007); Cardillo & Pratt (2013); see also Mast (1998); Mast & Givnish (2002) and Ladiges <i>et al.</i> (2012)
Santalaceae	<i>Santalum</i>	Species	E–W lineages/ <i>in situ</i> speciation	Harbaugh & Baldwin (2007)
Chenopodiaceae	SWWA Camphorosmeae	Species	<i>In situ</i> speciation	Cabrera <i>et al.</i> (2011)
Fabaceae	<i>Acacia acuminata</i> vs. <i>A. oldfieldii</i>	Species	<i>In situ</i> speciation	Byrne <i>et al.</i> (2002) and Byrne (2007)
Fabaceae	<i>A. lobulata</i> vs. <i>A. verrucula</i>	Species	<i>In situ</i> speciation	Byrne <i>et al.</i> (2001) and Byrne (2007)
Fabaceae	<i>A. sciophanes</i> vs. <i>A. anfractuosa</i>	Species	<i>In situ</i> speciation	Byrne <i>et al.</i> (2001) and Byrne (2007)
Fabaceae	<i>A. acuminata</i>	Populations	Phylogeographic structure	Byrne <i>et al.</i> (2002) and Byrne (2007)
Fabaceae	<i>A. verrucula</i>	Populations	Phylogeographic structure	Byrne <i>et al.</i> (2001) and Byrne (2007)
Hemerocallidaceae	<i>Stypandra glauca</i>	Populations	Phylogeographic structure	Tapper <i>et al.</i> (2014 <i>b</i>)
Myrtaceae	<i>Calothamnus quadrifidus</i> complex	Populations	Phylogeographic structure	Nistelberger <i>et al.</i> (2014)
Myrtaceae	<i>Eucalyptus caesia</i>	Populations	Phylogeographic structure	Byrne (2007) and Byrne & Hopper (2008)
Myrtaceae	<i>E. loxophleba</i>	Populations	Phylogeographic structure	Byrne & Hines (2004); Byrne (2007); see also Hines & Byrne (2001)
Myrtaceae	<i>E. marginata</i>	Populations	Phylogeographic structure	Wheeler & Byrne (2006); Byrne (2007); see also Byrne (2008)
Myrtaceae	<i>Kunzea pulchella</i>	Populations	Phylogeographic structure	Tapper <i>et al.</i> (2014 <i>a</i>)
Proteaceae	<i>Lambertia orbifolia</i>	Populations	Phylogeographic structure	Byrne (2007); see also Byrne <i>et al.</i> (1999)
Santalaceae	<i>Santalum spicatum</i>	Populations	Phylogeographic structure	Byrne <i>et al.</i> (2003); Byrne (2007); see also Byrne (2008)
Undated studies				
Hydatellaceae	<i>Trithuria</i>	Species	Ancient relicts	Saarela <i>et al.</i> (2007) and Iles <i>et al.</i> (2012)
Goodeniaceae	SWWA Goodeniaceae	Species	E–W lineages/ <i>in situ</i> speciation	Jabaily <i>et al.</i> (2012)
Myrtaceae	<i>Beaufortia</i> suballiance	Species	E–W lineages/ <i>in situ</i> speciation	Brown <i>et al.</i> (2001)
Myrtaceae	<i>E.</i> subgenus <i>Eucalyptus</i>	Species	E–W lineages/ <i>in situ</i> speciation	Ladiges <i>et al.</i> (2010); see also Ladiges <i>et al.</i> (2012)
Myrtaceae	<i>Kunzea</i>	Species	E–W lineages/ <i>in situ</i> speciation	de Lange <i>et al.</i> (2010)

