How Was the Australian Flora Assembled Over the Last 65 Million Years? A Molecular Phylogenetic Perspective

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Keywords

vicariance, dispersal, fire, climate change, diversification, turnover, ecological opportunity, sclerophylly

Abstract

Australia has a mostly dry, open, fire-shaped landscape of sclerophyllous and xeromorphic flora dominated by eucalypt and acacia trees, with diverse shrubs from a few families such as Myrtaceae, Proteaceae, and Fabaceae. Using molecular phylogenies to test hypotheses derived from the fossil record, we review the principal forces that transformed the ancestral Gondwanan rainforest through the Cenozoic. Today's vegetation is a mix of ancient radiations that have persisted in Australia through dramatic climate change since before the breakup of Gondwana, and more recent lineages whose ancestors arrived by trans-oceanic dispersal. Signatures in the fossil record of lineage turnover and trait evolutionary change are detected in phylogenies, but often at earlier dates. The Australian biota is a sample of the wider region, with extinction of some taxa and radiation of others (due to chance and opportunity), but biotic and abiotic interactions have resulted in a unique flora and fauna.

INTRODUCTION

This review considers the evolution of the Australian flora through the processes that shaped its transition from its Gondwanan heritage to that of the present-day island-continent. We do not attempt to tell the whole story but concentrate on the major evolutionary and ecological changes and especially on the insights gained through molecular studies.

Certain features of the Australian flora and vegetation are considered distinctive; they are the result of unique interactions among the historical heritage, climate, soils, and long isolation of the island-continent. These include fire-dependence, sclerophylly, xeromorphy, dominance by a few taxa (e.g., Myrtaceae, Proteaceae, and genera *Eucalyptus*, *Acacia*, and *Triodia*), and high species diversity with narrow endemism in two contrasting environments: the wet tropics of the northeast and the Southwest Australian Floristic Region (SWAFR) with its Mediterranean climate (**Figure 1**). We assess whether the 30 Ma of isolation of this continent have resulted in a unique flora or whether Australia has no more than a somewhat modified sample of the global flora.

In the late Cretaceous, Australia was part of Gondwana and close to the South Pole, and the vegetation was largely a dark, wet forest of conifers, ferns, *Ginkgo*, and angiosperms belonging to Casuarinaceae, Proteaceae, and *Nothofagus* (Hill 2004). Today (**Figure 1**) there is little (if any) of this kind of landscape and instead Australia consists mostly of open habitat and, in the temperate south, is dominated by sclerophyll plants such as eucalypts (sclerophyll biome). The vast, central arid biome is hummock grassland of *Triodia* or open shrubland dominated by *Acacia* or chenopods (Amaranthaceae), depending upon soil type (**Figure 1**). Across the tropical north is the monsoonal biome (savannah), consisting largely of open grassy woodland (eucalypts, acacias, and various tropical trees); here, too, *Triodia* is prominent on poor soils. The everwet biome is restricted to an archipelago of rainforest pockets strung along the east coast.

We structure our review around the following five major drivers that are hypothesized to have shaped the evolution of the Australian flora:

1. Biogeographic processes: continental drift resulting in speciation by vicariance when Australia was isolated at the end of the Eocene, followed by transoceanic dispersal and establishment of immigrant lineages after isolation (Crisp & Cook 2009).
2. Fire, which created open communities and likely led to the dominance of eucalypts (Bond & Midgley 2012, Crisp et al. 2011, Lamont & He 2012).
3. Climate change: three global cooling events during the Cenozoic (the last 65 Ma) caused floristic turnover as the everwet biome contracted and others expanded (Byrne et al. 2008, 2011; McGowran et al. 2004).
4. Geomorphological and pedological processes, especially prolonged weathering of the landscape, favored the dominance of sclerophylly and specialized adaptations for extracting nutrients from deficient soils (Huston 2012, Lambers et al. 2011, Orians & Milewski 2007, Pate & Verboom 2009). These processes likely contributed to allopatric speciation (e.g., by splitting populations) and sympatric speciation (e.g., by creating soil mosaics).
5. Ecological opportunities due to the formation of new habitats, evolution of new mutualisms, key innovations, and release from antagonists likely resulted in adaptive radiations.

BIOGEOGRAPHIC ORIGINS: GONDWANAN RELICS OR OCEANIC TRAMPS?

The longstanding controversy about why closely related organisms occur in widely separated landmasses, such as the southern continents, has stood since Hooker and Darwin had opposing ideas in the nineteenth century. Joseph Hooker (1853) and his contemporary Alfred Russell

Gondwana: ancient supercontinent that separated into the present-day landmasses Africa, Antarctica, Australia, Madagascar, India, New Caledonia, New Zealand, and South America

Sclerophylly: a syndrome in woody plants of tough, long-lived leaves, large quantities of lignin, and well-defended carbon-rich but nutrient-poor tissues

Xeromorphy: phenotypic traits adaptive to arid conditions; can be confused with sclerophylly arising from other causes, e.g., nutrient deficiency

Southwest Australian Floristic Region (SWAFR): an internationally recognized biodiversity hotspot

Biome: a large-scale biotic region characterized by climate, evolutionary history, and growth forms of the dominant plants

Vicariance: allopatric speciation of populations following their geographic separation by geological or climatic processes, such as continental drift

Allopatric: refers to populations or species that are separated by a wide geographic gap
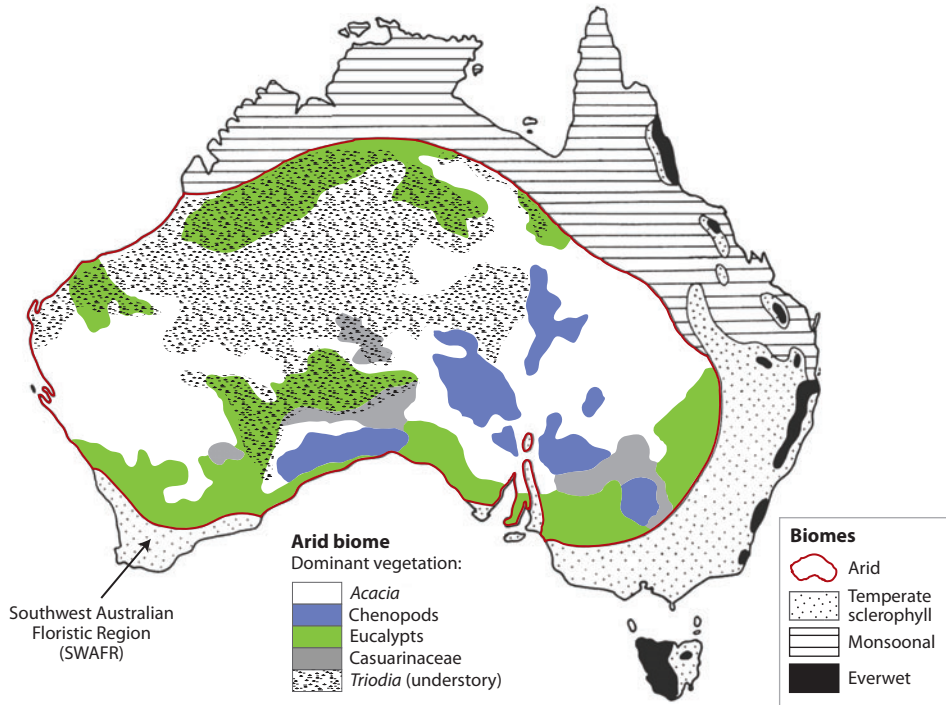
Figure 1

Contemporary biomes of Australia with the dominant vegetation mapped in the arid biome, which is outlined in red. The sclerophyll and monsoonal biomes are dominated mainly by eucalypts and acacias. The everwet biome is mostly rainforest. Based on Crisp et al. (2004) and Kershaw et al. (1994).

Wallace (1860) believed that some continents were once contiguous, forming a supercontinent, and that the present landmasses became isolated as intervening land sank beneath the oceans. Charles Darwin (1855), however, posited that dispersal explained the separation of related plants in the Southern Hemisphere and conducted experiments testing the longevity and flotation of seeds in seawater. When Wegener's (1915) idea of continental drift was finally accepted, the idea of vicariance became the dominant paradigm to explain the southern distributions.

More recently, the presence of young fossil taxa shared across landmasses (e.g., Pole 1993) and molecular dating that indicates some divergences that are too young to be the result of vicariance (e.g., Crisp et al. 2009) have led to a revival of the idea that long-distance dispersal has likely played a major role in the distribution of plants in the Southern Hemisphere—including in the assembly of the Australian flora.

How Many Australian Plant Lineages Date Back to Gondwana Compared with Those that Dispersed from Overseas After Isolation?

We compiled data for 85 dated clades of vascular plants from our own studies and published literature (details and data in **Supplemental Text** and **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) and found that 38 clades (45%) likely originated in Gondwana and 41 (48%) likely arrived via dispersal (**Figure 2**). The geographic source of 6 clades (7%) remained undetermined either because

Supplemental Material

Sympatric: refers to populations or species that co-occur, where distance is no barrier to gene flow

Key innovation: a novel adaptive trait that enables a lineage to exploit new habitat or resources and adaptively radiate

Adaptive radiation: refers to evolutionary diversification of a single lineage, in which species adapt to multiple distinct ecological niches
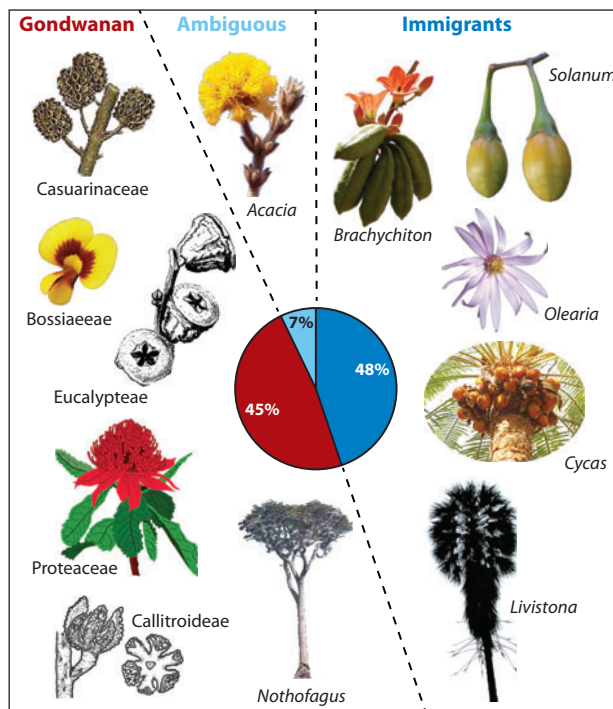
Figure 2

Geographic origins of 85 Australian vascular plant clades, illustrated by exemplar taxa. Pie chart shows proportion reconstructed as Gondwanan, i.e., present before isolation of Australia at 33 Mya (*red*, 45%), versus immigrants following isolation, i.e., by transoceanic dispersal (*dark blue*, 48%), or ambiguous (*light blue*, 7%).

the stem included the time when Australia became isolated (**Figure 3**) or because the clade had a worldwide sister group, or both. Most of these clades were endemic Australian families (e.g., Austrobaileyaceae and Cephalotaceae), and their unclear biogeographic origins are comparable with the problem of how and when *Amborella* (which is the sister group to all other angiosperms) got to New Caledonia (Grandcolas et al. 2008).

