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SYNTHESIS

Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota

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ABSTRACT

Aim The mesic biome, encompassing both rain forest and open sclerophyllous forests, is central to understanding the evolution of Australia's terrestrial biota and has long been considered the ancestral biome of the continent. Our aims are to review and refine key hypotheses derived from palaeoclimatic data and the fossil record that are critical to understanding the evolution of the Australian mesic biota. We examine predictions arising from these hypotheses using available molecular phylogenetic and phylogeographical data. In doing so, we increase understanding of the mesic biota and highlight data deficiencies and fruitful areas for future research.

Location The mesic biome of Australia, along the eastern coast of Australia, and in the south-east and south-west, including its rain forest and sclerophyllous, often eucalypt-dominated, habitats.

Methods We derived five hypotheses based on palaeoclimatic and fossil data regarding the evolution of the Australian mesic biota, particularly as it relates to the mesic biome. We evaluated predictions formulated from these hypotheses using suitable molecular phylogenies of terrestrial plants and animals and freshwater invertebrates.

Results There was support for the ancestral position of mesic habitat in most clades, with support for rain forest habitat ancestry in some groups, while evidence of ancestry in mesic sclerophyllous habitats was also demonstrated for some plants and herpetofauna. Contraction of mesic habitats has led to extinction of numerous lineages in many clades and this is particularly evident in the rain forest component. Species richness was generally higher in sclerophyllous clades than in rain forest clades, probably due to higher rates of net speciation in the former and extinction in the latter. Although extinction has been prominent in rain forest communities, tropical rain forests appear to have experienced extensive immigration from northern neighbours. Pleistocene climatic oscillations have left genetic signatures at multiple levels of divergence and with complex geographical structuring, even in areas with low topographical relief and few obvious geographical barriers.

Main conclusions Our review confirms long-held views of the ancestral position of the Australian mesic biome but also reveals new insights into the complexity of the processes of contraction, fragmentation, extinction and invasion during the evolution of this biome.

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Keywords

Australian mesic zone, biogeography, evolutionary history, phylogeny, phylogeography, rain forest, sclerophyll.

INTRODUCTION

The mesic zone biota is critical to understanding the evolution of Australia's biodiversity although the continent is now dominated by arid and semi-arid habitats. Historically, the Australian biota was thought to have multiple biogeographical origins, comprising a mix of relict lineages and 'invasive' elements. Until the 1960s it was widely held that either (1) Australian lineages were derived from Asian taxa by successive waves of colonization, the distinctiveness of a group being proportional to the age of the colonization wave that generated it, or (2) successive waves of colonization from Asia were superimposed on original Australian elements (Mayr, 1944; Keast, 1961; Darlington, 1965). In the late 20th century, with the development of plate tectonic theory, progress on interpretation of the Australian fossil plant record, and biogeographical analyses of extant taxa, the view emerged that the biota of the Australian mesic zone in general, and of the rain forest habitats in particular, is ancient. In this view, the ancestral biota rafted with Australia as it drifted north over the last 50 million years (Myr) and became progressively isolated from the rest of the former supercontinent Gondwana (Barlow, 1981). During this time, climatic change is thought to have been responsible for fragmentation of the mesic zone biota, the decline of rain forest and the expansion of the drier-adapted sclerophyllous flora (Hill *et al.*, 1999; Hill, 2004). Keast (1981) synthesized a modified version of this view, that as Australia drifted north it harboured both a subtropical element of its biota with relationships to Africa and India, and a more southern, cold-adapted one 'that characterized cool temperate Antarctic and southern South America in the Eocene'.

The goal of this review is to address long-standing questions on the origins of the mesic zone's biota and its subsequent development. These include: Was the habitat of mesic biota ancestral to that of others? How did the mesic biota's elements diversify? Which processes drove biotic changes and how did those processes influence present-day biotic composition? Although humans have influenced the Australian biota for the last *c.* 50,000 years, our focus is limited to non-human impacts. In particular, we ignore the Late Pleistocene megafaunal extinction and increase in fire frequency, both of which appear to have had significant impacts on the mesic biota. The former has been examined by several authors (Miller *et al.*, 2005; Prideaux *et al.*, 2009, 2010; Grun *et al.*, 2010), and the latter by Bowman (2000) and Mooney *et al.* (2011). We begin by discussing several key hypotheses that are central to understanding evolution of the Australian biota (Table 1). We use the fossil record and our understanding of environmental change (plate tectonics, landscape development and climate change) to ensure that these hypotheses have sound logical and evidentiary bases. However, the rapidly increasing scope and resolution of molecular phylogenies, particularly when time-calibrated, has provided a large source of evidence independent of the traditional bases of environmental history (Crisp *et al.*, 2004; Hugall *et al.*, 2008). Accordingly, we then formulate predictions that can be used to test the hypotheses, and in particular review relevant molecular phylogenetic and phylogeographical evidence for the predictions. Rigorous statistical assessment of the predictions is beyond our scope here. We acknowledge that New Guinea is part of the Australian plate so, ideally, our discussion would include New Guinea. However, we restrict our scope to the biota of Australia, which has been subject to more intensive study than that of New Guinea.

AUSTRALIAN MESIC ZONE

The Australian mesic zone is defined here in a very broad sense to include areas having a mean annual precipitation : evaporation ratio of > 0.4 but excluding the monsoonal region in the north (Fig. 1). This zone includes the Wet Tropics rain forests in the far north-east and extends down the eastern and south-eastern coast, and has a disjunct region in the far south-west of the continent. The remainder of the continent is occupied by a large central and western arid and semi-arid zone and a monsoon zone in the north. The biogeographical and environmental history of these latter regions have been reviewed recently by Byrne *et al.* (2008) and Bowman *et al.* (2010), respectively.

Although much smaller in area than either the monsoon or the arid/semi-arid zones, the mesic zone nonetheless harbours greater biotic diversity at all taxonomic levels in most major plant and animal groups (Byrne *et al.*, 2008; Bowman *et al.*, 2010). The mesic zone comprises components of several communities, including all of Australia's alpine vegetation, and most of the rain forest and sclerophyllous communities (Crisp *et al.*, 2004, 2009). It varies from forest to heath, depending upon the interactions of fire, climate and soil fertility. The very wet ecosystems of the mesic zone (rain forest, swamps, wet heath and alpine) are surrounded by extensive sclerophyllous forests and heaths that are relatively wet for at least part of the year, typically growing on oligotrophic soils and subject to frequent fires. The mesic zone spans tropical to temperate latitudes, across which biota vary in their temperature tolerances, and has been placed in three broad categories – microtherm, mesotherm and megatherm – with optimal temperatures for plant growth of 10–14 °C, 19–22 °C and 26–28 °C, respectively (Nix, 1982).

Table 1 Hypotheses regarding the origins and evolution of the biota of the Australian mesic zone and relationships to Australia's other biota. Further details and pertinent references are given in the text.