Table 1. Continued

Taxa		Analysis	Biogeographic pattern/s	References
Chenopodiaceae	Salicornioideae/ <i>Halosarcia</i>	Species	<i>In situ</i> speciation	Shepherd <i>et al.</i> (2004)
Elaeocarpaceae	<i>Tetradlea</i>	Species	<i>In situ</i> speciation	Butcher <i>et al.</i> (2007)
Fabaceae	<i>Daviesia</i>	Species	<i>In situ</i> speciation	Crisp & Cook (2003c) and Rosauer <i>et al.</i> (2009)
Fabaceae	<i>Gastrolobium</i>	Species	<i>In situ</i> speciation	Chandler <i>et al.</i> (2001)
Fabaceae	<i>Oxylobium</i>	Species	<i>In situ</i> speciation	Crisp & Cook (2003a)
Lamiaceae	<i>Pityrodia scabra</i>	Species/populations	<i>In situ</i> speciation	Shepherd <i>et al.</i> (2013)
Myrtaceae	<i>E. diptera</i> complex	Species	<i>In situ</i> speciation	Burgman (1985)
Myrtaceae	<i>E.</i> subgenus <i>Eudesmia</i>	Species	<i>In situ</i> speciation	Gibbs <i>et al.</i> (2009)
Myrtaceae	<i>Eremaea</i>	Species/populations	<i>In situ</i> speciation	Coates & Hnatiuk (1989)
Myrtaceae	<i>Melaleuca uncinata</i> complex	Species	<i>In situ</i> speciation	Broadhurst <i>et al.</i> (2004)
Stylidiaceae	<i>Stylidium carcifolium</i> complex	Species	<i>In situ</i> speciation	Coates <i>et al.</i> (2003)
Fabaceae	<i>A. saligna</i> complex	Populations	Phylogeographic structure	Millar <i>et al.</i> (2011)
Myrtaceae	<i>E. angustissima</i> complex	Populations	Phylogeographic structure	Elliott & Byrne (2004)
Myrtaceae	<i>E. gomphocephala</i>	Populations	Phylogeographic structure	Nevill <i>et al.</i> (2014)
Myrtaceae	<i>E. kochii</i> complex	Populations	Phylogeographic structure	Byrne & Macdonald (2000)
Rutaceae	<i>Boronia inornata</i>	Populations	Phylogeographic structure	Burgman (1985)

SWWA, south-western Australian.

upon which we develop four working hypotheses to explain the diversity and diversification of the south-western Australian fauna (Fig. 9). Our goal here is to provide a temporal and spatial perspective on major patterns of distribution and diversification. This process effectively adopts a phylogenetic species concept, but in many cases this is matched with traditional biological or morphological characters used to define species, e.g. call structures in frogs (Roberts & Wardell-Johnson, 1995) or genitalic differences in millipedes (Edward & Harvey, 2010; Wojcieszek & Simmons, 2011). We also speculate – *post hoc* – as to what mechanisms may have fundamentally driven speciation and/or divergence among populations.

Our four models are graphically illustrated in Fig. 9, and each provides a spatial, temporal and topological perspective on patterns of speciation or divergence. These models are further outlined in detail below, supporting evidence being given at three levels: (i) primary, dated, quantitative datasets; (ii) otherwise quantitative (but undated) datasets; and (iii) additional candidate lineages that may have diverged under each model, but for which only qualitative data exist. A summary of fossil data for SWWA is also provided, given the importance of fossil taxa for the temporal calibration of phylogenies.

(1) Ancient relicts of the High Rainfall Province

A minority of the higher animal taxa (i.e. genera and families) endemic to SWWA belong to ancient Gondwanan or even Pangaean lineages, i.e. they diverged from extant sister-taxa before the final separation of Australia from Antarctica in the early Oligocene (>35 Mya) (see Model 1 in Fig. 9). Their sister-lineages may occur on other former Gondwanan or Pangaean land masses, or be currently distributed in south-eastern Australia (but with more distant relatives on

other continents). Most ancient relictual taxa will also be restricted to the HRP – and especially the Warren bioregion within that Province (see Fig. 9) – due to the buffered, mesic climate of the region. For example, the three species in the harvestman genus *Karripurcellia* are endemic to a small area of the Warren bioregion surrounding Pemberton (Giribet, 2003). The closest relatives of *Karripurcellia* are found in New Zealand, and the inferred divergence date for this lineage is in the Mesozoic (Giribet *et al.*, 2009, 2012).