Clade: a lineage or branch in a phylogeny comprising all the species descended from a single common ancestor

Sister groups: clades that share the same most recent common ancestor and therefore are the same evolutionary age

Is There a Signal in the Australian Flora of Speciation by Gondwanan Vicariance?

From the data in **Supplemental Table 1**, we extracted divergence times for sister-group pairs occurring in Australia and other landmasses (**Supplemental Table 2**). We partitioned these data geographically with respect to the overseas sister group, and we plotted the distribution of divergence times for each geographic partition (**Figure 4**). Only South America–Australia divergences show a strong pattern of vicariance: The median divergence time of the 21 samples is 33 Mya, which coincides with the opening of both Drake Passage between Patagonia and Antarctica and the Southern Ocean between Tasmania and Antarctica. Nevertheless, at least 50% of these divergences appear to be too old (45 to 91 Mya) or too young (5 to 24 Mya) to have been a result of Gondwanan vicariance, even after allowing for error in individual divergence-time estimates.

In **Figure 4**, all divergences in the other geographic categories (except World) are too young to be explained by Gondwanan (or Pangaean) vicariance, so they were presumably the result
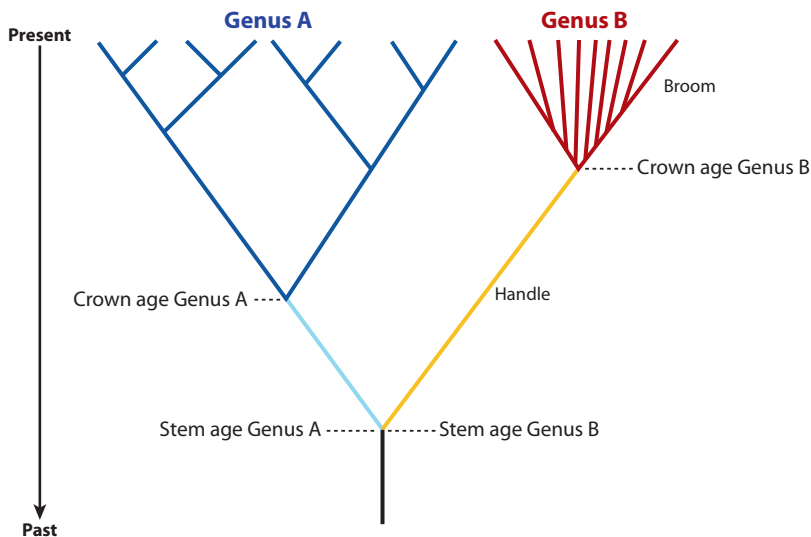
Figure 3

Stems, crowns, brooms, and handles. The crown of a group includes all the descendants of the most recent common ancestor (MRCA) of the extant taxa. The age of the crown is the time of that MRCA. The stem is the inferred lineage leading to the crown from the last common ancestor shared with another group, its sister group. Sister groups have the same-aged stems. Here, the crown of Genus A is in dark blue and its stem is in pale blue, and the crown of Genus B is in red and its stem is in gold. Genus B shows a broom and handle–shaped radiation—it has a long stem and a crown where the lineages radiated in only a short period of time, like the straws of a broom. Let us imagine that Genus A is endemic to Australia and is nested within a group occurring in Asia. In reconstructing the geographic origin of Genus A, its crown age represents the earliest time when we can be confident that the lineage was in Australia, and its stem age represents the earliest time that it could have been in Australia; that is, the length of the stem represents a period of uncertainty about the origin of the group in Australia. If the stem includes the time when Australia became isolated, then we cannot decide whether the lineage originated in situ (before that time) or arrived by dispersal later.

of dispersal. For example, the Tasman-Coral Sea east of Australia opened about 75 Mya; yet the oldest estimated divergence time for sister taxa in Australia and New Caledonia was about 42 Mya, and the oldest for Australia and New Zealand was about 59 Mya. This is consistent with multiple studies indicating that most, if not all, of the flora of these islands arrived by post-Gondwanan dispersal (Grandcolas et al. 2008, Wallis & Trewick 2009). Divergences between Australia and Africa, southeast Asia, or the pantropics would have to be dated older than 100 Mya to be vicariant as a result of continental drift, but none is sufficiently old; the oldest is dated about 51 Mya. Arrivals in Australia from the Northern Hemisphere are also young (some are Pleistocene in age) and clearly dispersed.

Does the Tropical Flora Have a Greater Proportion of Dispersed Taxa (e.g., from Asia and Africa) and Does the Temperate Flora Have More Gondwanan-Origin Taxa?

It has long been considered that different elements of the Australian flora had different geographic origins (Hooker 1860) and, moreover, that the temperate flora had a Gondwanan origin, whereas tropical taxa are hypothesized to have arrived by dispersal from Asia with increasing frequency as the Australian plate drifted north into tropical latitudes (e.g., Barlow 1981). These hypotheses are
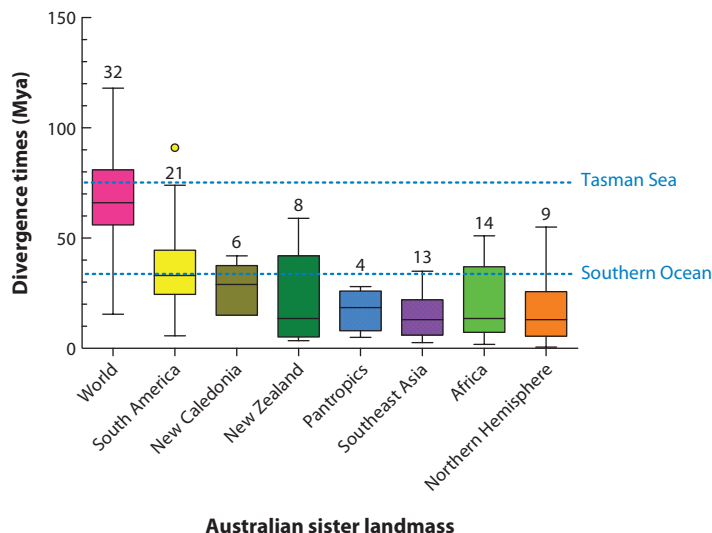
Figure 4

Times of divergence between Australian clades and their overseas sister groups, partitioned geographically. The boxes show the median and the 25th and 75th percentiles, whereas the error bars show the 2.5th and 97.5th percentiles; *n* (the number of divergences sampled) is shown above each plot. The open circle above the South American error bar is an outlier. Dotted lines indicate approximate oceanic opening times resulting from continental drift: The Tasman Sea separated Australia from New Zealand and New Caledonia, and the Southern Ocean separated Australia, Antarctica, and South America. The categories of World and Pantropics comprise lineages in which the ancestral area shared with Australia could not be reconstructed more precisely.

supported by analyses of the fossil record of woody rainforest taxa (Sniderman & Jordan 2011) and of dated molecular phylogenies of extant taxa (D.M. Crayn, C. Costion, M.G. Harrington, unpublished data). Australia shares with other southern landmasses both Gondwanan-age fossil plant taxa and their living descendants occurring in cool temperate rainforests. By contrast, extant taxa in warmer rainforests have close relatives in southeast Asia and a more recent fossil record, which has increased toward the present (Sniderman & Jordan 2011). Given that Australian rainforests (everwet biome) have contracted to a small fraction of their original extent (Byrne et al. 2011, Hill et al. 1999, Martin 2006), these hypotheses require testing with flora from other biomes. Here, we ask whether the apparent trend through time in geographic origins of the flora reflects differences in the ages of biomes. The everwet and sclerophyll biomes were present in Gondwana, whereas the monsoonal, arid, and alpine biomes have more recent origins, postdating the mid-Miocene. At this time, global climate became sharply cooler, drier, and more seasonal, and mountain building occurred in some regions such as southeast Australia, leading to the origin and expansion of the monsoonal, arid, and alpine biomes (Bowman et al. 2010; Byrne et al. 2008, 2011; Crisp et al. 2009; Hill 2004; Macphail 2007).

Supplemental Material

We inferred the ancestral biome (where possible) of Australian clades (**Supplemental Table 3**) and constructed a 2×2 contingency table that partitioned clades by geographic clade origin and biome age, i.e., whether the biome originated before or after the mid-Miocene. We found that lineages in the younger biomes are overwhelmingly dispersed into Australia; conversely, all clades that were already in Australia before it was isolated originated in the older sclerophyll and everwet biomes (Fisher's exact two-tailed test, $P = 0.00061$). This test is somewhat simplistic because Australia's everwet biome includes tropical rainforest, which Sniderman & Jordan (2011) found

to have received recent colonists from Asia. However, their definition of warm (mesothermal and megathermal) rainforests includes dry rainforest and vine thicket, which we consider to be part of the monsoonal biome (cf. Bowman et al. 2010). Nevertheless, it seems clear that the increasing trend through time toward immigration of taxa by dispersal reflects ecological opportunity resulting from the origin and expansion of new biomes (especially monsoonal and arid) following global climatic change in the Miocene. This trend also reflects Australia's drift into tropical latitudes and increasing proximity to southeast Asia.