Hypotheses	Evidence underlying the hypotheses	Testable predictions
1. The ancestors of the biota of Australia were organisms of mesic environments	Palaeoclimatic evidence for warm, wet climates in the Palaeogene (prior to 32 Ma), including the dominance of mesic lineages in the fossil record	The mesic biome should optimize as ancestral on phylogenies of lineages with mesic, and arid and/or monsoon biome representatives
2. Rain forest organisms were the ancestors of the present Australian biota	Strong representation in the Palaeogene fossil record of taxa now characteristic of rain forest	Rain forest environments should optimize as ancestral on phylogenies of lineages with both rain forest and sclerophyllous lineages
3. Lineages of Asian origin became an important component of the Australian mesic biota in the last 20 Myr	Interaction between the Southeast Asian plate and the Australian plate around 20 Ma, disjunct distribution of extant taxa and the relatively modest number of extant taxa present in the fossil record prior to this date	Asian lineages appear in the mesic biota in the last 20 Myr
4. Rain forest communities suffered extinction and contraction to refugia during the Neogene, contrasting with expansion of sclerophyll lineages	Palaeoclimatic evidence for late Neogene aridification of Australia, including fossil evidence for extinctions in rain forest lineages, and disappearance of rain forest taxa from areas that are now unsuited to rain forest	Rain forest lineages should have fewer species than their sister lineages in mesic sclerophyll communities
5. Climatic fluctuations in the Quaternary caused range expansions and contractions of mesic biota	Ice core and marine records of cycling in climate and atmospheric CO_2, fossil evidence of vegetation changes	Phylogeographical patterns among mesic areas should reveal genetic signatures of high diversity with localized endemism from long term persistence through multiple climatic cycles

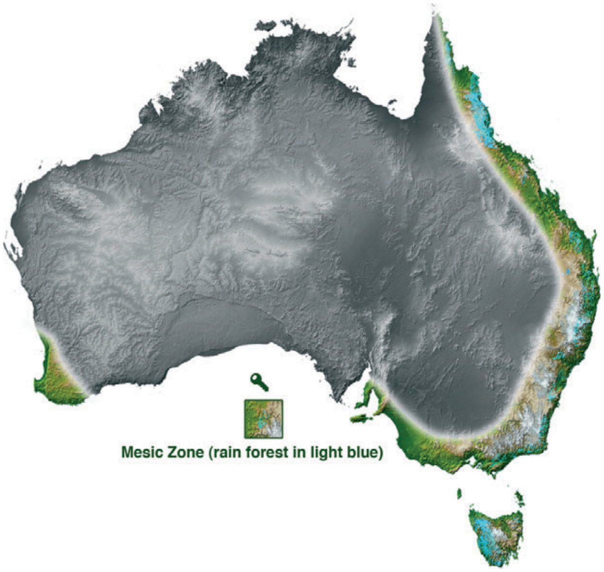

Figure 1 The mesic zone of Australia as defined in this paper.

GEOLOGICAL AND PALAEOCLIMATIC FRAMEWORKS

To understand the establishment of present climates in Australia and their impact on the biota, some understanding of Australia's history of isolation and aridification in response to the global Cenozoic cooling trend is necessary. This has been reviewed extensively elsewhere (Quilty, 1994; Lear *et al.*, 2000; Zachos *et al.*, 2001; Hall, 2002), particularly in relation to the complex spatio-temporal details of the aridification of Australia (Bowler, 1982; Kershaw *et al.*, 1994; Fujioka *et al.*, 2005, 2009; Byrne *et al.*, 2008; Williams *et al.*, 2009). The key point relevant to this review is that geological and palaeoclimatic evidence confirms the transition from widespread very wet, aseasonal climates in the Palaeogene to the present-day dominance of xeric and seasonal climates (Fig. 2). Our concern in this paper is the response of the Australian biota, especially its mesic components, to these dramatic changes across the continent in space and time.

It is clear that Australia became much drier between the Eocene and the present (Fig. 2). This resulted in expansion of the arid zone to cover *c.* 70% of the continent, and contraction of mesic environments. Ever-wet forests are now restricted to western Tasmania and an archipelago of small areas scattered near the eastern seaboard (Fig. 1). However, the exact timing of climatic drying is poorly known. The Late Miocene and Pliocene have often been interpreted as the first major period of climatic drying in Australia. Evidence for the development of open vegetation during the Oligocene and Early Miocene comes from the first appearance across a wide region of pollen of some plant groups typical of modern, open vegetation, including Asteraceae, Amaranthaceae (including chenopods), Poaceae and *Acacia* (e.g. Macphail *et al.*, 1994; Macphail, 2007). Further evidence comes from palaeoecological studies of vertebrate faunas that suggest the Late Oligocene and Late Miocene were dominated by open forests, with the warmer mid-Miocene being characterized by rain forests at Riversleigh,

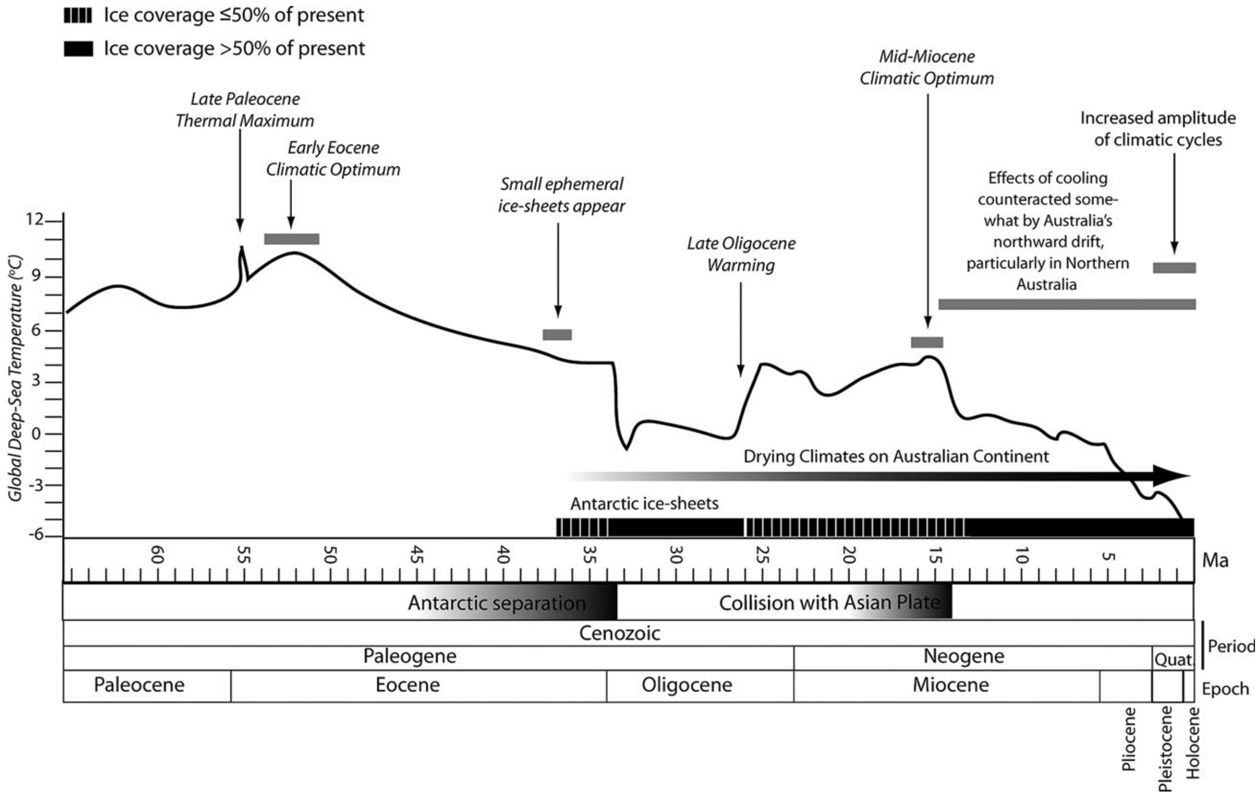

Figure 2 Summary of the palaeoclimate for the Australian continent since 65 Ma, adapted from fig. 2 of Zachos *et al.* (2001). It should be noted that the drop in global deep-sea temperatures in the late Neogene was not reflected in the climate across the whole of the Australian continent, being counteracted to some degree by Australia's drift northward; southern regions of Australia would have been affected more than northern latitudes by the global temperature decrease. There is convincing evidence that the separation of Australia from Antarctica (i.e. the presence of deep water in the Tasmania–Antarctic Passage) was complete by the early Oligocene but could have taken place up to 10 Myr prior to this date (Truswell, 1997). Similarly, there is evidence for the Australian and Asian Plates being in contact by the mid-Miocene, but the process could have been complete any time in the preceding 5 Myr (Hall, 2002). 'Quat.' = Quaternary.

which today is a seasonally dry savanna (Travoullon *et al.*, 2009). Macrofossils of Casuarinaceae species with sunken stomata (Guerin & Hill, 2006), an adaptation to seasonal water stress, appear in Oligocene deposits, indicating declining water availability. Similarly, pollen attributable to the eucalypt group (*sensu* Ladiges *et al.*, 1983) started to contribute significantly to pollen floras at this time (Truswell *et al.*, 1985; Martin, 1994). Nevertheless, the persistence of a number of rain forest taxa in southern, central and north-western Australia in the Oligocene implies that there was relatively high water availability over much of the continent (Truswell *et al.*, 1985; Martin, 1994; Macphail & Stone, 2004).