(a) Relevant dated datasets

Lepidogalaxiid fish (*Lepidogalaxias*; Near *et al.*, 2012; Fig. 4A); parastacid crayfish (*Engaewa*; Schultz *et al.*, 2009; see also Crandall *et al.*, 1999; Horwitz & Adams, 2000; Burnham *et al.*, 2012; Fig. 4G); pettalid harvestman (*Karripurcellia*; Giribet *et al.*, 2009, 2012; see also Boyer *et al.*, 2007; Boyer & Giribet, 2007); and peripatopsid onychophorans (*Kumbadjena*–*Occiperipatoides* lineage; Muriene *et al.*, 2013) (Fig. 5, left panel).

(b) Additional quantitative datasets

Chelid turtles (*Pseudemydura*; Shaffer *et al.*, 1997; Georges *et al.*, 1998); myobatrachid frogs (*Spicospina*; Read *et al.*, 2001; see also Roberts *et al.*, 1997; Edwards & Roberts, 2011; Fig. 4C); migid trapdoor spiders (*Moggridgea*; Griswold & Ledford, 2001; Cooper *et al.*, 2011; Fig. 4I); and carthaeid moths (*Carthaea*; Zwick *et al.*, 2011).

(c) Other candidate lineages

Phalangiid harvestman (*Hesperopilio*; Shear, 1996; Shultz & Cekalovic, 2006; Groh & Giribet, 2014);

pseudotyranochthoniid pseudoscorpions (*Pseudotyranochthonius*; Harvey & Štáhlavský, 2009); pionid water mites (*Larri*; Harvey, 1998); and meropeid scorpion flies (*Austromerope*; Abbott *et al.*, 2007; Machado *et al.*, 2013; Fig. 4L).

(2) South-western endemism due to early to mid-Miocene vicariance

For numerous lineages now endemic to south-western Australia (i.e. a few higher taxa, but mostly intra-generic clades or species), progressive aridification, plus marine incursions and eventual uplift and exposure of the calcareous Nullarbor divide throughout the early and mid-Miocene resulted in the eventual separation of south-western taxa from related forms in south-eastern Australia (see Model 2 in Fig. 9). Although some animal data hint at an extended process of isolation up until the later Miocene (~8 Mya) or earlier isolation in the Oligocene, this model is relatively explicit in proposing that vicariant climatic or edaphic boundaries were in place for most endemic reptile, frog, fish and less vagile invertebrate lineages by the mid-Miocene ~12–14 Mya.

(a) Relevant dated datasets

Honey possum (*Tarsipes*; Bininda-Emonds *et al.*, 2007; see also Kavanagh *et al.*, 2004); elapid snakes (*Elapognathus*, *Neelaps (calonotus)*; Sanders *et al.*, 2008); pygopodid lizards (*Aprasia*, *Delma*, *Pletholax*; Jennings *et al.*, 2003); myobatrachid frogs (*Crinia*, *Geocrinia*, *Heleioporus*, *Limnodynastes*, *Metacrinia–Myobatrachus–Arenophryne (MMA)* lineage, *Pseudophryne*; Barendse, 1984; Roberts & Maxson, 1985, 1986, 1989; Morgan *et al.*, 2007; see also Read *et al.*, 2001); hylid frogs (*Litoria*; Roberts & Maxson, 1985; Burns & Crayn, 2006); freshwater fish (*Galaxiella*, *Nannoperca*; Unmack *et al.*, 2011, 2012); parastacid crayfish (*Cherax*; Munasinghe *et al.*, 2004; Schultz *et al.*, 2009; see also Austin & Knott, 1996); archaeid spiders (*Zephyrarchaea*; Rix & Harvey, 2012c; Fig. 4H); and chironomid midges (*Stictocladus*; Krosch & Cranston, 2013) (Fig. 5). For a summary of relevant dated plant datasets, see Table 1 and Crisp & Cook (2007).