TRANSFORMATION BY FIRE

Fire-Adapted Communities Occurred from the Cretaceous Onward

Today, wildfires recurrently disturb communities in all temperate to warm, periodically dry regions of Australia (Bowman 2000, Bradstock et al. 2012) and the world (Bond & Midgley 2012, Bowman et al. 2009). Australia is considered the most fire-prone continent because a greater proportion of the total area is occupied by flammable communities than elsewhere (Bowman 2000, Bradstock et al. 2012). Fire regimes vary from monsoonal savannah (burned every 2–5 years) to temperate, wet eucalypt forests that experience infrequent (decades- to century-scale) but disastrous fires that can destroy communities and kill hundreds of people (Bradstock 2010).

Fire structures ecosystems (Bradstock et al. 2012, Pausas & Keeley 2009), for example, by controlling the boundary between rainforest and sclerophyll forest or savannah (Bond & Midgley 2012, Bowman 2000). Over evolutionary time, some plants adapt to fire (Keeley et al. 2011, Pausas & Keeley 2009) and, by identifying traits that are adaptive to particular fire regimes, the temporal history of fire regimes can be traced using molecular phylogenies (Crisp et al. 2011, He et al. 2011, Lamont & He 2012, Simon & Pennington 2012). This approach provides evidence independent of that from the physical environment, such as the geological record of atmospheric O_2 and CO_2 levels, temperature, precipitation, seasonality, and climatic conduciveness to ignition of wildfires (Beerling & Osborne 2006, Bond & Scott 2010).

The geological record of inertinite, a distinctive form of fossil charcoal resulting from wildfire (Bond & Scott 2010), and charcoalified flowers (Cantrill et al. 2011), shows that fire occurred worldwide with high frequency through the Cretaceous and Paleocene. Such evidence is almost unknown from Australia prior to the Oligocene (Kershaw et al. 2002), though the record has not been investigated systematically (M. Macphail, personal communication). Nevertheless, late Cretaceous sites from Antarctica (c. 83 Mya; Eklund et al. 2004) and New Zealand (c. 70 Mya; Cantrill et al. 2011) have yielded charcoalified mesofossils of diverse seed plant taxa, including angiosperms.

Recently, molecular phylogenetic studies tracing fire-adaptive traits through time suggest that fire was a selective force in Cretaceous and Paleogene communities that included eucalypts (c. 60 Mya; Crisp et al. 2011) and Proteaceae (88 Mya; Lamont & He 2012), notably the endemic Australian genus *Banksia* (60 Mya; He et al. 2011) (**Figure 5b**). Eucalypts have unique epicormic structures in their bark that are specialized for postfire resprouting. They could be an evolutionary modification of epicormic buds that resprout following drought or mechanical damage. However, epicormic buds of most noneucalypt species studied to date are located close to the bark surface, where they are often killed by fire (Burrows 2013). In eucalypts, these structures are narrow, radially oriented strips of cells of meristematic appearance, which are best developed within the innermost bark or even the outermost wood (Burrows 2013). Thus, at least some of the bud-forming cells have the full thickness of the bark as protection and can still regenerate after higher intensity fires (Burrows 2013). This structure has been found in all major eucalypt
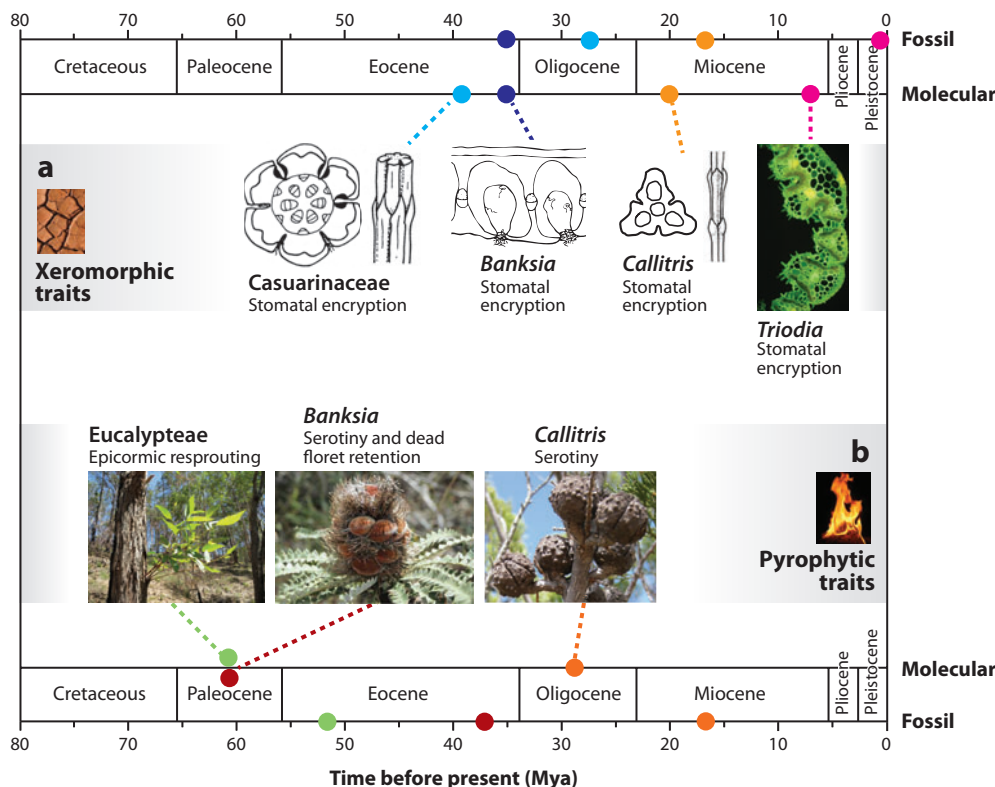
Figure 5

Origination times of (*a*) arid-adaptive (xeromorphic) and (*b*) fire-adaptive (pyrophytic) traits in exemplar clades, as inferred from molecular dating and the fossil record. Molecular dates are shown by colored dots on timelines, with links to traits by dashed lines. Dots with matching colors but no dashed line show the respective first appearances of traits in the fossil record. The molecular date is older in every case except stomatal encryption in *Banksia*. Sources: Casuarinaceae and *Banksia* line drawings (Hill 1994); *Triodia* leaf section (Watson & Dallwitz 1992 onward). Other photos by M.D.C.

lineages, growth forms, and Australian regions and can be unambiguously reconstructed as having originated in the most recent common ancestor of all eucalypts, c. 60 Mya (Crisp et al. 2011). In a similar phylogenetic study of the evolution of fire-adaptive traits in *Banksia*, a key component of Australian sclerophyll communities, He et al. (2011) found that serotiny (on-plant seed storage until burning) and dead floret retention (which enhances burning) co-originated with the first appearance of ancestral *Banksia* 60.8 Mya (**Figure 5b**).

Where Were Fire-Dependent Communities in the Cool, Wet Late Eocene?

Around 55–50 Mya, the world's climate was very warm and wet (Eocene climatic optimum: McGowran et al. 2004), and angiosperm-dominated tropical rainforests proliferated worldwide (Bond & Midgley 2012), including Australia (Hill et al. 1999, Macphail 2007). This was followed by progressive cooling after 50 Mya, though the climate continued to be wet (Bond & Scott 2010, Macphail 2007, McGowran et al. 2004), ending the long run of conditions conducive to wildfires. What happened to the fire-dominated communities during the Eocene?

Several lines of evidence and inference suggest that flammable communities existed, at least in some places, in Australia-Gondwana through the Eocene. First, trait mapping on molecular phylogenies suggests that multiple fire-adapted taxa were present during the late Eocene or earlier (≥35 Mya). These reconstructions imply that the descendants of these ancestors passed through the Eocene, retaining their fire adaptations to the present, e.g., the eucalypts and Proteaceae described above. Fire-stimulated flowering dates at least to the late Eocene in some other Australian taxa: Droseraceae (>41 Mya), Haemodoraceae (>48 Mya), and Loranthaceae (>45 Mya) (Lamont & Downes 2011). Legumes in Australian sclerophyll communities have hard seeds that are quickly dispersed by ants and buried, where they are protected from fire and germinate soon after burning (Orians & Milewski 2007). A diverse legume group in this biome, the pea-flowered Bossiaeeae, dates to the Eocene (44–51 Mya; Crisp & Cook 2009).

Second, there is evidence, independent of fossil floras, of seasonally dry climate, which is an important determinant of the flammability of vegetation (Bowman et al. 2009). Global climatic modeling indicates that Australia had a seasonally dry monsoon-like climate in the mid-late Eocene, even though it was technically not a monsoon; this is because of the high paleolatitude (Huber & Goldner 2012): Cape York was c. 30°S and Tasmania was c. 60°S (McGowran et al. 2004). Although global climate cooled significantly through the late Eocene, it was always much warmer than today (McGowran et al. 2004).

Third, by matching pollen (Macphail 2007, his table 7) and leaf (Greenwood 1996) morphology of fossil assemblages with those of present-day taxa and communities, paleobotanists have inferred monsoonal climates from mid- to late Eocene floras in central and northern Australia (Greenwood 1996, Martin 2006, Pole & Bowman 1996), especially in the northwest (Macphail 2007). However, dates for some of these floras are uncertain (e.g., Pole & Bowman 1996), climatic inferences from the morphology of assemblages are contentious (Greenwood 2005, Hill 2004), and there is some danger of circularity in using this approach for making paleoecological inferences.

Fourth, even today rainforest and flammable sclerophyll exist as mosaics. The high plateau of the Gibraltar Range in northern New South Wales experiences a temperate climate with reliable rainfall exceeding 1,500 mm annually and, on the deep, rich basalt-derived soils, supports tall rainforest. This forms a mosaic with sclerophyll communities (heath and eucalypt forest) growing on granite that weathers to highly nutrient-deficient sandy soil. Fossil evidence supports similar scenarios: Several Eocene sites in central and northern Australia have been characterized as mosaics. For example, central Australia was reconstructed as experiencing seasonal rainfall, with rainforest restricted to the well-watered valley bottoms (riparian) and sclerophyll vegetation on the slopes and ridges (Macphail 2007, Martin 2006). At mid- to late Eocene sites from south-west Western Australia reconstructed as *Nothofagus*-dominated rainforest, a high diversity of sclerophyll plants (which were likely flammable), particularly Myrtaceae and Proteaceae, has been reported (Hill & Merrifield 1993, Itzstein-Davey 2007), which is consistent with the phylogenetic reconstructions by Lamont et al. (2011, Lamont & He 2012).

