Deep history of wildfire in Australia

Robert S. Hill[A,C] and Gregory J. Jordan[B]

[A]School of Biological Sciences, The University of Adelaide, SA 5005, Australia.

[B]School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tas, 7001.

[C]Corresponding author. Email: bob.hill@adelaide.edu.au

Abstract. Australian plant species vary markedly in their fire responses, and the evolutionary histories of the diverse range of traits that lead to fire tolerance and fire dependence almost certainly involves both exaptation and traits that evolved directly in response to fire. The hypothesis that very long term nutrient poverty in Australian soils led to intense fires explains much of the unusual Australian species' responses to fire, as does near global distribution of evidence for fire during the Cretaceous, possibly driven by high atmospheric oxygen level. Recent descriptions of leaf fragments from a Late Cretaceous locality in central Australia provide the first fossil evidence for ancient and possibly ancestral fire ecology in modern fire-dependent Australian clades, as suggested by some phylogenetic studies. The drying of the Australian climate in the Neogene allowed the rise to dominance of taxa that had their origin in the Late Cretaceous, but had not been prominent in the rainforest-dominated Paleogene. The Neogene climatic evolution meant that fire became an important feature of that environment and fire frequency and intensity began to grow to high levels, and many fire adaptations evolved. However, many plant species were already in place to take advantage of this new fire regime, and even though the original drivers for fire may have changed (possibly from high atmospheric O_2 levels, to long hot, dry periods at different times in different parts of the continent), the adaptations that these species had for fire tolerance meant they could become prominent over much of the Australian continent by the time human colonisation began.

Introduction

Many species within the Australian vegetation have evolved so that they can persist or even thrive in the presence of a ~~high~~ natural fire regime with varying frequency and/or intensity. However, it is not clear how and when the necessary adaptations evolved, and whether a response to fire was the major driver.

Much has been written about the adaptation of the Australian vegetation to fire, but these adaptations must be characteristics of individual species. Dobzhansky (1956) defined an adaptive trait as "an aspect of the developmental pattern which facilitates the survival and/or reproduction of its carrier in a certain succession of environments". If this definition is applied to the species that make up the Australian vegetation, then the relationship of each species to fire can be explained by how the adaptations of that species influences its capacity to tolerate fire and its level of dependence on fire. However, it is also possible that many of the apparent adaptive traits exhibited by plant species to fire may in fact be exaptations (Bradshaw *et al.* 2011a), with the primary evolutionary driver having been present in the very distant past. Keeley *et al.* (2011) have noted that fire has been present in the global environment for a long time, and certainly was available to be a primary driver for adaptation in the vast majority of taxa that make up the living biota. The resolution of the primary drivers of adaptation is an important issue for several branches of biological science, and perhaps most notably for those studying the plant fossil record.

Australian plant species vary markedly in their fire tolerance, in terms of both fire intensity and fire frequency. Fire intolerant species are those that will be lost locally in response to even mild fire regimes. Such species are found in many vegetation types in Australia, but they are most characteristic of some woody alpine, mangrove and rainforest vegetation. In some instances, they may represent open vegetation types that have persisted in a similar form since the Cretaceous (Jordan *et al.* 2016). If these vegetation types are burnt there may be a large time gap before significant regeneration occurs (e.g. Kirkpatrick *et al.* 2010) and many of the species that comprise these vegetation types are usually killed by fire with no obvious regeneration strategy to assist in fire recovery.

However, most plant species in Australia have some degree of fire tolerance. The capacity of a species to persist under different fire regimes (notably the patterns of fire frequency, intensity and size) is likely to depend on which of the many possible reproductive and/or vegetative adaptations the species has (Bowman *et al.* 2012).

Many Australian plant species are fire dependent to at least some degree (Hill in press). Fire dependence may be a cost of adaptation to fire rather than an adaptation to fire itself. This situation arises when the capacity to outcompete other species after a fire comes at the cost of being unable to compete in the absence of fire. The rainforest-associated giant eucalypts (such as *Eucalyptus regnans*, *E. grandis*) are an excellent example. These species can only regenerate after the removal of a forest canopy and the fire-induced soil modification, including the replacement of the soil microbiome (Tng *et al.* 2014; Tng *et al.* 2012). The seedlings then undergo intense light competition,

leading to the need for very rapid growth, which may only be attained if the seedling's resources are not expended on other traits, such as shade tolerance (Tng *et al.* 2012).