Sedimentological evidence and the appearance of saline evaporites in south-eastern and south-western Australia (An *et al.*, 1986; Zheng *et al.*, 1998, 2002; Pillans & Bourman, 2001; Clarke & Pillans, 2002) imply an impact of major aridification in the mesic zone within the past *c.* 1 million years. There is strong evidence from many parts of the world for cycling of climates over the Quaternary [currently defined as the period from 2.58 million years ago (Ma) to the present (Ogg & Pillans, 2008)]. The early Quaternary was characterized by low amplitude, high frequency [20 to 40 thousand year (kyr)] cycles, then from the mid-Quaternary [780 thousand years ago (ka)], global climate was dominated by high amplitude glacial/interglacial cycles of *c.* 100 kyr duration (Zachos *et al.*, 2001; Maslin & Ridgwell, 2005).

FOSSIL EVIDENCE FOR CHANGES IN THE MESIC ZONE BIOTA

Pollen data from Miocene deposits (Martin, 1987, 1998; Kershaw *et al.*, 1994) chart the changing nature of forest communities in the Murray River Basin of south-eastern Australia. Prior to this time most evidence suggests the widespread presence of rain forest (Hill, 2004). General drying is interpreted where communities that included species from the highly drought-sensitive *Nothofagus* subgenus *Brassospora* were replaced by forests dominated by Araucariaceae and Myrtaceae in the Early Miocene, and by more xeric forests dominated by Myrtaceae–Casuarinaceae in the Middle Miocene. Similarly, several phases of extinction of rain forest mammals are moderately well documented (Archer *et al.*, 1999; Long *et al.*, 2002). The first of these occurred around the early to mid-Miocene, and a second phase of extinction occurred from the mid-Pliocene. The third phase was more recent, around 300 ka, and the record from Mt Etna in central eastern Queensland, where only small pockets of rain forest occur today, indicates that even up to that time there was a high diversity of rain forest vertebrates despite earlier extinctions (Hocknull, 2002; Hocknull *et al.*, 2007).

Fossil records indicating change in vegetation during the early climatic cycles of the Quaternary are mostly restricted to south-eastern Australia. Pollen and macrofossil data suggest strong cycling of vegetation types with wetter climates in inferred interglacials prior to the current one (Colhoun & van de Geer, 1998; Sniderman *et al.*, 2009; Sniderman, 2011). Global extinctions of plant species (Jordan, 1997) and regional extinctions of plant genera (Sniderman, 2011) in the early Quaternary (2.58–0.78 Ma) suggest large impacts of the early climatic cycles. One site from south-eastern Australia shows warmer climates with significantly wetter summers than at present throughout the period from 1.79 to 1.55 Ma (Sniderman *et al.*, 2009). Evidence from fossil beetles demonstrates that through the Quaternary to as recently as the last interglacial, there has been significant and ongoing contraction of rain forest faunas paralleling the plant-based evidence (Porch *et al.*, 2009; Sniderman *et al.*, 2009).

Fossil evidence from sites in south-eastern Australia and the Wet Tropics region of north-eastern Australia show that rain forest was more extensive during the last interglacial than at the present (Kershaw & van der Kaars, 2007; Kershaw *et al.*, 2007; Porch *et al.*, 2009). For much of the last 100 kyr until the end of the Pleistocene, most south-eastern Australian pollen records are dominated by pollen of herbs and grasses, particularly Asteraceae and Poaceae (Kershaw & van der Kaars, 2007), with pollen of sclerophyllous trees present in trace amounts. This implies that trees were rare and/or confined to sheltered landscape refugia, although records from present-day high rainfall regions (McKenzie, 1995; Colhoun & van de Geer, 1998) suggest locations of some larger-scale forest refugia. On the Atherton Tableland in far north Queensland, pollen of rain forest taxa was almost completely replaced by that of sclerophyllous *Eucalyptus* and Casuarinaceae around the Last Glacial Maximum (LGM), *c.* 25–15 ka (Kershaw *et al.*, 2007). The assembly of modern vegetation communities commenced around 14 ka, with re-establishment of localized rain forests in the north and in parts of Tasmania, and widespread sclerophyllous communities across remaining areas.

The vertebrate fossil record through the Quaternary generally remains too patchy and poorly dated to demonstrate overall biotic response to cyclic changes during this time. However, several cave sequences show local responses within the vertebrate fauna to change during the last two or three glacial cycles (Prideaux *et al.*, 2007). Fossils from sites in the extreme southwest of Western Australia show changes in the vertebrate fauna as the vegetation altered from heathland to forest in the late Quaternary (Balme *et al.*, 1978; Merrilees, 1979). Similarly, large adjustments in geographical range between glacial and post-glacial phases are observed in late Quaternary cave fossil records from south-eastern Australia (Morris *et al.*, 1997; Aplin *et al.*, 2010).

HYPOTHESES

Hypothesis 1. The ancestors of the biota of Australia were organisms of mesic environments

The notion that the ancient biota of Australia was restricted to mesic habitats has grown from the well-established environmental history of Australia. The plant fossil record provides evidence that the biota during the early Cenozoic occupied climates much wetter than now (Fig. 2) and that there was a later transition to biota adapted to present-day drier climates. Thus, a range of taxa constrained to mesic environments were present through most of Australia, including the heart of the arid zone (Macphail, 2007). These taxa include southern conifers, for which experimental evidence supports the assumption that climatic preferences of some plant groups have not changed drastically through time, and that current bioclimatic distributions of these taxa are guides to past climates (see Brodribb & Hill, 1998; Hill & Brodribb, 1999; Macphail, 2007). Moreover, a recent meta-analysis of phylogenies of Southern Hemisphere plant groups (Crisp *et al.*, 2009) has confirmed that transition between biomes is a rare evolutionary process. Under an assumption of habitat constancy, a far less complete animal fossil record also supports the existence in the Cenozoic of mesic-adapted mammal and reptile faunas (Godthelp *et al.*, 1992, 1999; Hand *et al.*, 1994; Archer *et al.*, 1999; Long *et al.*, 2002; Hocknull *et al.*, 2007). Further testing of the hypothesis of mesic ancestry can be achieved through assessing the prediction that the mesic biome should optimize as ancestral on phylogenies of lineages that contain mesic, and arid and/or monsoon biome representatives.

Hypothesis 2. Rain forest organisms were the ancestors of the present Australian biota

A more restrictive version of Hypothesis 1 that has acquired the status of dogma is that the ancestral biota of Australia comprised a rain forest community (Schodde & Calaby, 1972; Johnson & Briggs, 1975) from which the sclerophyllous and arid zone lineages evolved (Rowe *et al.*, 2011). Fossil evidence supports great antiquity (reaching into or beyond the Palaeogene) of at least some elements of the contemporary Australian rain forest biota (e.g. Long *et al.*, 2002; Morley, 2002; Hill, 2004). In particular, many of the plant groups in microthermal rain forest have a fossil record extending back at least 30 Myr but only a small proportion of the clades in the much more diverse mega- and meso-thermal rain forests are represented by such old fossils (Carpenter *et al.*, 1994; Greenwood & Christophel, 2005; Sniderman & Jordan, 2011). If Australia was more-or-less covered in rain forest at the time of isolation, then rain forest should optimize as ancestral on molecular phylogenies of groups that have both rain forest and non-rain forest taxa.