In summary, although direct geological evidence of fire in the late Eocene of Australia-Gondwana is lacking, circumstantial evidence, including that from molecular phylogenies, suggests that fire-dependent communities could have existed in northern Australia. The charcoal record should be investigated there.

CLIMATE CHANGE

At the end of the Eocene, the tectonic separation of Australia and South America from Antarctica opened the Southern Ocean and changed the world's climate. Onset of the Antarctic circumpolar
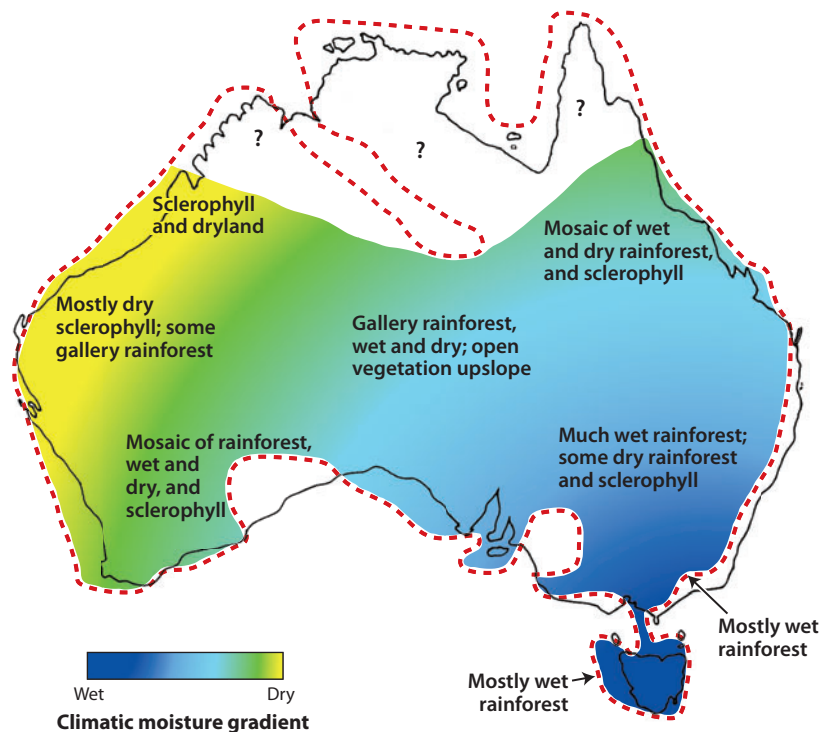
Figure 6

Reconstruction of Australian vegetation at the Oligocene-Miocene boundary (c. 23 Mya), about 12 Ma after isolation. Continuous black outline shows contemporary coastline, and dashed red outline shows early Miocene coastline. Wet rainforest is characterized by *Nothofagus*, dry rainforest by Araucariaceae, open sclerophyll vegetation by eucalypts, and dryland by Asteraceae and Poaceae. This map is necessarily simplified, being based on pollen from ~12 widely separated sites; no data are available for most of the continent. Based on Kershaw et al. (1994) and Macphail (2007).

current steepened the temperature gradient from the Equator to the South Pole, causing Antarctica to glaciate and initiating cooler, more seasonal climates worldwide (McGowran et al. 2004, McLoughlin 2001). The impact on Australia was complicated by its northward drift, resulting in warmer climates in the north, despite cooling in the south (McGowran et al. 2004). Global cooling and drying continued to the present, with periods of amelioration punctuated by three episodes of sharp drops in global temperature: the cooling event marking the Eocene-Oligocene boundary (c. 33 Mya), a second event initiating aridification in the mid-Miocene (c. 14 Mya), and a third event late in the Pliocene (4–2 Mya) (McGowran et al. 2004) leading to formation of the central Australian desert (Fujioka et al. 2009, Martin 2006). Southern Hemisphere fossil floras from high latitudes, including Australia, record relatively little extinction at the end of the Cretaceous (Barreda et al. 2012, Macphail 2007), whereas the Eocene-Oligocene event initiated major changes. Rainforests contracted and gymnosperms declined while open, sclerophyllous and xeromorphic vegetation increased as drier and more seasonal biomes expanded: initially, the sclerophyll biome, and later, the alpine, monsoonal, and arid biomes (Hill 2004, Hill et al. 1999, Kershaw et al. 1994, Macphail 2007, McLoughlin et al. 2011) (**Figure 6**).
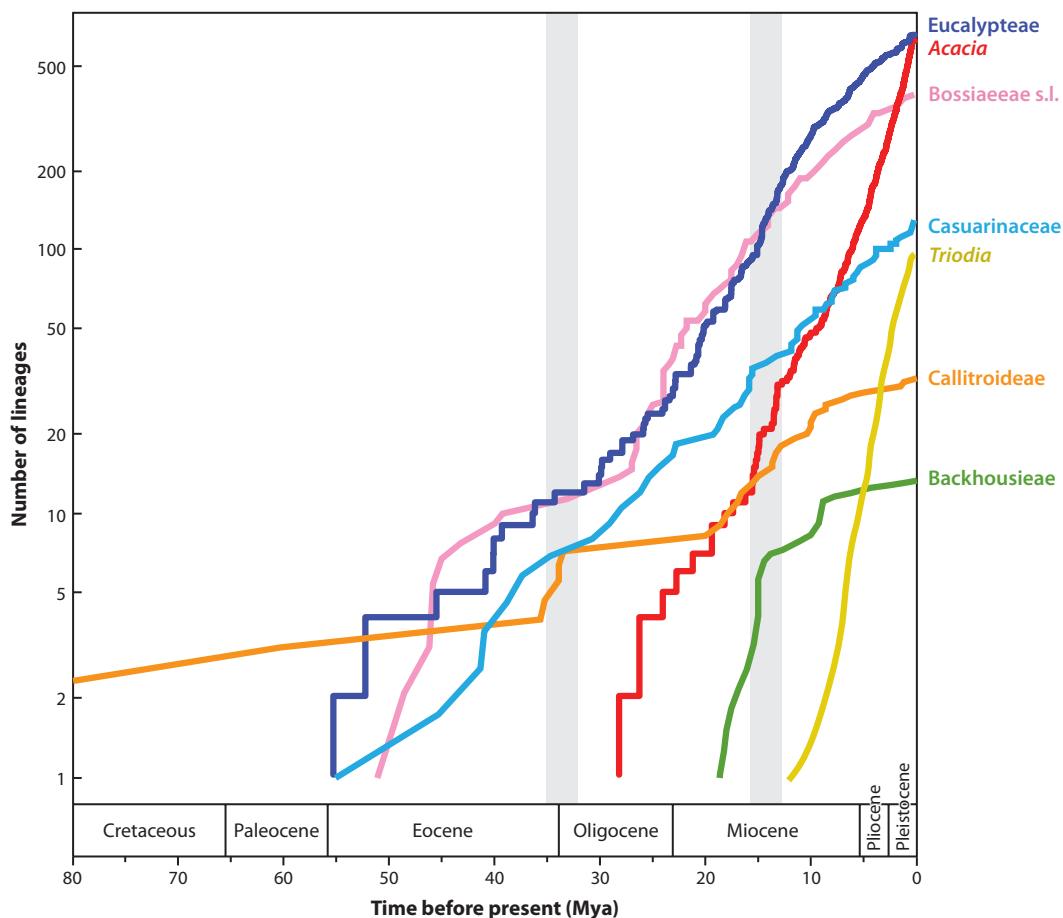
Figure 7

Lineages-through-time (LTT) plots from dated phylogenies of seven Australian plant groups. An increase in diversification rate appears as a steepening in the slope of the LTT plot, e.g., in *Acacia* from 15 Mya; conversely, a decreasing slope indicates a decreasing diversification rate, e.g., in Eucalypteae, Callitroideae, and Bossiaeeae from 15 Mya. A major extinction event leaving survivors that reradiated is visualized as a plateau followed by an abrupt steepening in the slope of the plot, e.g., in Callitroideae about 35 Mya and 20 Mya. Each gray bar indicates a global cooling and aridification event. See text for discussion of the links between these events and diversification in these lineages. Sources: Eucalypteae and *Acacia* (A.H. Thornhill, J.T. Miller, M.D. Crisp, L.G. Cook, paper in preparation); Fabaceae tribe Bossiaeeae sensu lato (Crisp & Cook 2009); Casuarinaceae (L.G. Cook, A. Toon, M.D. Crisp, unpublished data); Cupressaceae subfamily Callitroideae (M.D. Crisp, S. Sakaguchi, Y. Isagi, D. Bowman, unpublished data); Myrtaceae tribe Backhousieae (Harrington et al. 2012); and *Triodia* (A. Toon, M.D. Crisp, L.G. Cook, unpublished data).

Aridification: Contrasting Trends in Diversification as Some Biomes Contracted and Others Expanded

Molecular phylogenies of multiple Australian plant lineages show signatures of diversification shifts, as predicted from the geological record of fossils and paleoclimates. Changes in slopes of lineages-through-time (LTT) plots, likely reflecting extinctions of everwet-biome lineages, are evident in peas (Bossiaeeae), cypresses (Callitroideae), and possibly also eucalypts and Casuarinaceae from about the time of the end-Eocene cooling event (**Figure 7**). Australian representatives of these taxa are either absent or minimally represented in the everwet biome today, but

Lineages through time (LTT): a plot of the number of species accumulating toward the present, estimated from a dated phylogeny

Cupressaceae (cypresses) and Casuarinaceae (she-oaks) were conspicuous components of this biome in the Eocene fossil record (Hill 2004, Hill & Brodribb 1999, Macphail 2007). Eucalypts have essentially no Paleogene fossil record in Australia (Hill 1994), though in the Eocene they grew on rainforest margins in the Patagonian region of Gondwana (Hermsen et al. 2012), where they are now extinct.