As noted above, the evolutionary histories of the diverse range of traits that lead to fire tolerance and fire dependence are probably complex, and almost certainly involve some exaptation as well as some traits that evolved directly in response to a high fire frequency, although the roles of these are very controversial (Bowman *et al.* 2014; Bradshaw *et al.* 2011a; Bradshaw *et al.* 2011b; Keeley *et al.* 2011).

A major controversy in understanding how fire has moulded the evolution of the Australian biota revolves around how old fire traits are. One long held view is that fire adaptation is a relatively recent phenomenon, largely (or even entirely) arising as the Australian climates became drier during the Neogene (~23 million years ago). In particular, the Early Eocene (56 to 47.8 million years ago) was a very wet period, with very little or no charcoal in the fossil record (Martin 1996). Certainly, pollen of genera of conifers that are now exclusively or predominantly in very wet and fire free habitats (e.g. *Lagarostrobos, Dacrydium* and *Dacrycarpus*) can be found in virtually all fossil deposits across Australia from this time (Macphail 2007). However, the contemporaneous fossil record from western and central Australia is sparse and the old view is challenged by recent research on the history of fire. Amongst the most interesting change in perception is the hypothesis that very long term nutrient poverty in Australian soils led to intense fires, along with evidence that fires were extremely widespread in the Late Cretaceous (Brown *et al.* 2012), playing a major role in the global radiation of flowering plants (Bond and Scott 2010). Both of these concepts are of critical importance for our understanding of the co-existence of terrestrial vegetation with fire.

Nutrient Poverty/Intense Fire Theory

Orians and Milewski (2007) developed what they termed the "Nutrient Poverty/Intense-Fire Theory", which postulates that most anomalous features of organisms and ecosystems of Australia "are the evolutionary consequences of adaptations to nutrient poverty, compounded by intense fire that tends to occur as a result of nutrient poverty". This innovative hypothesis suggests that the combination of plants growing in plentiful light and periodically adequate water, but on low nutrient soils, produce carbohydrates in excess of what the plant can combine with essential elements to form the basic structure of the plant. This excess carbohydrate can then be used for other aspects of the plant body, including well-defended foliage, large quantities of lignified tissue, and sugar-rich exudates. The rapid accumulation of nutrient-poor biomass provides fuel for fires, which in turn further deplete the nutrient status of the soil. Additionally, some authors suggest that scleromorphic leaves may be more flammable than those from other vegetation types (e.g. De Lillis *et al.* 2009), although

the controls on flammability are complex. This has the capacity to be a self-supporting strategy over a very long period of time (millions of years), and the abundance of heavily lignified tissues allows the evolution of large woody fruits that provide strong insulation for seeds during fire, as well as large underground lignotubers and thick bark that also protect meristematic tissues during the heat of a fire.

A Middle Eocene (47.8 to 37.8 million year old) fossil from the Kennedy Range of north-western Australia is certainly consistent with this hypothesis. *Banksia archaocarpa*, (McNamara and Scott 1983) is a massively woody structure remarkably similar in general form to modern cones of a suite of *Banksia* species from fire prone western Australia (Fig. 1).

Figure 1. *Banksia archaeocarpa* holotype (WAM P79.42), from the Merlinleigh Sandstone, eastern Kennedy Range, Western Australia. Scale bar = 2cm.

Evidence from perhaps the best example of the interaction of fire with the vegetation from the pre-human fossil record – the Eocene to Miocene Latrobe Valley coal of southeastern Victoria – aligns well with that described by Orians and Milewski (2007). The fire-prone phases in the coals are dominated by scleromorphic leaves, often with spiny margins, and large, woody fruits that would protect the seeds from the heat of the fire (e.g. *Banksia*, Casuarinaceae, *Callitris*). Blackburn and Sluiter (1994) described the coal floras in detail, utilising both microfossils (spores and pollen as well as charcoal particles) and macrofossils (mostly leaves and shoots). They reported very high charcoal quantities in the darkest coals, which were dominated by relatively dryland vegetation, containing such modern taxa as monocotyledons, including Typhaceae, Sparganiaceae and Restionaceae, Proteaceae, including *Banksia*, *Xylomelum* and others, Myrtaceae, including *Baeckea*, *Leptospermum* and *Melaleuca*, and many other taxa. The paler coals, with much lower charcoal levels, were dominated by rainforest taxa and included many conifers and ferns. Sluiter et al. (in press) provide an update on the Latrobe Valley coal floras and demonstrate the complexity of these environments, and it is clear we still have much to learn about the fire ecology in these ancient environments. While the ecology of the coals is difficult to reconstruct, it seems likely that at one extreme we see fire adapted species in a complex and diverse vegetation that would be recognisable today, and at the other extreme, we see rainforest vegetation consisting of species with ~~low~~ little or no tolerance of fire.