Hypothesis 3. Lineages of Asian origin became an important component of the Australian mesic biota in the last 20 Myr

Although early views that most of the Australian biota originated from Southeast Asia (Hooker, 1860; Mayr, 1944; van Steenis, 1962) have long been abandoned, there has clearly been extensive biotic interchange between the two regions. This is apparent from well-documented, disjunct distributions of a range of plants and animals (e.g. Webb *et al.*, 1984; Barker *et al.*, 2004; Jonsson *et al.*, 2008). Australia and Southeast Asia have not been connected by continuous land for more than 100 Myr, but the intervening water gaps are now relatively narrow. After *c.* 25 Ma when the Australian plate collided with Sundaland and associated microplates (Hall, 2002), biotic interchange between the regions may have become considerably more likely than prior to that time (Morley, 2002). Views on the significance of the Asian contribution to the Australian biota have varied markedly. Thus, Truswell *et al.* (1987) and Kershaw *et al.* (2005) concluded that there was little evidence for a massive influx of Southeast Asian plants into Australian rain forests following the Sunda-Sahul collision, whereas Morley (1998, 2002) and Sniderman & Jordan (2011) argued for extensive migration of plant taxa in both directions since *c.* 20 Ma. This hypothesis predicts that immigrant lineages will be nested subclades within clades that are older than 20 Myr and that have representative taxa in both Australia and Southeast Asia. We use the 20 Ma threshold because this is soon after the first evidence for the collision of continental crust in Sulawesi, at approximately 25 Ma (Hall, 2002).

Hypothesis 4. Rain forest communities suffered extinction and contraction to refugia during the Neogene, contrasting with expansion of sclerophyll lineages

The clear fossil evidence for extreme reduction in rain forest area and extinction of rain forest taxa (see above) suggests that extinction may have greatly exceeded speciation in rain forest communities. Changes in extinction rates are difficult to infer from molecular phylogenies in the absence of fossil evidence (Morlon *et al.*, 2010; Rabosky, 2010), but a difference in net diversification rate predicts that rain forest clades will have lower species richness compared to their sister clades in sclerophyllous ecosystems.

Hypothesis 5. Climatic fluctuations in the Quaternary influenced distributions of mesic biota

The climatic oscillations of the Quaternary produced glacial/interglacial conditions throughout the Northern and Southern Hemispheres. The effects of these oscillations on the biota are well documented, particularly in temperate Europe (e.g. Taberlet *et al.*, 1998; Hewitt, 2004) and have also been demonstrated in other Northern Hemisphere biotas (e.g. Brunsfeld *et al.*, 2001; Calsbeek *et al.*, 2003; Lessa *et al.*, 2003; Kadereit *et al.*, 2004; Soltis *et al.*, 2006), and in arid environments (see Byrne *et al.*, 2008). The climatic fluctuations evident in the palaeoecological records leave signatures of expansion and contraction in phylogeographical structure. It is also expected that these fluctuations would have led to expansion and contraction of the Australian mesic biota. These signatures may reflect influences of multiple glacial cycles as they will not have been over-written by extinctions due to glaciation, as occurred in the northern temperate zone. Glaciation in Australia was restricted to relatively small regions of Tasmania and the Kosciuszko Massif (Barrows *et al.*, 2001). Across much of the mesic zone, xeric conditions during the Plio-Pleistocene glacial cycles would have caused range contraction and local extirpations of populations, more so than extinctions of species across their entire ranges (Colhoun *et al.*, 1996; Hope *et al.*, 2004). We predict that fine-scale and occasionally even deep phylogeographical structuring should be recovered, especially in rain forests. As a result, phylogeographical patterns should reveal genetic signatures of localized high diversity and localized endemism of lineages from long-term persistence through multiple climatic cycles. Depending on local topography and climatic gradients, this could manifest as marked phylogeographical structure at fine, as well as broad geographical scales.

APPROACH AND METHODS

Support for predictions derived from the five hypotheses above was evaluated using molecular phylogenies that include mesic zone biota. We assessed relevant molecular phylogenies that have estimates of dating, and multiple taxa of Australian terrestrial plants and animals. For predictions derived from Hypotheses 1 and 2, phylogenies that dated to, or earlier than, 30 Ma were trait-mapped using parsimony in Mesquite (Maddison & Maddison, 2007) as applied by Crisp *et al.* (2009) to determine whether the most recent common ancestor (MRCA) was reconstructed as inhabiting the mesic zone. The 30 Myr minimum age limit was applied to constrain analyses to lineages that had ancestors present on the Australian landmass at the time of deep ocean separation of Australia from Antarctica, and hence the remainder of Gondwana. To evaluate support for Hypothesis 3, we identified geographical disjunctions between Australian rain forest taxa and their non-Australian closest relatives, and estimated whether the divergence times were < 20 Ma, at which time the Australian and Asian plates began to interact. For the prediction derived from Hypothesis 4, phylogenies that included sister clades of rain forest and sclerophyllous taxa were assessed to determine whether the rain forest clade was species poor compared with its sclerophyll sister. The prediction of Hypothesis 5 was assessed from a survey of phylogeographical literature.

RESULTS

Prediction 1. The mesic biome should optimize as ancestral on phylogenies of lineages with mesic and arid and/or monsoon biome representatives

Evaluation of DNA-based phylogenies that had nodes dated at 30 Ma or earlier strongly supported the hypothesis that the mesic zone is ancestral for both plants and animals. Mesic ancestry was evident in the majority of plant phylogenies including wet forest and sclerophyllous elements, e.g. Casuarinaceae (Steane *et al.*, 2003; Crisp *et al.*, 2004), *Callitris* (Pye *et al.*, 2003), eucalypts (Myrtaceae tribe Eucalypteae: Crisp *et al.*, 2004), and Proteaceae (Jordan *et al.*, 2005, 2008; Barker *et al.*, 2007; Sauquet *et al.*, 2009).

For birds, mesic ancestry was inferred from all phylogenies for passerines, particularly oscine passerines (Barker *et al.*, 2002, 2004; Ericson *et al.*, 2002, 2003; Chesser & ten Have, 2007) and for parrots among non-passerines (Wright *et al.*, 2008; Schweizer *et al.*, 2010). Recent estimates of divergence times based on multi-gene molecular datasets (e.g. Drummond *et al.*, 2006; Beck, 2008) reveal that the mammal fauna at 30 Ma included representatives of the two extant monotreme families and at least 13 extant marsupial families. Trait mapping of occupied biomes among these groups of mammals has not been done on rigorously derived phylogenies but mesic origins are inferred for *Rattus* (Rowe *et al.*, 2011) and two ecologically diverse marsupial lineages – macropodoids (kangaroos and their allies) and peramelids (bandicoots) (Meredith *et al.*, 2008a,b). Other marsupial groups are essentially restricted to mesic and monsoonal environments, including pseudocheirid and petaurid possums (Meredith *et al.*, 2010). In both cases, phylogenies suggest mesic origins.

In the few cases of invertebrate phylogenies that are dated, or for which it is generally strongly accepted that the extant fauna is of Australian origin, all taxa are exclusively mesic and do not show transitions to other biomes. These include *Ornithoptera* (birdwing butterflies) that occur in rain forest and sclerophyll (Braby *et al.*, 2005), *Delias* butterflies found in cool temperate wet forests and cloud forests (Braby & Pierce, 2007), *Paralamyctes* centipedes (Giribet & Edgecombe, 2006) and glow worms (Diptera: Keroplatidae) (Baker *et al.*, 2008) that occur only in the mesic zone.

Many more studies of Australian plant and animal taxa, particularly reptiles and invertebrates, are not informative for Prediction 1 either because they apparently dispersed into Australia only after the isolation of the continent or because studies did not include nodes dating back to the isolation of Australia 30 Ma. Among radiations that are less than 30 Ma, the skinks, agamid lizards, elapid snakes, dasyurid marsupials and Australo-Papuan hydromyin rodents (*sensu* Lecompte *et al.*, 2008) all probably have mesic forest ancestry. Within each of these taxa there have been subsequent arid or dry forest radiations from the mesic ancestors, e.g. *Ctenotus*, *Lerista* and *Carlia* skinks, amphibolurin dragons, knob-tail geckos, *Neobatrachus* and *Helioporus* frogs (Mahoney *et al.*, 1996; Morgan *et al.*, 2007; Rabosky *et al.*, 2007; Dolman & Hugall, 2008; Hugall *et al.*, 2008; Skinner & Lee, 2009; Oliver & Bauer, 2011). In contrast, the diplodactyloid gecko lineages that include the Carphodactylidae, Diplodactylidae and Pygopodidae, which have ancient Australian origins (Oliver & Sanders, 2009), show no distinct association of early phylogenetic lineages with the mesic zone.