Phylogenies of numerous other taxa show evidence of extinction and reradiation at the end of the Eocene. *Nothofagus* had a major end-Eocene extinction preceding radiation of the four extant subgenera across Southern Hemisphere landmasses (Cook & Crisp 2005). One lineage within the *Nothofagus* subgenus *Brassospora* tracked everwet, mesothermal rainforest as it contracted northward to the tropics, surviving today only in New Guinea and New Caledonia (Hill 2004). By contrast, other subgenera—*Nothofagus*, *Lophozonia*, and *Fuscospora*—adapted to the cooling, more seasonal climates in the south, where they expanded in the post-Eocene fossil record, in both Patagonia (Barreda & Palazzesi 2007) and Australia (Hill 2001, 2004), which is consistent with the dated phylogeny (Cook & Crisp 2005). Similarly, the family Tremandraceae (now in synonymy) diverged from within the rainforest family Elaeocarpaceae during the Paleocene, and it underwent a rapid radiation from the late Eocene (Crayn et al. 2006). Tremandraceae occurs in the sclerophyll biome; the plants are subshrubs, and its rate of molecular evolution (measured by counting substitutions in DNA sequences) is about double that of its rainforest sisters (Crayn et al. 2006). The end-Eocene climate change probably caused extinction of the rainforest members of this clade, with the survivor being that which had shifted adaptively and subsequently radiated in the sclerophyll biome.

Gymnosperms were abundant in the Australian fossil record after the end of the Cretaceous (Macphail 2007), including the last surviving representatives of the Bennettitales in the world (McLoughlin et al. 2011). Low extant diversity of gymnosperms results largely from major extinctions seen in the Cenozoic fossil record (Hill 2004, Hill & Brodribb 1999, McLoughlin et al. 2011); peaks occur soon after the end-Eocene and mid-Miocene climate-change events (Niklas 1997). Dated molecular phylogenies of gymnosperms worldwide show broom-shaped clades (**Figure 3**) (Crisp & Cook 2011, Nagalingum et al. 2011), which is consistent with extinction and reradiation (Crisp & Cook 2009). Few gymnosperm lineages have survived the Cenozoic, and diversification rate modeling shows that the low gymnosperm diversity can be explained by increased extinction against a background of unchanging speciation rate (Crisp & Cook 2011).

Rainforest began to contract markedly from 25 Mya (Hill et al. 1999, e.g., their figure 70; also Kershaw et al. 1994), and rainforest-adapted Callitroideae (*Austrocedrus*, *Fitzroya*, *Libocedrus*, and *Papuacedrus*) are well represented in the Australian Oligocene macrofossil record but are now extinct in Australia (Hill & Brodribb 1999). A second plateau occurs in the LTT of Callitroideae from 33 to 20 Mya (**Figure 7**), falling between the end-Eocene and mid-Miocene cooling events. This plateau might represent extinction of these taxa or, alternatively, decreasing speciation rate as available niche space for rainforest-adapted Callitroideae decreased. The sharp upturn in the callitroid LTT slope at 20 Mya marks the radiation of the dry-adapted lineages of *Callitris* (M. Crisp, S. Sakaguchi, Y. Isagi, D. Bowman, unpublished data). More extinctions of rainforest taxa occurred at the mid-Miocene cooling event. For example, Backhousieae shows an LTT plateau (**Figure 7**) at this time, likely reflecting extinction as its biome contracted (Harrington et al. 2012).

In the sclerophyll flora, Crisp & Cook (2007) found evidence of a spike in allopatric speciation events linked to mid-Miocene aridification by comparing divergence times in plant sister taxa in southeast and southwest Australia. Populations were probably split across the Great Australian Bight by coincident climatic change and elevation of the calcareous Nullarbor plateau. From the mid-Miocene onward, several sclerophyll lineages (eucalypts, Bossiaeeae, and Callitroideae)
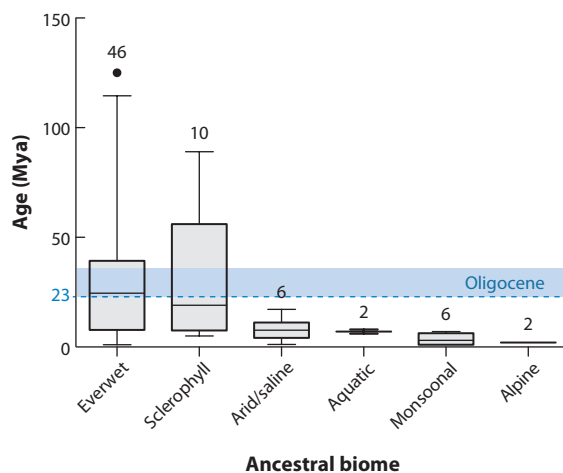
Figure 8

Ages of crown-groups of individual lineages grouped by inferred ancestral biome for Australian plant clades. Those originating in the sclerophyll and everwet biomes are much older than others, none of which is older than 23 Mya. Blue bar represents the Oligocene (34–23 Mya). The boxes show the median and the 25th and 75th percentiles, whereas the error bars show the 2.5th and 97.5th percentiles, and *n* is shown above each plot. The alpine biome includes temperate grassland.

showed a gradual decrease in diversification rate (**Figure 7**), possibly reflecting ecological limits to diversity (Rabosky 2009) as the monsoonal and arid biomes expanded, possibly into space previously occupied by the sclerophyll biome. Only *Acacia*, Casuarinaceae, and *Triodia* show no evidence of a diversification rate slowdown during this period (**Figure 7**). Both *Acacia* and *Triodia* are diverse and dominant in the arid and monsoonal regions (Gonzalez-Orozco et al. 2011, Rice & Westoby 1999) and likely radiated with the expansion of these biomes. Other arid-adapted lineages arrived by transoceanic dispersal, established and diversified as the dry biomes expanded, e.g., chenopods (Amaranthaceae) (Kadereit & Freitag 2011) and *Lepidium* (Brassicaceae) (Mummenhoff et al. 2004). For details and other examples, see **Supplemental Table 1**.

▶ Supplemental Material

The black dot above the Everwet error bar represents an outlier. In geologically young biomes, clades would have commenced diversifying only after the biome originated or expanded. To test this prediction, we grouped clades from **Supplemental Table 1** according to their reconstructed ancestral biome. Those with ambiguous reconstructions were omitted, including all endemic Australian families. For clades lacking a dated crown group (**Figure 3**), we used half the age of the stem; omitting these made little difference to the result (**Supplemental Table 3**). We found that, for all Australian biomes younger than the Eocene (arid, monsoonal, and alpine), crown ages of clades were also correspondingly younger; in fact, all dated from the Neogene or later (<23 Mya; **Figure 8**). Crown ages for sclerophyll and everwet biomes vary widely, but their median ages are older than the oldest crown ages in younger biomes (**Figure 8**).

Trait Evolution in Response to Climate Change

Sclerophyll traits evolved in response to oligotrophic soils and, in the Australian fossil record, date back as far as the Cretaceous, at least in Proteaceae. Based on trends inferred from the macrofossil record, sclerophyllous traits might have been modified for drought tolerance (exapted for xeromorphy) as the Australian climate became drier from the Oligocene onward, in families

such as Casuarinaceae, Myrtaceae, Proteaceae, and Cupressaceae (Guerin & Hill 2006, Hill 1994, Hill & Brodribb 2001, Paull & Hill 2010). For example, stomata sunken deeply into pits or grooves (found in Casuarinaceae, Cupressaceae, Proteaceae, and *Triodia*) are considered to be adaptive to drought, whereas other forms of stomatal protection, such as a covering by a layer of hairs, have more ambiguous functions and are not necessarily drought-adaptive (Jordan et al. 2008). Also, trends toward smaller leaves in *Nothofagus* fossils have been attributed to post-Eocene climatic cooling in southern Australia (Hill 2001).

There has been limited testing of these fossil-based hypotheses in a physiological and phylogenetic framework. In the conifer family Podocarpaceae, phylogenetic mapping suggested that some podocarp lineages adapted to tropical forests after evolving unique (for conifers) angiosperm-like leaf traits (Biffin et al. 2012). In Proteaceae, phylogenetic ancestral state reconstruction found that few (5 or 6) transitions explained nearly all species' occurrences in dry habitats and, within these dry-environment clades, deep stomatal encryption evolved several times (Jordan et al. 2008). However, some of these dry-climate clades dated to the Paleogene or earlier, before the onset of aridification in Australia (Jordan et al. 2008). Earlier than expected phylogenetic dates for transitions could be an artifact of extinction of wet-adapted taxa (Crisp & Cook 2012, Jordan et al. 2008) or, if the older dates are accurate, the transitions might have occurred in habitats that were seasonally or topographically dry and unrepresented by fossils (Hill & Merrifield 1993). Encryption of stomata in *Casuarina* and *Allocasuarina* originated by c. 39 Mya (**Figure 5a**) and in *Triodia* by c. 7 Mya (A. Toon, M.D. Crisp, L.G. Cook, unpublished data).

There is much potential for further testing of fossil-based hypotheses of trait evolution linked to environmental change through evolutionary time. Phylogenetic methods are developing rapidly, both for linking clade diversification to trait evolution (e.g., Eastman et al. 2011) and for incorporating fossils directly into the modeling (Slater et al. 2012).

SOILS AND TOPOGRAPHY

Many Australian soils are ancient, highly weathered, and therefore nutrient-deficient, especially in exchangeable phosphorus and nitrogen (Lambers et al. 2011, McKenzie et al. 2004, Orians & Milewski 2007). Such oligotrophic soils likely exert strong selection for efficient nutrient-assimilation and -conservation strategies and consequently drive phenotypic and phylogenetic diversification (Hopper 2009). One consequence of nutrient deficiency is sclerophylly, in which plants develop small, tough, long-lived leaves and woodiness. Additionally, there may be a feedback between sclerophylly and fire because sclerophyll plants allocate large amounts of expendable energy to carbon-based lignified tissue, which accumulates as persistent, flammable litter (Orians & Milewski 2007). Early origins (Paleocene or earlier; **Figure 5**) (Hill & Brodribb 2001) and sustained prevalence of sclerophylly likely led to early dominance of some taxa, such as Proteaceae and eucalypts. Some sclerophyll traits were probably preadapted to xeromorphy (Hill & Brodribb 2001) and could have favored continued dominance of these taxa following aridification.