(b) Additional quantitative datasets and other candidate lineages

A large number of southern Australian animal genera have endemic lineages in south-western Australia, and listing all such examples is beyond the scope of this study. Ordinal taxa with key lineages that may have diverged under this model include squamate reptiles, testudine tortoises, siluriform fish and most orders of terrestrial arthropods. This model of divergence may also be relevant to two monotypic genera of mammals (*Parantechinus*, *Setonix*) and birds (*Purpurecephalus*, *Quoyornis*; see also Loynes, Joseph & Keogh, 2009; Christidis *et al.*, 2011) endemic to SWWA, although data are largely lacking except for *Purpurecephalus* (Schweizer *et al.*, 2011, 2012).

(c) Remarks

This classic model of the Miocene ‘islandisation’ of SWWA is developed on a suite of divergence estimates from both vertebrate and invertebrate taxa, and is explicit in identifying the mid-Miocene as an important climactic phase in the final dissolution of remnant east–west connectivity and gene flow. However, this model is clearly an inappropriate working hypothesis for most mammals and birds (and possibly other highly vagile taxa, e.g. see Hawlitschek *et al.*, 2011), given the apparent primacy of the Plio–Pleistocene in generating patterns of south-western endemism in these groups (see Fig. 5, ‘Tier 2 divergences’).

(3) Derived xeric adaptation

This model of *in situ* speciation during the Miocene – an extension to ‘Hypothesis 1’ of Byrne *et al.* (2011) – predicts that for lineages now widespread throughout SWWA, basal or early-branching clades are restricted to the HRP, with derived species occurring in more xeric inland habitats of the TRP or SCP (see Model 3 in Fig. 9). This model explains patterns in clades with multiple basal taxa in the HRP and only one or a very few xeric-adapted species (see upper cladogram for Model 3 in Fig. 9), the latter diverging from HRP taxa relatively late, in the very late Miocene or Pliocene (Figs 7B and 8A). This model also explains patterns in clades with only one or a very few basal species in the HRP and an equal or greater diversity of species in more xeric regions (see lower cladogram for Model 3 in Fig. 9), indicating that for another subset of south-western taxa, an initial first major pulse of speciation during the mid-Miocene (i.e. 15–12 Mya) was associated with the early divergence of more arid-adapted lineages from their plesiomorphic, mesic-adapted sister-taxa (Fig. 7A, C). We propose that for both scenarios, a long period of Miocene range contraction (with or without *in situ* mesic zone speciation) was broken by the evolution, in the Miocene or Pliocene, of more arid-adapted species that then underwent significant range expansion. This was possibly in response to the transition to winter rainfall patterns and the rapid climatic changes that occurred during the Pliocene (Byrne *et al.*, 2008).

(a) Relevant dated datasets

Diplodactylid lizards (*Diplodactylus*; Oliver *et al.*, 2009; see also Oliver, Hutchinson & Cooper, 2007); pygopodid lizards (*Aprasia*; Jennings *et al.*, 2003); and myobatrachid frogs (*Crinia*, *Heleioporus*, *Metacrinia–Myobatrachus–Arenophryne (MMA)* clade; Barendse, 1984; Maxson & Roberts, 1985; Roberts & Maxson, 1989; Edwards, 2007; Morgan *et al.*, 2007; see also Read *et al.*, 2001) (Figs 6, 7A–C and 8A).

(b) Additional quantitative datasets

Scincid lizards (*Ctenotus*; Kay & Keogh, 2012) and micropholcommatid spiders (*Raveniella*; Rix *et al.*, 2010).

(c) Other candidate lineages

Although specifying additional candidate lineages for this model in the absence of a phylogeny is difficult, derived xeric adaptation could be considered a null hypothesis for any of the many lineages in SWWA with endemic species restricted to the HRP and congeners found in the TRP or SCP.

(4) Allopatric speciation in mesic zone refugia

This model of *in situ* speciation predicts that susceptible mesic-adapted lineages experienced allopatric speciation during the mid-late Miocene and Pliocene as a result of the vicariant isolation and contraction of formerly continuous (mesic) habitats (see Model 4 in Fig. 9). In SWWA, this model is especially relevant to taxa from the HRP (especially the Warren bioregion) and the southern SCP, where numerous mesic refugia can still be found in forested, montane and coastal regions (Fig. 8C, D). It is also relevant to more inland taxa, isolated on habitat ‘islands’ (e.g. granite outcrops, mountain peaks). Increasingly severe aridification is proposed to have driven population contraction into isolated refugia, with persistent xeric barriers driving subsequent allopatric speciation.