In summary, Prediction 1 received extensive support from all biotic groups except for the diplodactyloid geckos.

Prediction 2. Rain forest environments should optimize as ancestral on phylogenies with both rain forest and sclerophyllous lineages

Evaluation of phylogenies for Prediction 2 shows some support from plants but there are limited data available for other groups. In plants, the rain forest environment optimized as ancestral in phylogenies of Elaeocarpaceae (Crayn *et al.*, 2006), Casuarinaceae (Steane *et al.*, 2003; Crisp *et al.*, 2004), *Alectryon* (Edwards & Gadek, 2001), Styphelioideae (Quinn *et al.*, 2003) and Proteaceae subfamily Grevilleoideae, but not the family as a whole (Jordan *et al.*, 2005). For birds, the results of Hawkins *et al.* (2005) suggest rain forest origins for many avian lineages now living in drier habitats (see also Norman *et al.*, 2007) (Fig. 3). Among mammals, rain forest is predicted to be a likely ancestral habitat for peramelids, macropodoids, pseudocheirids and petaurids (Beck, 2008), although for several of these groups it is necessary to include New Guinean taxa in phylogenies to obtain this result.

Prediction 3. Asian immigrant lineages appear in the mesic biota in the last 20 Myr

Very few dated phylogenies exist that inform this issue directly. However, undated phylogenies provide numerous examples in which a single species or lineage exists in Australia that is either shared with locations outside Australia or embedded within diverse groups that are widespread outside Australia (e.g. northern neighbours, Asia, Africa, America). Evaluation of dated phylogenies revealed strong support for this prediction in herpetofauna and birds, and some support in plants and invertebrates.

In the herpetofauna, numerous groups show evidence of immigration into Australia from Asia followed by radiation of lineages within Australia, e.g. the gekkonid genera *Gehyra* (Sistrom *et al.*, 2009) and *Heteronotia* (Fujita *et al.*, 2010), agamids that show a strong pattern of diversification from rain forest ancestors (Hugall *et al.*, 2008), elapid snakes (Keogh, 1998; Keogh *et al.*, 1998; Sanders *et al.*, 2008), blindsnakes (Vidal *et al.*, 2010), homalopsid snakes (Alfaroa *et al.*, 2008) and pythons (Rawlings *et al.*, 2008). Some groups show multiple colonizations from Southeast Asia, e.g. lygosomine skinks (Honda *et al.*, 2000).

Although there are few dated plant phylogenies, there is a wealth of evidence for recent immigration of plant species into the mesic zone. Based on phylogenetic analyses and geographical

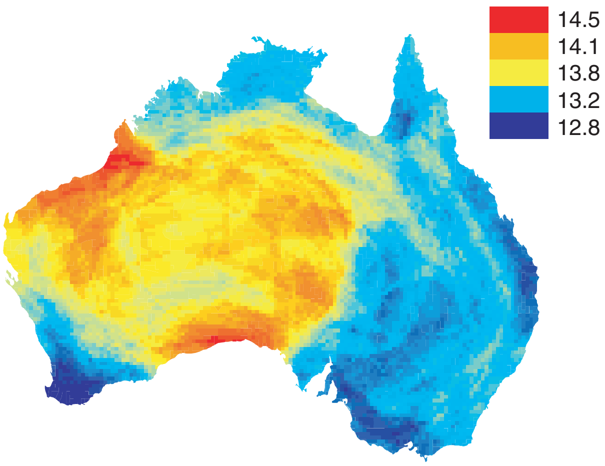

Figure 3 Mesic origin of bird fauna in Australia. Geographical patterns of mean root distance (MRD) resolved at the family level for Australian birds using cell size of 27.5 × 27.5 km, based on the tree of Sibley & Ahlquist (1990). Cells are coloured according to the calculated MRD value, a measure of the level of evolutionary development of the local avifauna. Cells with high values support species that are, on average, closely related; cells with low values support a predominance of distantly related taxa. Thus, the mesic zone avifauna is characterized more by species-poor lineages, while the arid zone is characterized by bird taxa from more species-rich families. Figure adapted from Hawkins *et al.* (2005).

distribution data, there are many hundreds of plant taxa that are probably recent immigrants from Asia and beyond, but only a few examples are given here. Studies by Crisp *et al.* (2010) and Pfeil & Crisp (2008) support the hypothesis for *Livistona* palms and *Citrus* (Rutaceae), respectively. A dated phylogeny for *Aglaia australiensis* and *A. meridionalis* (Meliaceae) shows that these species represent an isolated lineage that entered Australia from Southeast Asia within the last 10 Myr (Muellner *et al.*, 2008) (Fig. 4). Various area cladograms of plants indicate immigration of subgeneric lineages of *Pseuduvaria* (Annonaceae) (Su *et al.*, 2008) and *Rhododendron* (Ericaceae) (Webb & Ree, in press). Some of the Australian figs (*Ficus*, Moraceae), such as *F. benjamina*, probably represent invasive lineages whereas others do not, such as species in section *Malvanthera* (Rønsted *et al.*, 2008).

Invertebrates that appear to have arrived in Australia only after isolation from Antarctica include multiple bee groups (Lowe & Crozier, 1997; Leys *et al.*, 2002; Danforth *et al.*, 2004; Schwarz *et al.*, 2004, 2006; Fuller *et al.*, 2005; Schiffer *et al.*, 2007), and some cockroaches and termites (Thompson *et al.*, 2000; Maekawa *et al.*, 2003). For camaenid land snails, the phylogenetic evidence is consistent with relatively recent (Miocene) colonization and subsequent radiation through the mesic zone (Hugall *et al.*, 2002; Hugall & Stanisic, 2011).

Among birds, the clearest evidence from molecular phylogenetic studies of post-20 Ma immigrant lineages being present in the mesic zone come from kingfishers (Moyle *et al.*, 2006), drongos (Pasquet *et al.*, 2007), monarch flycatchers (Filardi & Moyle, 2005), and the members of the suborder Passeridae of passerine birds (Ericson *et al.*, 2002; Barker *et al.*, 2004). The ancestors of the passeridan songbirds dispersed from Australo-Papua and extant passeridan lineages returned and speciated in Australia in both mesic and arid habitats.

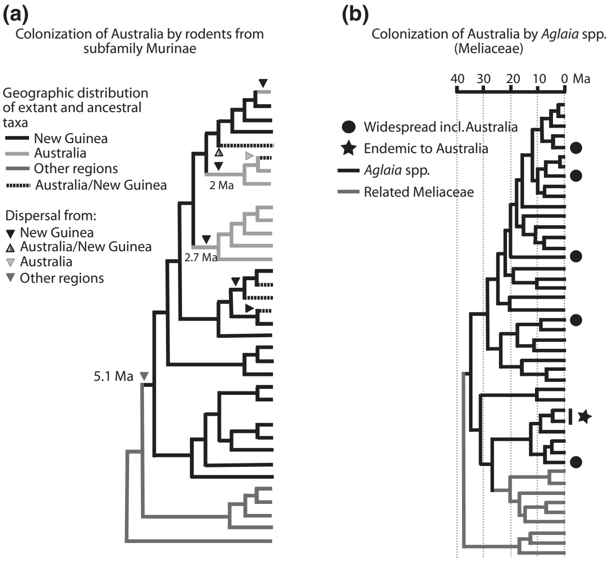

Figure 4 Dated molecular phylogenies provide evidence that many lineages have entered Australia within the last 10–20 Myr, after the collision of the Sahul and Sunda shelves. (a) Colonization of Australia by rodents from subfamily Murinae. Parsimony reconstruction of dispersal events, showing one of two equally parsimonious dispersal scenarios, and estimated dates (Ma) of dispersal events (next to branches). Figure adapted from Rowe *et al.* (2008). (b) Bayesian chronogram based on a maximum parsimony tree obtained from ITS sequences of *Aglaia* and related Melioideae taxa (adapted from Muellner *et al.*, 2008). Black branches represent *Aglaia* species. Grey branches represent other genera. Most taxa are widespread across regions in Southeast Asia and the Pacific Islands (e.g. Malay archipelago, New Guinea, Solomon Islands). Circles represent species of *Aglaia* that are present in Australia as well as other areas of Southeast Asia. The star represents two species of *Aglaia* (*A. australiensis* and *A. meridionalis*) that are endemic to Australia.