Disjunctions in the distributions of extant Australian taxa are often attributed to aridity barriers, for example, across dry corridors between rainforest belts in eastern Australia (e.g., Bell et al. 2012) and between riparian habitats in central and northern Australia (Edwards et al. 2012, Kondo et al. 2012). Less attention has been given to topography and soils as causal factors, perhaps because relief is generally low in the Australian landscape. Nevertheless, gaps between the sandstone plateaus (islands in the savannah sea) of the monsoonal north (Bowman et al. 2010), the deep Hunter Valley on the eastern coast (Di Virgilio et al. 2012), and isolated granite outcrops in the southwest (Hopper 2009) have all been implicated in genetic isolation and speciation of biota. In the

temperate south, exposure of the limestone plateau of the Nullarbor Plain, separating acidic soils, has been hypothesized as the cause of vicariant speciation in plants adapted to acidic soils on either side (Crisp & Cook 2007). This hypothesis was supported by significant clustering of southwest-southeast divergence-time estimates, coinciding with the geological age of the Nullarbor (c. 15 Mya), which also became a topographic and climatic barrier at that time (Crisp & Cook 2007).

Less clear is the role of soil mosaics in speciation and diversification, which likely involves ecological, rather than geographic, barriers to gene flow. Ecological speciation in the face of gene flow has been controversial but is supported by recent theoretical (Gavrilets 2003) and empirical (Papadopulos et al. 2011, Peakall et al. 2010) research. Soil mosaics have likely contributed to evolution of high plant diversity in the SWAFR, where nutrient deficiency is particularly acute and sclerophylly is prevalent (Hopper 2009, Lambers et al. 2011). There is a global correlation between nutrient-deficient soils (resulting from great age or rapid weathering) and high plant species diversity and endemism (Huston 2012). Australia fits this pattern, especially in regions of moderately low precipitation (Huston 2012, Pekin et al. 2012). However, there is little agreement on a mechanism linking nutrient deficiency of soils per se to high diversity.

Rather, the mechanism might be fine-scale patterning of soils, allowing geographic overlap, which contributes to high levels of biodiversity. Studies across multiple taxa, including angiosperm families, suggest that environmental heterogeneity (habitat complexity) is an important factor contributing to high diversification rates (reviewed by Vamosi & Vamosi 2012). In a biodiverse region of eastern New South Wales, which includes a mosaic of oligotrophic (sandstone, granitic) and richer (shale, basaltic) soils, fine-scale floristic turnover is correlated with lithological turnover (Di Virgilio et al. 2012). In the SWAFR, excavation of sites has shown that dominant plants (eucalypts and *Banksias*) modify the edaphic environment, creating root channels and impervious subsurface pavements, increasing the complexity of the soil mosaic, and restructuring the vegetation (Pate & Verboom 2009, Verboom & Pate 2006).

Recent studies based on molecular phylogenies have suggested that soil mosaics allow geographic overlap and/or coexistence of closely related species. An analysis of fine-scale community composition in the SWAFR found spatial clustering of phylogenetic diversity with a high degree of niche turnover (i.e., local endemism) that was correlated with soil variables (Sander & Wardell-Johnson 2011). Also in the SWAFR, Merwin et al. (2011) found that closely related *Banksia* species were co-occurring and edaphically specialized to different soils with fine-scale turnover. In the Fabaceae tribe Bossiaeeae sensu lato, species have smaller geographic ranges in the SWAFR compared with their sister groups in southeast Australia, likely because climatic gradients are steeper in the SWAFR (L.G. Cook, L.W. Popple, M.D. Crisp, N.B. Hardy, unpublished data) (cf. the high-diversity transitional rainfall zone of Hopper & Gioia 2004). In *Daviesia*, there is more geographic overlap between clades in the SWAFR than in southeast Australia, possibly reflecting specialization across fine-scale soil mosaics and a longer history in the SWAFR (L.G. Cook, L.W. Popple, M.D. Crisp, N.B. Hardy, unpublished data).

ECOLOGICAL OPPORTUNITY

Adaptive radiations are thought to arise from various kinds of ecological opportunities (Yoder et al. 2010). These include new habitats, key innovations, and release from antagonists. Ecological opportunities can lead to adaptive radiations by relaxing stabilizing selection and triggering diversifying selection on populations (Yoder et al. 2010). As discussed above, climate change has opened new biomes that have been successfully exploited by lineages after evolution of a key innovation, for example, stomata sunken into deep grooves in Proteaceae (Jordan et al. 2008). Animals, too,

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responded to the ecological opportunity arising from climate change by adaptively radiating into the open biomes concurrently with the plants, as shown by dated molecular phylogenies, e.g., Australo-Papuan magpies and butcherbirds, honeyeaters, kangaroos, and reptiles (Kearns et al. 2013). There are too many likely examples of ecological opportunity and its consequences in the Australian flora to discuss here in detail, so we briefly mention a few.

In an analysis of diversification rate variation within Myrtaceae (Biffin et al. 2010), two lineages had values that were significantly above expectation. These were the fleshy-fruited clades of tropical trees, Syzygieae and Myrteae, which include two of the largest plant genera in the world, with 1,000 or more species each (respectively, *Syzygium* and *Eugenia*). Both clades are pantropical, with most of their diversity occurring in extra-Australian rainforests that did not contract dramatically as Australian rainforests did during the Cenozoic. Biffin and colleagues hypothesized that long-distance dispersal of their fleshy fruits (a key innovation) promoted diversification of these clades, in contrast to the dry-fruited Myrtaceae clades that diversified more slowly.

Release from antagonists is one source of ecological opportunity. Plants have responded to herbivores by evolving defenses such as spines, irritating hairs, and toxic chemicals. In Australia, Myrtaceae has evolved an astonishing diversity and abundance of terpenes that defend the plants against herbivores as disparate as koalas and Christmas beetles (Keszei et al. 2010). The observed diversity of terpene synthases largely evolved before divergence of the major clades within the family (Keszei et al. 2010) and before the origins of fire-adaptive epicormic resprouting (Crisp et al. 2011). As the foliar glands that produce these aromatic oils also promote flammability of plants, epicormic resprouting could be the result of an ecological opportunity (to shift from rainforest to flammable biomes), originating as a by-product of a defense system. Whether the high diversity of Myrtaceae in Australia results from the shift to effective chemical defense or the subsequent shift to fire resistance merits further research.

Australia has a greater proportion of plant species dispersed by ants than any other continent and is the only one on which vegetation is dominated by myrmecochorous trees (Orians & Milewski 2007, p. 410). According to these authors, an ecological opportunity arose from the combination of nutrient poverty and intense fire. On nutrient-deficient soils, elaiosomes are costly to produce and, compared with larger seed-dispersers, ants are attracted to seeds producing very small elaiosomes. Unlike vertebrate dispersers such as birds, ants bury the seed effectively, protecting them from the extreme heat of wildfires.

A wide range of Australian taxa show specialized ecophysiological root adaptations for dealing with nutritionally deficient soils, especially in the SWAFR. These include mutualisms with diverse micro-organisms, such as mycorrhizae and bacteria, often associated with specialized nutrient-scavenging cluster-roots (Lambers et al. 2011, Pate & Verboom 2009). The legumes (Fabaceae) are well known for their mutualism with nitrogen-fixing bacteria and, unsurprisingly, the family is highly diverse on oligotrophic Australian soils. Phylogenetic analysis of both the bacteria and their hosts has revealed distinct phylogenetic communities of *Bradyrhizobium* on Fabaceae in monsoonal tropics versus the temperate SWAFR (Stepkowski et al. 2012).

The converse of ecological opportunity leading to adaptive radiations is an ecological change resulting in decreasing diversification, or ultimately extinction, such as contraction of the everwet biome, discussed in the earlier section, "Trait Evolution in Response to Climate Change." Giant lemurs in southern Madagascar were the likely dispersers of large-seeded trees, and their extinction during the past 2,000 years has been implicated in major changes in semiarid communities (Crowley et al. 2011). In central Australia, genetic differentiation among populations of *Macrozamia* is surprisingly high, given their young estimated age, and it is hypothesized that this results from extinction of herbivorous megafauna such as *Diprotodon* or *Genyornis* that likely dispersed

their large seeds (Ingham et al. 2013). Lack of dispersal opportunity makes these populations vulnerable to extinction.

In the ancestrally bee-pollinated legume tribe Bossiaeeae sensu lato, multiple transitions to bird pollination have occurred during the past 20 Ma (A. Toon, M. Crisp, L. Cook, unpublished data). Diversification rates have been significantly lower in the bird-pollinated clades than in their bee-pollinated sister clades, and the transitions are possibly irreversible, owing to an evolutionary ratchet. Bossiaeeae species commonly coexist in communities with dominant bird-pollinated plants of Myrtaceae and Proteaceae, which attract honeyeater birds that could have created ecological opportunity for bee-bird transitions. However, the ecological opportunity seems not to have resulted in significant diversification, compared with the bee-pollinated sister lineages.

CONCLUSION

To What Extent Is the Australian Flora Unique?

Of the distinctive features of the Australian flora listed in the Introduction, most are not unique. Sclerophylly is characteristic of floras in regions having oligotrophic soils (often with a Mediterranean climate), such as the Cape region of South Africa, California, and the Mediterranean (Hopper 2009, Orians & Milewski 2007), and xeromorphic traits recur in arid regions everywhere. Similarly, fire as a selective force is present anywhere in the world with a temperate to warm, periodically wet-dry climate and open vegetation (Bond & Midgley 2012). These traits are considered characteristic of Australia mainly because nowhere else do sclerophyll, arid, and fire-dependent communities occupy such a large proportion of the continental area. Although the diversity hotspots are significant within Australia, the SWAFR is not unique because the other four Mediterranean regions are all recognized hot spots (Hopper 2009, Myers et al. 2000). The Australian wet tropics is not even a globally recognized hot spot, in contrast to much more extensive tropical rainforest regions elsewhere, such as the entire neighboring southeast Asian-Malesian region (Myers et al. 2000).