(a) Relevant dated datasets

Archaeid spiders (*Zephyrarchaea*; Rix & Harvey, 2012c; Fig. 4H); migid spiders (*Moggridgea*; Cooper *et al.*, 2011; Fig. 4I); amphispodid isopods (*Amphisopus*; Gouws & Stewart, 2013); chironomid midges (*Archaeochlus*; Martin *et al.*, 2002); and peripatopsid onychophorans (*Kumbadjena*; Murielle *et al.*, 2013) (Figs 6 and 8C, D).

(b) Additional quantitative datasets

Myobatrachid frogs (*Geocrinia* (*rosea* complex); Read *et al.*, 2001; Driscoll & Roberts, 2007; see also Wardell-Johnson & Roberts, 1993); stiphidiid spiders (*Baiami*; Gray, 1981, 1992); and parastacid crayfish (*Engaewa*; Horwitz & Adams, 2000; Burnham *et al.*, 2012).

(c) Other candidate lineages

Idiopid spiders (*Cataxia*; Main, 1985); garypid pseudoscorpions (*Synsphyronus*; Harvey, 1987, 1996, 2011); pseudotyranochthoniid pseudoscorpions (*Pseudotyranochthonius*; Harms & Harvey, 2013); iulomorphid millipedes (*Atelomastix*, *Samichus*; Edward & Harvey, 2010) and bothriembryontid snails (*Bothriembryon*; Iredale, 1939; Breure & Whisson, 2012).

(5) Other models?

Numerous other patterns of diversity can be seen among the south-western Australian biota, where explicit models of historical biogeography cannot be inferred due to the lack of appropriate quantitative data. For example, many lineages show a diversity of co-occurring taxa in both the HRP and/or SCP/TRP, including *Neobatrachus* frogs (a complex of four or five sympatric species), numerous speciose reptile genera

of the sandplains north and south of Geraldton (e.g. *Lerista*; Skinner *et al.*, 2008; Skinner, 2010), and *Cherax* freshwater crayfish in the HRP, among many others (Figs 7D and 8B). Various processes may be involved in generating these patterns, including polyploidy (Mahony *et al.*, 1996; Roberts *et al.*, 1996; Mable & Roberts, 1997; Roberts, 1997a,b) or complex interactions between climate variation and substrate heterogeneity (Edwards *et al.*, 2012; Levy *et al.*, 2012). Reptile datasets also hint at the potential importance of the SCP and TRP as ancestral areas for lineages that subsequently expanded into the arid zone (Skinner, 2010; Lee *et al.*, 2013). Listing or discussing all such patterns and possible processes is beyond the scope of this review, but any future testable interpretation must have a strong foundation in appropriate phylogenetic dating or ecological and phenotypic approaches to analysing the biogeographic signal.