Among mammals only Australo-Papuan rats and mice (Hydromyini) showed evidence for post-20 Ma immigration into Australia (Lecompte *et al.*, 2008; Rowe *et al.*, 2008) (Fig. 4). Dated phylogenies suggest that phalangerid and petaurid possums may have evolved in New Guinea or Sulawesi during the late Tertiary and invaded Australia during the Pleistocene (Raterman *et al.*, 2006; Malekian *et al.*, 2010). Although bats have been present in Australia since the Eocene (Hand *et al.*, 1994), many lineages presumably arrived through the course of the mid- to late Tertiary (Hand, 2006), coming from both the New World [mysticinids, now extinct in Australia but persisting in New Zealand (see Hand *et al.*, 1998)] and the Old World (all other groups). Unfortunately, relatively few Australian bats have been included in global phylogenetic studies, hence estimates of arrival times for most groups are based exclusively on the fossil record.

In summary, where phylogenies are available for testing Prediction 3, it appears that immigrant lineages are mostly Asian, generally entered Australia after 20 Ma, and some have undergone habitat diversification across mesic and arid zones.

Prediction 4. Rain forest lineages should have fewer species than their sister lineages in mesic sclerophyll communities

Although data are limited, there was support for this prediction of less speciation and/or greater extinction in rain forest compared to sclerophyll in birds and plants. Mammal phylogenies did not support this prediction and show some outstanding examples of explosive diversification in non-mesic environments (e.g. macropodoid and dasyurid marsupials, and the hydromyin rodents; Aplin, 2006).

Among birds, although phylogenetic studies with complete taxon sampling are few, some groups provided reliable data. The Meliphagoidea generally (Gardner *et al.*, 2010), *Acanthiza* thornbills (Nicholls, 2001) and the Maluridae (fairy-wrens, emu-wrens and grasswrens) (Schodde & Weatherley, 1982; Schodde, 2006; Christidis *et al.*, 2010; Driskell *et al.*, 2011; Lee *et al.*, in press) support the prediction because their greatest diversity is in non-rain forest environments across Australia and New Guinea.

Many published plant studies did not contain representatives of both rain forest and sclerophyll biomes and thus were not useful for testing this hypothesis. Evaluation of the ten phylogenies that did include appropriate data yielded support for the hypothesis. Examples of groups that have a species-poor lineage in the rain forest and a highly diversified group of species in the sclerophyll biomes include Proteaceae (e.g. Banksiinae, Persoonioideae and Hakeinae) (Barker *et al.*, 2007; Sauquet *et al.*, 2009), Casuarinaceae (Steane *et al.*, 2003; Crisp *et al.*, 2004), *Callitris* (Pye *et al.*, 2003), Elaeocarpaceae *sensu lato* [i.e. including the Tremandraceae (Crayn *et al.*, 2006)] and *Eucalyptus* (Crisp *et al.*, 2004).

Most mammals showed evidence of higher species diversity in sclerophyllous lineages than in their sister rain forest lineages, although it is worth noting that there are few phylogenetic studies of Australian bats, which are a prominent component of rain forest fauna. Only a few mammal phylogenies show relatively species-poor branches in rain forest environments, i.e. *Murexia*/*Antechinus* (Armstrong *et al.*, 1998; Krajewski *et al.*, 2007), Hypsiprymnodontidae (Burk *et al.*, 1998), Potoroidae and Burramyidae (Archer *et al.*, 1999), and Australo-Papuan Muridae (Lecompte *et al.*, 2008; Rowe *et al.*, 2008). In contrast, Australo-Papuan *Rattus* showed equivalent flourishes of rapid diversification in each of mesic, sclerophyll and arid zones although with mesic origins overall (Rowe *et al.*, 2011). There is evidence for rapid radiation in arid or monsoonal lineages relative to mesic (primarily rain forest) lineages in both *Sphenomorphus* (Rabosky *et al.*, 2007) and *Eugongylus* (Dolman & Hugall, 2008) lineages of lygosomine skinks.

In summary, molecular phylogenies generally supported the prediction that rain forest lineages have fewer extant species than their sister lineages from sclerophyllous communities. Extinction in rain forests is inferred as the reason for relatively species-poor lineages in this biome and is consistent with the fossil evidence for extinction as the primary driving force behind paucity of rain forest taxa.

Prediction 5. Phylogeographical patterns among mesic areas should reveal genetic signatures of high diversity with localized endemism from long-term persistence through multiple climatic cycles

Review of phylogeographical analyses for this prediction reveals high levels of intra-specific differentiation between divergent lineages in mesic taxa in all biotic groups. These genetic signatures also occur among regions that would be expected to have been fragmented through climatic cycling within all geographical areas of the mesic zone (Fig. 5).

There are significant levels of genetic structure within various species in Tasmania (McKinnon *et al.*, 2004; Steane *et al.*, 2006; Macqueen *et al.*, 2009; Worth *et al.*, 2009, 2010; Nevill *et al.*, 2010), and also evidence of biotic connectivity between western Tasmania and western Victoria (e.g. Otway Ranges), particularly for eucalypts (McKinnon *et al.*, 2004), birds (Murphy *et al.*, 2011), mammals (Macqueen *et al.*, 2009), reptiles (Chapple *et al.*, 2005) and frogs (Schauble & Moritz, 2001; Symula *et al.*, 2008). Phylogeographical studies of the widespread cool temperate rain forest plants, *Nothofagus cunninghamii* and *Tasmannia lanceolata,* reveal strong patterns of geographical partitioning of chloroplast haplotypes that significantly pre-date the LGM (Worth *et al.*, 2009, 2010) indicating persistence of the species within multiple parts of their current ranges, including drier regions such as eastern Tasmania and, for *T. lanceolata*, western Victoria.

Species restricted to wet forests and alpine areas in south-eastern Australia show strong molecular divergence between patches indicating long-term isolation, for example, the plants *Eucalyptus nitens* (Byrne & Moran, 1994), *E. regnans* (Nevill *et al.*, 2010), *Lagarostrobos franklinii* (Clark & Carbone, 2008), the mammal *Burramys parvus* (Osborne *et al.*, 2000; Mitrovski *et al.*, 2007), and the lizard *Cyclodomorphus praealtus* (Koumoundouros *et al.*, 2009). At Tallaganda in the Great Dividing Range, multiple taxa of springtails and flatworms show spatially congruent patterns in the face of impacts at multiple time scales since the Pliocene (Garrick *et al.*, 2004, 2007, 2008; Sunnucks *et al.*, 2006).

Terrestrial species with distributions along the east coast show strong patterns of genetic differentiation with separation of genetic lineages in the northern and central regions and in the south-eastern corner, e.g. marsupials (Houlden *et al.*, 1999; Zenger *et al.*, 2003; Brown *et al.*, 2006), rodents (Jerry *et al.*, 1998), birds (Nicholls & Austin, 2005; Joseph *et al.*, 2008; Donnellan *et al.*, 2009; Joseph & Omland, 2009), lizards (Chapple *et al.*, 2005; Moussalli *et al.*, 2005; Dubey & Shine, 2010; Edwards & Melville, 2010), snakes (Keogh *et al.*, 2003; Dubey *et al.*, 2010; Sumner *et al.*, 2010) and frogs (James & Moritz, 2000; Schauble & Moritz, 2001; Symula *et al.*, 2008).