The isolation of Australia as an island-continent for the past 33 Ma is considered biogeographically significant (Barlow 1981). Even so, the large number of taxa that have established there via transoceanic dispersal during that period shows that it has not been especially isolated. Nevertheless, isolation might have been an important filter, resulting in a biased sample of the world's biota, as is well known from studies on smaller islands (Whittaker & Fernández-Palacios 2007). This could have led to some clades, which established before others, occupying a range of niche space that is dominated by other taxa in the rest of the continents (Whittaker & Fernández-Palacios 2007). Perhaps this explains the dominance of Australia's drier forests and woodlands by so few taxa (eucalypts and acacias), in contrast to elsewhere. Historical contingency or idiosyncratic events early in the evolutionary history of a clade, particularly if resulting in a large geographic range, are considered factors in the evolution of dominance and high diversity of particular clades (Vamosi & Vamosi 2012). Eucalypts made the transition to the sclerophyll biome early, in the Paleocene, and when this biome expanded after the end of the Eocene, they were well positioned to dominate the biome and influence its subsequent evolution, perhaps competitively excluding immigrating trees. Moreover, the flammability of eucalypts, combined with their extraordinary capacity to resprout epicormically after severe fires, could have reinforced this early advantage. *Acacia*, although possibly immigrant rather than Gondwanan in origin, was present from about the beginning of the Oligocene (Macphail & Hill 2001) and could also have gained advantage from an early presence just as the sclerophyll

biome was expanding. As a nitrogen-fixing legume, it would have been preadapted to oligotrophic soils.

In conclusion, the Australian flora is mostly a modified sample of the global flora, with some distinctive characteristics resulting from idiosyncratic events (rise to dominance by particular flammable, sclerophyll lineages) early in its existence as an island.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

LITERATURE CITED

Barlow BA. 1981. The Australian flora: its origin and evolution. In *Flora of Australia*. Vol. 1. *Introduction*, ed. AS George, pp. 25–75. Canberra: Aust. Gov. Publ. Serv.

Barreda V, Palazzesi L. 2007. Patagonian vegetation turnovers during the Paleogene-early Neogene: origin of arid-adapted floras. *Bot. Rev.* 73:31–50

Barreda VD, Cúneo NR, Wilf P, Currano ED, Scasso RA, Brinkhuis H. 2012. Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. *PLoS ONE* 7:e52455

Beerling DJ, Osborne CP. 2006. The origin of the savanna biome. *Glob. Change Biol.* 12:2023–31

Bell RC, MacKenzie JB, Hickerson MJ, Chavarria KL, Cunningham M, et al. 2012. Comparative multi-locus phylogeography confirms multiple vicariance events in co-distributed rainforest frogs. *Proc. R. Soc. B* 279:991–99

Biffin E, Brodribb TJ, Hill RS, Thomas P, Lowe AJ. 2012. Leaf evolution in Southern Hemisphere conifers tracks the angiosperm ecological radiation. *Proc. R. Soc. B* **279:341–48**

Biffin E, Lucas EJ, Craven LA, Ribeiro da Costa I, Harrington MG, Crisp MD. 2010. Evolution of exceptional species richness amongst lineages of fleshy-fruited Myrtaceae. *Ann. Bot.* 106:79–93

Bond WJ, Midgley JJ. 2012. Fire and the angiosperm revolutions. *Int. J. Plant Sci.* 173:569–83

Bond WJ, Scott AC. 2010. Fire and the spread of flowering plants in the Cretaceous. *New Phytol.* 188:1137–50

Bowman DMJS. 2000. *Australian Rainforests: Islands of Green in a Land of Fire.* Cambridge, UK: Cambridge Univ. Press

Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, et al. 2009. Fire in the Earth system. *Science* 324:481–84

Bowman DMJS, Brown GK, Braby MF, Brown JR, Cook LG, et al. 2010. Biogeography of the Australian monsoon tropics. *J. Biogeogr.* 37:201–16

Bradstock RA. 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Glob. Ecol. Biogeogr.* 19:145–58

Bradstock RA, Gill AM, Williams RJ, eds. 2012. *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World*. Melbourne, Aust.: CSIRO

Burrows GE 2013. Buds, bushfires and resprouting in the eucalypts. *Aust. J. Bot.* 61:331–49

Byrne M, Steane DA, Joseph L, Yeates D, Jordan GJ, et al. 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *J. Biogeogr.* 38:1635–56

Uses phylogenetic mapping to show that podocarp conifers adapted to tropical forests after evolving angiosperm-like leaf traits.

Byrne M, Yeates DK, Joseph L, Kearney M, Bowler J, et al. 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Mol. Ecol.* 17:4398–417

Cantrill DJ, Wanntorp L, Drinnan AN. 2011. Mesofossil flora from the Late Cretaceous of New Zealand. *Cretac. Res.* 32:164–73

Cook LG, Crisp MD. 2005. Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. *Proc. R. Soc. B* 272:2535–44

Crayn DM, Rossetto M, Maynard DJ. 2006. Molecular phylogeny and dating reveals an Oligo-Miocene radiation of dry-adapted shrubs (former Tremandraceae) from rainforest tree progenitors (Elaeocarpaceae) in Australia. *Am. J. Bot.* 93:1328–42

Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, et al. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458:754–56

Crisp MD, Burrows GE, Cook LG, Thornhill AH, Bowman DMJS. 2011. Flammable biomes dominated by eucalypts originated at the Cretaceous–Palaeogene boundary. *Nat. Commun.* 2:193

Crisp MD, Cook LG. 2007. A congruent molecular signature of vicariance across multiple plant lineages. *Mol. Phylogenet. Evol.* 43:1106–17

Crisp MD, Cook LG. 2009. Explosive radiation or mass extinction? Interpreting signatures in molecular phylogenies. *Evolution* 63:2257–65

Crisp MD, Cook LG. 2011. Cenozoic extinctions account for low diversity of extant gymnosperms compared with angiosperms. *New Phytol.* 192:997–1009

Crisp MD, Cook LG. 2012. Phylogenetic niche conservatism: What are the underlying evolutionary and ecological causes? *New Phytol.* 196:681–94

Crisp MD, Cook LG, Steane DA. 2004. Radiation of the Australian flora: What can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philos. Trans. R. Soc. B* 359:1551–71

Crowley BE, Godfrey LR, Irwin MT. 2011. A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. *Am. J. Primatol.* 73:25–37

Darwin C. 1855. Does sea-water kill seeds? *Gard. Chron.* 21:356–57

Di Virgilio G, Laffan SW, Ebach MC. 2012. Fine-scale quantification of floral and faunal breaks and their geographic correlates, with an example from south-eastern Australia. *J. Biogeogr.* 39:1862–76

Eastman JM, Alfaro ME, Joyce P, Hipp AL, Harmon LJ. 2011. A novel comparative method for identifying shifts in the rate of character evolution on trees. *Evolution* 65:3578–89

Edwards RD, Crisp MD, Cook LG. 2013. Niche differentiation and spatial partitioning in the evolution of two Australian monsoon tropical tree species. *J. Biogeogr.* 40:559–69

Eklund H, Cantrill DJ, Francis JE. 2004. Late Cretaceous plant mesofossils from Table Nunatak, Antarctica. *Cretac. Res.* 25:211–28

Fujioka T, Chappell J, Fifield LK, Rhodes EJ. 2009. Australian desert dune fields initiated with Pliocene-Pleistocene global climatic shift. *Geology* 37:51–54

Gavrilets S. 2003. Models of speciation: What have we learned in 40 years? *Evolution* 57:2197–215

Gonzalez-Orozco CE, Laffan SW, Miller JT. 2011. Spatial distribution of species richness and endemism of the genus *Acacia* in Australia. *Aust. J. Bot.* 59:600–8

Grandcolas P, Murienne J, Robillard T, Desutter-Grandcolas L, Jourdan H, et al. 2008. New Caledonia: a very old Darwinian island? *Philos. Trans. R. Soc. B* 363:3309–17

Greenwood DR. 1996. Eocene monsoon forests in central Australia? *Aust. Syst. Bot.* 9:95–112

Greenwood DR. 2005. Leaf form and the reconstruction of past climates. *New Phytol.* 166:355–57

Guerin GR, Hill RS. 2006. Plant macrofossil evidence for the environment associated with the Riversleigh fauna. *Aust. J. Bot.* 54:717–31

Harrington MG, Jackes BR, Barrett MD, Craven LA, Barrett RL. 2012. Phylogenetic revision of Backhousieae (Myrtaceae): Neogene divergence, a revised circumscription of *Backhousia* and two new species. *Aust. Syst. Bot.* 25:404–17

He T, Lamont BB, Downes KS. 2011. *Banksia* born to burn. *New Phytol.* 191:184–96

Hermsen EJ, Gandolfo MA, del Carmen Zamalao M. 2012. The fossil record of *Eucalyptus* in Patagonia. *Am. J. Bot.* 99:1356–74

Discusses phylogenies of 11,000 Southern Hemisphere plants that show transoceanic dispersal was most common between similar habitats.

Shows how shapes of phylogenies and LTTs can be used to infer diversification shifts, including extinction.