(6) Fossils

Dated fossils are of great value in calibrating molecular clocks for phylogenetic or character evolution studies, and have been used in that context in SWWA for studies on *Banksia* evolution (Cardillo & Pratt, 2013) and floral evolution in relation to fire (Lamont & He, 2012). Unfortunately, the fossil record for fauna from SWWA is relatively limited. Martin (2008) reported fossils from a number of insect groups, including Coleoptera, Blattodea, Hemiptera, Mecoptera, Neuroptera, Grylloblattodea and Diptera dating back to the early Jurassic (~190–200 mya), allowing some possibility of future dating of hexapod lineages. There are also a number of vertebrate fossils from SWWA, although these are limited to deposits in Pleistocene-aged caves in the Leeuwin-Naturaliste Block (e.g. Prideaux *et al.*, 2010). These deposits report either extant taxa (e.g. frogs and reptiles; Tyler, 1994; Hollenshead, Mead & Swift, 2011) or a mix of modern and recently extinct mammal species, with arguments about the relative roles of climate variation, initial human invasions and post-European impacts on fauna (Prideaux *et al.*, 2010). Mid-Pleistocene vertebrate fossils (primarily mammals, one lizard species) have also been reported from cave deposits on the central Nullarbor Plain (Prideaux *et al.*, 2007), but are uninformative in the context of dating any available south-western Australian phylogenies. For some vertebrate groups (e.g. frogs and mammals), fossil deposits across Australia offer some opportunities for calibration of deeper cladogenic events with implications for the south-western Australian fauna. The Riversleigh deposits in Queensland (Oligocene–Miocene), similar deposits in the adjacent Northern Territory and from Murgon in south-eastern Queensland (early Eocene) all contain frog fossils mostly referable to modern genera (Tyler, 1994), although none of this material has previously been used to calibrate trees (e.g. Read *et al.*, 2001) or has been relevant to phylogenetic analyses of anurans from SWWA (e.g. Morgan *et al.*, 2007).

Despite the relative paucity of data, there is strong potential for plant and animal fossils to be used for phylogenetic dating, and to generate new insights into the evolution of the

south-western Australian biota. There is a good spread of fossil ages for animals (e.g. frogs: Pleistocene to early Eocene; Tyler, 1994), dates are available for the evolution of specific character states in plants (Lamont & He, 2012) and there is a sophisticated capacity to reconstruct historical environments used by fossil faunas (Prideaux *et al.*, 2007). That material must now be expanded, for example by using the remarkably diverse invertebrate fossil fauna reported by Martin (2008), and married to targeted, phylogenetic data.

V. FUTURE DIRECTIONS

(1) Research priorities

In this review we have highlighted congruent spatial and temporal patterns of divergence among co-occurring taxa in SWWA, to elucidate the history of the region's biota. There is a remarkably small amount of data available for plants, which is surprising given the incredible floristic diversity of SWWA, the relatively comprehensive level of taxonomic understanding of the region's flora and the concomitant volume of literature dedicated to explaining this diversity. And while we now have a good understanding of the spatial distribution of plant species richness and endemism (Hopper & Gioia, 2004), plus patterns of evolution in a limited array of taxa (e.g. Crisp & Cook, 2007; Rosauer *et al.*, 2009; Cardillo & Pratt, 2013), we still do not truly understand evolutionary history in most plant groups – recently exemplified by an analysis of spatial patterns of orchid diversity (Phillips *et al.*, 2011). That study used species occurrence data to infer numerous evolutionary mechanisms generating diversity, but had no underlying quantitative phylogenetic support. Clearly, understanding these sorts of evolutionary problems requires: (i) a more extensive application of quantitative phylogenetic methods; (ii) rigorous taxon sampling of endemic lineages to uncover a more complete picture of relationships and to resolve finer-scale patterns (e.g. Cardillo & Pratt, 2013); and (iii) the use of new or evolving approaches in biogeography to test adequately more complex ecological models of speciation and population divergence (e.g. Edwards *et al.*, 2012; see also Schluter, 2009 for review). This seems especially important given the likely discordance between processes of plant and animal speciation in SWWA, in both space and time (see Anacker & Strauss, 2014).

For animals, although the available data highlight a number of key mechanisms that may have been critical in driving patterns of diversity in SWWA, much also remains to be understood. The datasets we have analysed are strongly biased towards vertebrates, which give a prejudiced view of patterns of speciation in SWWA. Clearly, more studies on south-western Australian invertebrate taxa are required, across all phyla. The available data for invertebrates show some compelling evidence for fine-scale differentiation and local endemism, within topographically diverse areas (e.g. the Stirling Range; Cooper *et al.*, 2011; Rix & Harvey, 2012c) as well as in comparatively featureless landscapes (e.g. the