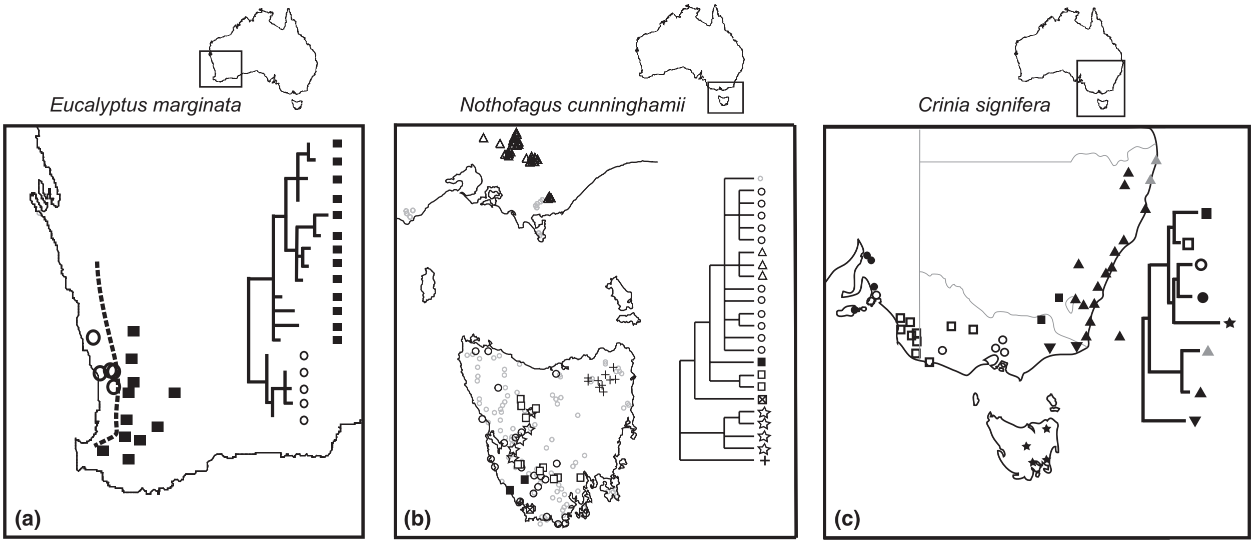

Figure 5 Examples of phylogeographical structure in Western Australia, Tasmania and south-eastern Australia. (a) Phylogeography of chloroplast haplotypes of *Eucalyptus marginata* in south-western Western Australia. Chloroplast diversity was structured into two geographically distinct lineages – coastal (circles) and forest (squares) – separated by the geomorphological boundary of the Darling Scarp that separates the Coastal Plain from the Darling Plateau (dashed line). Figure adapted from Wheeler & Byrne (2006). (b) Distribution of chloroplast haplotypes of *Nothofagus cunninghamii* across its natural range of Tasmania and Victoria. Distinct phylogeographical structure can be seen with particular haplotypes being restricted to Victoria, north-eastern Tasmania and western Tasmania. The evidence suggested that there were multiple glacial refugia for this species across Tasmania and in the highlands of Victoria. Figure adapted from Worth *et al.* (2009). (c) Geographical distribution in south-eastern Australia of mitochondrial haplotypes found in the common froglet, *Crinia signifera*. Distinct geographical partitioning of major haplotype clades can be observed, as well as partitioning of haplotype sub-clades within those clades. Figure adapted from Symula *et al.* (2008).

Divergence between these major regions is generally dated to the Late Miocene–Pliocene, suggesting reinforcement of genetic patterns over multiple climatic cycles, although phylogeographical structure in squirrel gliders between eastern coastal and south-eastern inland regions reflects Late Pleistocene influences (Pavlova *et al.*, 2010). Two notable exceptions are geographically disjunct mesic species with no phylogeographical structure, the sooty owl *Tyto tenebricosa* complex (Norman *et al.*, 2002) and *Eucalyptus grandis* (Jones *et al.*, 2006). Within the major regions there is also genetic structuring representing later Pleistocene influences in all organisms. Species that have more restricted distributions within the major regions also show similar patterns of genetic structure, e.g. reptiles on the central coast (Colgan *et al.*, 2009). The broad patterns of lineage divergence within many species reflect common responses of population contractions due to climatic change. Species-specific patterns of lineage distribution within regions may reflect influences over different time scales or differing ecological tolerances.

In freshwater systems, species with low mobility typically show the vicariance that would be anticipated from historical isolation of drainages. For example, a suite of decapods (*Caradina* spp., *Euastacus* spp.) found throughout the east coast of Australia show drainage-based endemism reflecting Pliocene and Pleistocene influences (Hurwood & Hughes, 2001; Chenoweth & Hughes, 2003; Baker *et al.*, 2004; Page & Hughes, 2007). Perhaps not surprisingly, species with aerial life-stages, such as *Trichoptera* (caddis flies), tend not to show strong endemicity at the drainage system level as dispersal counteracts development of genetic endemism (Baker *et al.*, 2003; Schultheis & Hughes, 2005). Nonetheless, if barriers are sufficient, such subdivision can be seen in some flying insects that are good dispersers, such as Late Pleistocene divergence in the widely-distributed butterfly *Heteronympha merope* (Norgate *et al.*, 2009).

In a major research programme on fauna in the Australian Wet Tropics, phylogeographical patterning has been analysed in a framework of detailed modelling of potential distributions for the LGM and Holocene. Species display very high levels of genetic endemism in inferred rain forest refugia that are highly congruent across major animal groups, including snails, beetles, mammals, reptiles and birds (reviewed in Moritz *et al.*, 2009). The rain forest distribution in the Wet Tropics shows a major geographical break at the Black Mountain Corridor, and comparative phylogeography suggests that there is considerable temporal heterogeneity in divergence times of various groups across this break (Joseph *et al.*, 1995; Moussalli *et al.*, 2005; Moritz *et al.*, 2009). Phylogeographical studies on plants in the Wet Tropics are more limited, but genetic disjunction across this break has been demonstrated in some, but not all, *Elaeocarpus* species (Rossetto *et al.*, 2007, 2009). Substantial phylogeographical structure, sometimes congruent across taxa, has also been demonstrated for rain forests of central and southern Queensland (McGuigan *et al.*, 1998; Moritz *et al.*, 2000; Stuart-Fox *et al.*, 2001).

In the south-western mesic region of Western Australia divergent lineages occur in several species of frog (Edwards, 2007; Morgan *et al.*, 2007; Edwards *et al.*, 2008), and in the small heath dragon, *Rankinia adelaidensis*, where one lineage occurs on the west coast and one on the south-west coast (Melville *et al.*, 2008). Divergent lineages are also evident in several plant species through the south-west botanical province (Byrne & Macdonald, 2000; Wheeler & Byrne, 2006). In birds, phylogeographical structure is apparent between the south-western and south-eastern mesic regions and appears to have been established variously from the Early to Late Pleistocene (Donnellan *et al.*, 2009; Joseph *et al.*, 2009; Guay *et al.*, 2010; Murphy *et al.*, 2011) and even earlier in *Melithreptus* honeyeaters (Toon *et al.*, 2010).

In summary, this prediction, which has not been reviewed previously, indicates that there is considerable phylogeographical structuring and localized endemism across all biotic groups in the mesic zone, concordant with the hypothesis that many elements of the mesic biota have shown localized persistence and limited mobility through climatic fluctuations during the Quaternary. Notwithstanding that much of this idiosyncratic diversity probably reflects unresolved and undescribed species-level taxonomy, phylogeographical structuring is greater than might be expected and occurs both within and between mesic regions, even within those not expected to have experienced extremes of climate, and within regions with low topographical relief and few geographical barriers.