Past Atmospheric Oxygen Levels

It has been proposed that changes in levels of oxygen in the atmosphere drove major changes in the incidence of fire globally (Glasspool and Scott 2010). Levels of atmospheric oxygen substantially above current levels lead to almost inevitable fire, whereas low levels more-or-less preclude fire (Belcher *et al*. 2010). However, reconstructions of past oxygen levels in the atmosphere have been remarkably incongruent (e.g. Robinson 1989, Hansen and Wallmann 2003, Bergman *et al.* 2004, Arvidson *et al.* 2006, Berner 2006, Belcher 2009, Glasspool and Scott 2010, Tappert *et al.* 2013). In particular, Tappert *et al.* (2013) places the atmospheric oxygen level below 15% (i.e. below the threshold required for wildfire to be sustained) for most of the past 250 million years. This is incompatible with the presence of charcoal in the fossil record: for example, abundant macrocharcoal remains in the Lower Cretaceous in England (Watson and Alvin 1996) and Nova Scotia (Falcon-Lang *et al.* 2016).

Recently, Glasspool and Scott (2010) used fossil charcoal levels to provide alternative estimates of past atmospheric oxygen levels. While there is a danger that this is circular when the resulting re-

construction is then used to explain past fire history, there is significant logic to the approach Glass-pool and Scott take, and they avoid some of the problems that other reconstructions face. With these assumptions in place, the reconstruction by Glasspool and Scott (2010) appears to provide great utility in understanding the interaction between atmospheric oxygen, terrestrial vegetation and fire over the very long term (Fig. 2). Glasspool and Scott's (2010) evidence suggests that atmospheric oxygen levels were sufficiently high for fire to be a constant companion to the contemporaneous terrestrial vegetation for a very long period of Earth history - hundreds of millions of years (Fig. 2). Over the last decade there has been a strongly emerging recognition of the significance of the Creta-ceous environment in which angiosperms probably evolved and certainly diversified and assumed dominance in the vegetation. Many authors have assumed that the flowering plants evolved at a time of high natural fire frequency and that they must have been adapted to those high frequencies (e.g. Friis *et al.* 2011). Most of the early angiosperm fossils now recorded are charcoalified, and suggest small plants growing in open vegetation. Furthermore, this low stature combined with small seeds suggests life history characteristics that traditionally would have been regarded as r-selected species, typified by species that produce large numbers of seeds that germinate and mature quickly, and can make good use of ephemeral resources. Trees appear to have been absent from the flower-ing plant life forms until the Late Cretaceous (Friis *et al.* 2011).
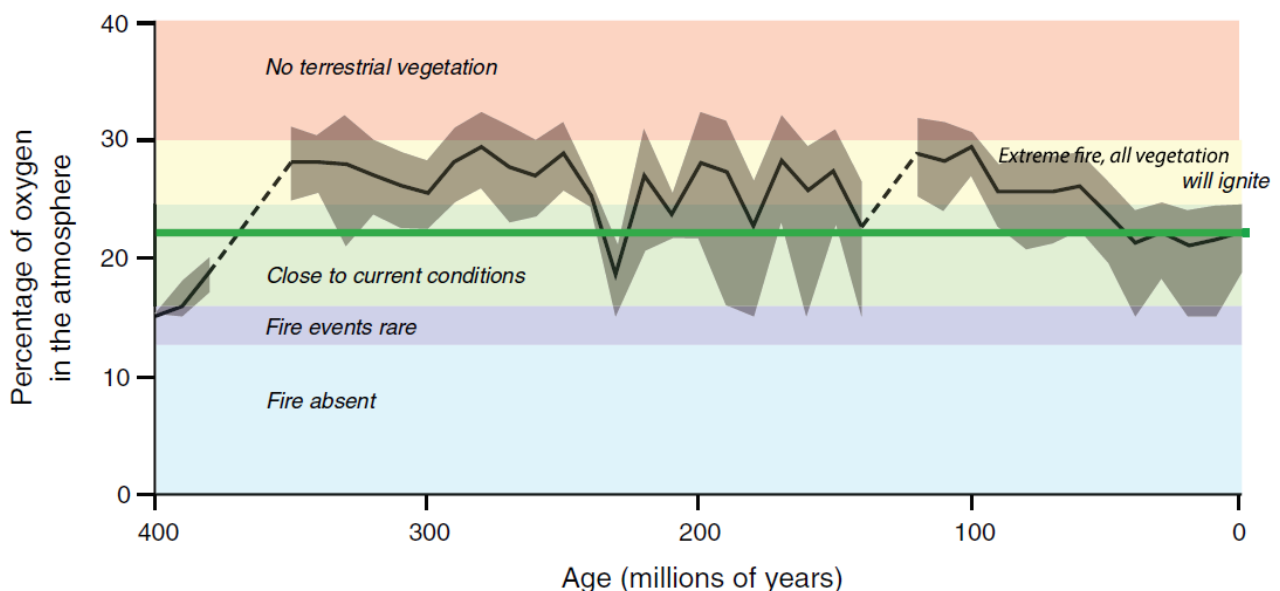