Hill RS. 1994. The history of selected Australian taxa. In *History of Australian Vegetation: Cretaceous to Recent*, ed. RS Hill, pp. 390–419. Cambridge, UK: Cambridge Univ. Press

Hill RS. 2001. Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): the contribution of the fossil record. *Aust. J. Bot.* 49:321–32

Hill RS. 2004. Origins of the southeastern Australian vegetation. *Philos. Trans. R. Soc. B* 359:1537–49

Hill RS, Brodribb TJ. 1999. Southern conifers in time and space. *Aust. J. Bot.* 47:639–96

Hill RS, Brodribb TJ. 2001. Macrofossil evidence for the onset of xeromorphy in Australian Casuarinaceae and tribe Banksieae (Proteaceae). *J. Mediterr. Ecol.* 2:127–36

Hill RS, Merrifield HE. 1993. An early Tertiary macroflora from West Dale, southwestern Australia. *Alcheringa* 17:285–326

Hill RS, Truswell EM, McLoughlin S, Dettman ME. 1999. The evolution of the Australian flora: fossil evidence. In *Flora of Australia*. Vol. 1. *Introduction*, ed. AE Orchard, pp. 251–320. Melbourne, Aust.: ABRS/CSIRO

Hooker JD. 1853. Introductory essay. In *Flora Novae-Zelandiae*. Part I. *Flowering Plants*, ed. JD Hooker, pp. i–xxxix. London: Lovell Reeve

Hooker JD. 1860. Introductory essay. In *Flora Tasmaniae*. Vol. 1. Part III. *Dicotyledones*, ed. JD Hooker, pp. i–cxxviii. London: Lovell Reeve

Hopper SD. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322:49–86

Hopper SD, Gioia P. 2004. The south-west Australian floristic region: evolution and conservation of a global hotspot of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 35:623–50

Huber M, Goldner A. 2012. Eocene monsoons. *J. Asian Earth Sci.* 44:3–23

Huston MA. 2012. Precipitation, soils, NPP, and biodiversity: resurrection of Albrecht's Curve. *Ecol. Monogr.* 82:277–96

Ingham JA, Forster PI, Crisp MD, Cook LG. 2013. Ancient relicts or recent dispersal: How long have cycads been in central Australia? *Divers. Distrib.* 19:307–16

Itzstein-Davey F. 2007. Changes in the abundance and diversity of Proteaceae in south-western Australia: a review of an integrated palaeoenvironmental study. *Geogr. Res.* 45:43–53

Jordan GJ, Weston PH, Carpenter RJ, Dillon RA, Brodribb TJ. 2008. The evolutionary relations of sunken, covered, and encrypted stomata to dry habitats in Proteaceae. *Am. J. Bot.* 95:521–30

Kadereit G, Freitag H. 2011. Molecular phylogeny of Camphorosmeae (Camphorosmoideae, Chenopodiaceae): implications for biogeography, evolution of C-4-photosynthesis and taxonomy. *Taxon* 60:51–78

Kearns AM, Joseph L, Cook LG. 2013. A multilocus coalescent analysis of the speciational history of the Australo-Papuan butcherbirds and their allies. *Mol. Phylogenet. Evol.* 66:941–52

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* 16:406–11

Kershaw AP, Clark JS, Gill AM, D'Costa DM. 2002. A history of fire in Australia. In *Flammable Australia: The Fire Regimes and Biodiversity of Australia*, ed. RA Bradstock, JE Williams, AM Gill, pp. 3–25. Cambridge, UK: Cambridge Univ. Press

Kershaw AP, Martin HA, McEwen Mason JRC. 1994. The Neogene: a period of transition. In *History of the Australian Vegetation: Cretaceous to Recent*, ed. RS Hill, pp. 299–327. Cambridge, UK: Cambridge Univ. Press

Keszei A, Brubaker CL, Carter R, Kollner T, Degenhardt J, Foley WJ. 2010. Functional and evolutionary relationships between terpene synthases from Australian Myrtaceae. *Phytochemistry* 71:844–52

Kondo T, Crisp MD, Linde C, Bowman D, Kawamura K, et al. 2012. Not an ancient relic: the endemic Livistona palms of arid central Australia could have been introduced by humans. *Philos. R. Soc. B* 279:2652–61

Lambers H, Brundrett MC, Raven JA, Hopper SD. 2011. Plant mineral nutrition in ancient landscapes: High plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant Soil* 348:7–27

Lamont BB, Downes KS. 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecol.* 212:2111–25

Deconstructs putatively xeromorphic traits, testing their correlation with environmental variables on a dated phylogeny.

Lamont BB, He T. 2012. Fire-adapted Gondwanan Angiosperm floras evolved in the Cretaceous. *BMC Evol. Biol.* **12**:223

Macphail M. 2007. Australian palaeoclimates: Cretaceous to Tertiary. A review of palaeobotanical and related evidence to the year 2000. CRC LEME Spec. Vol. Open File Rep. 151. Bentley, Perth

Macphail MK, Hill RS. 2001. Fossil record of *Acacia* in Australia: Eocene to recent. In *Flora of Australia*, *Vol.* 11A: *Mimosaceae, Acacia Part 1*, ed. AE Orchard, AJG Wilson, pp. 13–29. Melbourne, Aust: ABRS/CSIRO

Martin HA. 2006. Cenozoic climatic change and the development of the arid vegetation in Australia. *J. Arid Environ.* 66:533–63

McGowran B, Holdgate GR, Li Q, Gallagher SJ. 2004. Cenozoic stratigraphic succession in south-eastern Australia. *Aust. J. Earth Sci.* **51**:459–96

McKenzie NJ, Jacquier DW, Isbell RF, Brown KL. 2004. *Australian Soils and Landscapes: An Illustrated Compendium*. Collingwood, Victoria: CSIRO

McLoughlin S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Aust. J. Bot.* 49:271–300

McLoughlin S, Carpenter RJ, Pott C. 2011. *Ptilophyllum muelleri* (Ettingsh.) comb. nov from the Oligocene of Australia: last of the Bennettitales? *Int. J. Plant Sci.* 172:574–85

Merwin L, He T, Lamont BB. 2011. Phylogenetic and phenotypic structure among *Banksia* communities in south-western Australia. *J. Biogeogr.* 39:397–407

Mummenhoff K, Linder P, Friesen N, Bowman JL, Lee JY, Franzke A. 2004. Molecular evidence for bi-continental hybridogenous genomic constitution in *Lepidium* sensu stricto (Brassicaceae) species from Australia and New Zealand. *Am. J. Bot.* 91:254–61

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–58

Nagalingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. 2011. Recent synchronous radiation of a living fossil. *Science* 334:796–99

Niklas KJ. 1997. *The Evolutionary Biology of Plants*. Chicago: Univ. Chicago Press

Orians GH, Milewski AV. 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biol. Rev.* **82**:393–423

Papadopulos AST, Baker WJ, Crayn D, Butlin RK, Kynast RG, et al. 2011. Speciation with gene flow on Lord Howe Island. *Proc. Natl. Acad. Sci. USA* 108:13188–93

Pate JS, Verboom WH. 2009. Contemporary biogenic formation of clay pavements by eucalypts: further support for the phytotarium concept. *Ann. Bot.* 103:673–85

Paull R, Hill RS. 2010. Early Oligocene *Callitris* and *Fitzroya* (Cupressaceae) from Tasmania. *Am. J. Bot.* 97:809–20

Pausas JG, Keeley JE. 2009. A burning story: the role of fire in the history of life. *BioScience* 59:593–601

Peakall R, Ebert D, Poldy J, Barrow RA, Francke W, et al. 2010. Pollinator specificity, floral odour chemistry and the phylogeny of Australian sexually deceptive *Chiloglottis* orchids: implications for pollinator-driven speciation. *New Phytol.* 188:437–50

Pekin BK, Boer MM, Wittkuhn RS, Macfarlane C, Grierson PF. 2012. Plant diversity is linked to nutrient limitation of dominant species in a world biodiversity hotspot. *J. Veg. Sci.* 23:745–54

Pole M. 1993. Keeping in touch: vegetation prehistory on both sides of the Tasman. *Aust. Syst. Bot.* 6:387–97

Pole MS, Bowman DMJS. 1996. Tertiary plant fossils from Australia's 'Top End'. *Aust. Syst. Bot.* 9:113–26

Rabosky DL. 2009. Ecological limits on clade diversification in higher taxa. *Am. Nat.* 173:662–74

Rice B, Westoby M. 1999. Regeneration after fire in *Triodia* R. Br. *Aust. J. Ecol.* 24:563–72

Sander J, Wardell-Johnson G. 2011. Fine-scale patterns of species and phylogenetic turnover in a global biodiversity hotspot: implications for climate change vulnerability. *J. Veg. Sci.* 22:766–80

Simon MF, Pennington T. 2012. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *Int. J. Plant Sci.* 173:711–23

Slater GJ, Harmon LJ, Alfaro ME. 2012. Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* 66:3931–44

Sniderman JMK, Jordan GJ. 2011. Extent and timing of floristic exchange between Australian and Asian rain forests. *J. Biogeogr.* 38:1445–55

Uses phylogenetic mapping in Proteaceae to infer Gondwanan origins of fire-adaptive traits and open flammable communities.

Details fossil-pollen reconstructions of climate and vegetation in Australia through the Cretaceous and Cenozoic.

Provides a comprehensive review of geological evidence for environmental change through the last 65 Ma.

Reviews the ecological feedbacks between oligotrophic soils, sclerophylly, and fire in Australia.

Stepkowski T, Watkin E, McInnes A, Gurda D, Gracz J, Steenkamp ET. 2012. Distinct *Bradyrhizobium* communities nodulate legumes native to temperate and tropical monsoon Australia. *Mol. Phylogenet. Evol.* 63:265–77

Vamosi SM, Vamosi JC. 2012. Perspective: causes and consequences of range size variation: the influence of traits, speciation, and extinction. *Front. Biogeogr.* 4:168–77

Verboom WH, Pate JS. 2006. Bioengineering of soil profiles in semiarid ecosystems: the 'phytotarium' concept. A review. *Plant Soil* 289:71–102

Wallace AR. 1860. On the zoological geography of the Malay Archipelago. *J. Proc. Linn. Soc. Lond. Zool.* 4:172–84

Wallis GP, Trewick SA. 2009. New Zealand phylogeography: evolution on a small continent. *Mol. Ecol.* 18:3548–80

Watson L, Dallwitz MJ. 1992 onward. *The grass genera of the world: descriptions, illustrations, identification, and information retrieval; including synonyms, morphology, anatomy, physiology, phytochemistry, cytology, classification, pathogens, world and local distribution, and references*. Version: 18th, December 2012. **http://delta-intkey.com/grass/index.htm**

Wegener A. 1915. *Die Entstehung der Kontinente und Ozeane*. Brunswick: Sammlung Vieweg

Whittaker RJ, Fernández-Palacios JM. 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford, UK: Oxford Univ. Press

Yoder JB, Clancey E, Des Roches S, Eastman JM, Gentry L, et al. 2010. Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.* 23:1581–96

Discusses hypotheses and evidence for causal links between ecological opportunity and adaptive radiation.

RELATED RESOURCES

Crisp MD, Trewick SA, Cook LG. 2011. Hypothesis testing in biogeography. *Trends Ecol. Evol.* 26:66–72

Losos JB. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.* 175:623–39

Ronquist F, Sanmartín I. 2011. Phylogenetic methods in biogeography. *Annu. Rev. Ecol. Evol. Syst.* 42:441–64