Swan Coastal Plain; Rix *et al.*, 2010). This propensity for short-range endemism in invertebrates (Harvey, 2002) may be related to limited dispersal capacity or micro-allopatry driven by substrate variation, the latter of which is considerable in SWWA (see online Fig. S3). Although there is little empirical evidence for either claim in invertebrates, empirical data for dispersal in vertebrates suggest that while some taxa disperse widely and show little genetic differentiation (Davis & Roberts, 2005), others exhibit more limited dispersal (Driscoll, 1998a, b; Edwards & Roberts, 2011) that in some cases can be explained by substrate variation (Edwards *et al.*, 2012; Levy *et al.*, 2012). Similarly, given the floristic diversity in SWWA and the abundance of speciose endemic plant clades, co-evolutionary studies of mutualistic, pollinating or phytophagous animal taxa may be informative. The major insect orders are perhaps the least understood and certainly the most diverse of all terrestrial fauna in SWWA, with important endemic radiations of phytophagous lineages (e.g. Miridae; Schuh & Weirauch, 2010) and strong pollinator fidelity in certain plant taxa (e.g. Orchidaceae; Gaskett, 2011).

The four models developed and summarised herein are necessarily based on a relatively small number of dated or otherwise quantitative datasets for a relatively small selection of taxa. While we are confident that these hypotheses are robust and well supported by available data, further testing is required to demonstrate the generality or otherwise of these models and potentially clarify relevant spatial or temporal details and variants. To this end, we have outlined relevant candidate taxonomic groups in Section IV that we expect will be informative in testing patterns of historical biogeography in SWWA. For example, peripatopsid onychophorans of the genus *Kumbadjena* (see Reid, 2002; Muriene *et al.*, 2013; Fig. 4O) are known to be highly diverse in the southern HRP, and further exploring their interspecific relationships and the timing of divergences will be valuable in clarifying patterns of speciation in the Warren bioregion. A secondary focus should also be taxa which exhibit idiosyncratic biogeographic patterns, or patterns otherwise not prescribed by the models outlined in Section IV. For example, diverse reptile communities in sandplain habitats along the Indian Ocean and Southern Ocean coastlines exhibit complex patterns of diversity at varying spatial scales, and these offer great potential for future research.

In this review we have presented an optimistic view of the value of phylogenetic analysis in understanding patterns of diversity, evolution and biogeography. Yet the foundation for an understanding of any biota is inevitably collection-based and taxonomic, in that relevant collections and taxonomic analyses are required to adequately inform and initiate biogeographic studies on specific taxa. In SWWA – as across Australia and many other regions of the world – a huge proportion of the terrestrial fauna remains undescribed at even the alpha taxonomic level, and we believe that a holistic appreciation of biogeographic patterns and processes in the region cannot begin to be achieved until this shortfall is addressed. However, a huge amount of phylogenetic work

can still be done on many well-known taxa – as well as on relatively poorly known groups with the assistance of DNA barcoding (e.g. Puillandre *et al.*, 2012) – and we feel strongly that these molecular phylogenetic studies should also lead to tangible taxonomic outcomes in their own right. Although there has always been a lag between ‘clade discovery’ *via* phylogeography and ‘clade documentation’ *via* taxonomy (Rix *et al.*, 2010), molecular studies are increasingly testing and refining species boundaries using ever more sophisticated methods, which themselves can be tested in this way (Camargo *et al.*, 2012). Molecular data must also be combined, where possible, with conventional morphological, behavioural and ecological characters. This will facilitate an accurate evaluation of species status (Edwards & Knowles, 2014) and avoid over- or under-splitting based exclusively on molecular data (e.g. Chappell, Treweek & Morgan-Richards, 2011; Marshall *et al.*, 2011).