SYNTHESIS

Evolutionary processes shaping the ancestral mesic biota

Our review of phylogenetic data from many biotic groups in the Australian mesic biome brings renewed and fresh support, as well as novel insights, to the longstanding notion of the biome's antiquity. Floristically, the current mesic zone biota has rain forest and sclerophyllous components. The fossil record supports the hypothesis of rain forest habitat being the most ancient component, as that element is represented through the Eocene prior to the break-up of Gondwana. Syntheses of molecular phylogenetic data from plants and birds were consistent with the plant fossil evidence for rain forest habitat being ancestral to sclerophyllous habitat. The fossil record also indicates co-occurrence of sclerophyllous and rain forest elements, although sclerophyllous components of the mesic zone became more common during and after the Oligocene coincident with the contraction of rain forest elements. This led to a change in composition of the mesic biota. Integration of molecular and fossil data thus reinforces the finding that some contemporary rain forest elements may have evolved from taxa inhabiting sclerophyllous habitat, and that some sclerophyllous elements have a long history of representation, perhaps in habitats peripheral to rain forest.

The major change in the mesic biota was contraction of a continent-wide biota to south-eastern, south-western and eastern coastal refugia. Major vicariance events affecting the mesic biome involved the separation of the eastern and western mesic areas through the uplift of the Nullarbor Plain and the formation of the central deserts (Crisp & Cook, 2007). The fossil record demonstrated the changing floristic composition of the biota throughout the Late Miocene and Pliocene. The contraction of the mesic biota in response to aridification also resulted in fragmentation, particularly of rain forest elements, but also of components of the present open forest community. Present-day rain forest communities in Tasmania and along the east coast of mainland Australia occur as patches within a matrix of sclerophyllous communities. Fragmentation of the eastern mesic region appears to have been driven primarily by climate change as the Australian continent drifted north. The drying, and increasingly seasonal, climate interacted with geographical disjunctions (e.g. the east–west barrier of the Great Dividing Range and several major river and/or mountainous areas that intersect the Great Dividing Range along its north–south axis) to form a chain of disjunct biotic regions (Nix, 1982).

Extinction of species is a likely consequence of major contraction and fragmentation of mesic environments. It would lead to fewer extant species and long, naked branches in the topologies recovered in phylogenetic analyses. Such patterns were recovered in molecular phylogenies, particularly in plants and birds, where low taxon diversity and long branches characterized rain forest lineages in comparison to sclerophyllous lineages. The latter showed clearly higher rates of diversification. The phylogenetic data are consistent with fossil evidence for high rates of extinction of plants throughout the Miocene and Pliocene, and the primary driving force behind paucity of extant rain forest taxa is extinction. This extinction had a biased influence on the biota because it occurred mainly among rain forest elements whereas sclerophyllous elements showed a contrastingly greater rate of net speciation. Against this trend, there has no doubt been some allopatric speciation in rain forest groups as once contiguous rain forest blocks became separated. Overall, these patterns and the processes we have identified show that variation in rates of extinction over different time frames have affected the patterns of diversity in the rain forest and sclerophyllous components of the mesic zone across Australia.

The large components of the mesic biota with *in situ* origins have been supplemented by dispersal of organisms into Australia, particularly from its near northern neighbours. This immigration largely followed from tectonic shifting of landmasses (as Australia approached Asia) and changed environmental conditions allowing geographical proximity of ecologically similar regions in present-day Southeast Asia and Australia. Few resolved phylogenies with sufficient taxon sampling across Australia, New Guinea and Southeast Asia were available to explicitly test the hypothesis of immigration into the Australian mesic zone from neighbouring northern biotas. However, some groups of mammals and many plant genera show a pattern of immigration that contradicts a trenchant, older notion of the mesic zone having been wholly resistant to invasions (see Introduction). Despite the possible niche availability in sclerophyllous environments, it appears that immigrant lineages have not established at higher rates in sclerophyllous systems than in rain forest systems. The finding that transoceanic colonization most often involves no change of biome (Crisp *et al.*, 2009) suggests that immigrant Asian taxa could have established in wet or monsoonal habitats in Australia rather than in mesic sclerophyll environments or relatively hostile arid/semi-arid environments.

Persistence of mesic biota through Quaternary climatic oscillations

It is clear that the mesic biota in Australia has not evolved as a single unit but has been fragmented over multiple time scales through its history. This fragmentation was particularly driven by increased inter-annual to orbital climatic variability and seasonality during the Quaternary. Phylogeographical analyses reveal highly divergent lineages in many taxa, and in most regions of the mesic zone, including sclerophyllous and rain forest communities. Divergence of lineages occurred during the Pliocene and Pleistocene, and they persisted and further diversified despite the climatic oscillations from the mid-Pleistocene and increased aridity leading to additional rounds of contraction in mesic environments. There are strong phylogeographical patterns in areas of high topographic relief, particularly in the tropical and subtropical rain forests, and the temperate forests of the south-eastern region. Genetic structuring is also evident in areas with subdued relief in the south-western region where there are few topographical features to promote vicariance. Even in currently widespread species in sclerophyllous habitat, the legacy of historical contraction of distributions is evident in genetic structure and phylogeographical patterns. Persistence of the biota through climatic oscillations over multiple glacial cycles has led to genetic signatures of high diversity and endemism in many localities, with few indications of major expansions. This is a notable contrast with patterns of recolonization following glaciation in the temperate biota of the Northern Hemisphere.

FUTURE DIRECTIONS

We have inferred major processes from geological and fossil evidence and examined their influences on the evolutionary history of the Australian mesic zone biota through analysis of phylogenetic data in the context of the palaeoclimatic and geological history of the Australian continent. Our understanding of the interactions and relative importance of contraction, extinction, fragmentation and invasion in driving major changes in the distribution and composition of the mesic biota has become clearer and more detailed. We have elucidated the influences of these processes at a continental scale but many more avenues of fruitful and informative investigation should be pursued to extend this work to a finer scale. We suggest the following areas as those that would yield further insights into the evolution of this ancient biome if an interdisciplinary approach similar to that we have taken is pursued:

1. Phylogenetic analyses (e.g. area cladograms) to establish the level of congruence between co-occurring taxa in isolated blocks of remnant rain forest.
2. Phylogenies of neglected lineages or biotic groups such as fungi, bryophytes, ferns, invertebrates and many aquatic vertebrates.
3. Further testing of the hypothesis that taxa in mesic sclerophyllous environments have evolved from rain forest ancestors.
4. Further investigation of the role of immigration/invasion in the current composition of the mesic biota and especially the drivers of these processes.
5. Explicit tests to establish whether the mesic zone has been more resistant to immigration than other biomes in Australia (e.g. arid, monsoonal).
6. Investigation of species richness and rates of extinction, speciation and evolution in sclerophyllous versus rain forest lineages; our review suggests interesting patterns but many more phylogenies are required to evaluate the role of these processes adequately.
7. Comparison of the patterns of lineage birth and death between mesic and non-mesic zones; our review did not investigate this aspect of interactions of the mesic biome with other biomes. Clarification of the temporal layering and heterogeneity that has been involved will require many more analyses of individual taxa, and the systematic inclusion of New Guinean taxa.
8. Tests for ancestry of sclerophyllous components in other biotic groups, not just plants and herpetofauna as has been shown here.
9. Explicit tests of diversification dynamics especially in plant taxa with reasonable fossil records, allowing for tests for changes in extinction rates.
10. Investigation of how the biogeographical and evolutionary dynamics of the semi-arid and mesic open woodlands and savannas relate to the neighbouring arid, monsoonal and mesic biomes.

CONCLUSIONS

The mesic biome has been influenced by various selective pressures over a range of geographical and temporal scales. Over longer time frames, increasing aridification has driven widespread contraction of the biome to occupy a relatively small area of the continent. Coincidently, the mesic zone has become the home of immigrant lineages from the north. More recently, cycling of arid and mesic conditions has led to both fragmentation and reunification of mesic environments. This has promoted strong patterns of regional variation both within and between species.

This review has facilitated a greater understanding of the organismal responses to climate and habitat change that will allow us to make predictions about the fate of Australia's mesic biota over the next century with more confidence. Further broad-ranging surveys of the biogeographical histories of different lineages will form an important source of information for understanding and predicting the biotic responses to long-term climatic and habitat change. In particular, knowledge of the level of resilience of mesic biota to long-term climatic change and its persistence through Quaternary climatic cycles will be required to identify refugia and develop climate change adaptation strategies.

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BIOSKETCH

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