(2) Conservation

Historical climate change and the responses of taxa to this change have been integral in generating patterns of diversity in south-western Australian taxa. Biotic responses to this climate change have been range contraction, population subdivision or extinction, as well as adaptation, speciation and range expansion. But what will happen in the future? Clearly, these processes may be repeated, and historical responses provide some indication of potential future responses of species to climate change (Moritz & Agudo, 2013). Quantitative biogeographic studies on south-western Australian taxa have the potential to provide crude yet nonetheless informative insights into a number of factors of conservation significance, including (but not limited to): (i) the location of possible habitat refugia (Keppel *et al.*, 2012); (ii) the identification of regions with the highest phylogenetic diversity or significant phylogenetic turnover (Rosauer *et al.*, 2009, 2013); (iii) the identification of short-range endemic taxa of conservation significance (Harvey *et al.*, 2011); (iv) the ability of species to disperse and track their ecological niches; (v) the capacity for species to tolerate wide or variable environmental conditions; and (vi) the identification of key ecological or physiological transitions necessary for the evolution of xeric-adapted lineages. Traditionally, systematics and biogeography have intersected with conservation biology in a rather poorly defined and usually indirect way, despite the significant insights these fields can offer in the face of severe anthropogenic change. In SWWA – with its high biodiversity, largely cleared landscapes and the predicted severity of climate change in the region (Smith *et al.*, 2000; IOCI, 2002; IPCC, 2007; Asseng & Pannell, 2013) – we envisage immediate benefit to conservation decision-makers from the discovery and description of new taxa (e.g. Oliver *et al.*, 2010) and short-range endemic species (e.g. Edward & Harvey, 2010; Harvey *et al.*, 2011), and from the identification of macro- and micro-refugia (Keppel *et al.*, 2012; Moritz & Agudo, 2013) and regions of highest phylogenetic endemism (Rosauer *et al.*, 2009). Certainly, with ever-increasing pressures on Australia’s only global biodiversity hotspot,

conservation management and planning must be informed by as much data as possible, and historical biogeographic studies bring another important dimension to this urgent process.

VI. CONCLUSIONS

(1) Our review demonstrates that we know much about the historical biogeography of animals in SWWA, due to an accumulation of dated quantitative phylogenetic studies over the last three decades. Available animal datasets are still strongly biased towards vertebrates, although invertebrate phylogenies for multiple lineages are beginning to provide comparative data.

(2) Quantitative biogeographic studies on south-western Australian animals provide evidence for at least four main mechanisms driving patterns of endemism in SWWA. Relictualism can be implicated in the distributions of at least several seemingly ancient taxa in the HRP. Vicariant isolation of lineages west of the Nullarbor divide has been fundamental in generating regional endemism, both during the early-mid Miocene and the Plio–Pleistocene. *In situ* speciation has generated significant endemic diversity in select lineages, especially less vagile fish, frogs, reptiles and invertebrates, while more recent population subdivision has led to lineage divergence in both less vagile and more widely distributed organisms.

(3) Review of the mechanisms driving divergence patterns has enabled us to derive testable models of historical biogeography for SWWA. From the data available we propose four such models to explain some of the strongest patterns seen among south-western Australian animal taxa. These models are explicit in providing a spatial, temporal and topological perspective on patterns of speciation or divergence, and all highlight the importance of post-Oligocene climate change in driving range contraction or separation (Models 1, 2, 4), as well as xeric adaptation (Model 3) in different taxa.

(4) The fauna of SWWA is rich in poorly studied lineages or clades for which dated phylogenetic data remain to be gathered or assessed. Numerous candidate lineages worthy of further study can be identified given what we know of their taxonomy, distributions or relationships, and it is critical that these taxa be studied in the future to help refine our understanding of the historical biogeography of the region, highlight gaps in our knowledge, and allow us to derive general postulates from quantitative (rather than qualitative) results. Other biogeographic models are clearly required to explain other idiosyncratic patterns of distribution seen in different taxa, and generating numerous datasets for suites of co-occurring lineages will help identify congruent signals.

(5) With the exception of vertebrates, for which the vast majority of known species are named, greater taxonomic research is required on all other phyla, to understand better the diversity and composition of the fauna of SWWA, and

to properly inform biogeographic studies and conservation efforts.

VII. ACKNOWLEDGEMENTS

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VIII. REFERENCES

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Fig. S1. Map showing rainfall in SWWA currently and during the Last Glacial Maximum (LGM) 21,000 years before present (ybp).

Fig. S2. Map showing temperature in SWWA currently and during the Last Glacial Maximum (LGM) 21,000 years before present (ybp).

Fig. S3. Map showing soil categories in SWWA.

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