Figure 2. Phanerozoic inertinite distribution and predictions of past atmospheric oxygen levels. Error bars = 1 standard deviation from the mean. Modified from Glasspool and Scott (2010).

The evidence for shrubby or herbaceous early angiosperms in a fire prone environment is increasingly common from the Northern Hemisphere, but until recently has been largely absent from the Southern Hemisphere, probably due to a shortage of fossils from appropriately aged sediments. However, there is evidence for relatively widespread Late Cretaceous fire from both Australia (see Carpenter in press) and elsewhere in the southern hemisphere (Manfroi *et al.* 2015). However, Carpenter *et al.* (2015) were the first to provide fossil evidence linking such fires during the Late Cretaceous (Campanian-Maastrichtian) with clades that now dominate Australia's flammable flora. Those authors described a Proteaceae-dominated open shrub vegetation associated with charcoal particles from central Australia, the first evidence of this vegetation type in Australia and a major advance in our knowledge of the form of early Proteaceae taxa. Furthermore, the macrofossils present show evidence of well-developed scleromorphy (low soil nutrients) and possibly some xeromorphy (low water availability).

When Did Australia's Fire Traits Evolve?

The clearest fossil evidence for the early presence of fire traits in the Australian flora is *Banksia archaeocarpa* (McNamara and Scott 1983) described above, which represents a massively woody infructescence consistent with being serotinous. Similar reproductive structures may eventually be discovered in much older sediments given the presence of leaf fragments that cannot be distinguished from extant *Banksia* in the Late Cretaceous of central Australia (Carpenter *et al.* 2015).

Molecular dating estimates of the age of fire-related traits in the Australian flora add to this story (Fig. 3). Overall, these studies suggest that almost all the fire traits considered arose after the Early Eocene, but there is very high uncertainty in almost all cases. Only one of these traits clearly precedes the Early Eocene (the deeply embedded meristems that allow stem resprouting in eucalypts (Crisp *et al.* 2011), and even this inference is impeded by a lack of information on the uncertainty of the age estimates. Several other traits may be this old, notably serotiny in *Banksia* (He *et al.* 2011), and possibly soil seed storage on the *Stirlingia*, *Synaphea* and the *Conospermum* clade (Lamont and He 2012)), but certainly could also postdate the Early Eocene.

Crisp *et al.* (2011) and Lamont and He (2012) also reconstructed the evolution of "biome flammability" and "occurrence in fire-prone habitats". Reconstructions of extrinsic characters such as these are problematic (Grandcolas *et al.* 2011). An ancestral state reconstruction infers evolution of a specific characteristic – thus, reconstructing the evolution of habitat implies that it is a map of some genetically determined feature that allows species to occupy that habitat. Thus, there is an implicit assumption that the traits being reconstructed are homologous unless ancestral state reconstruction
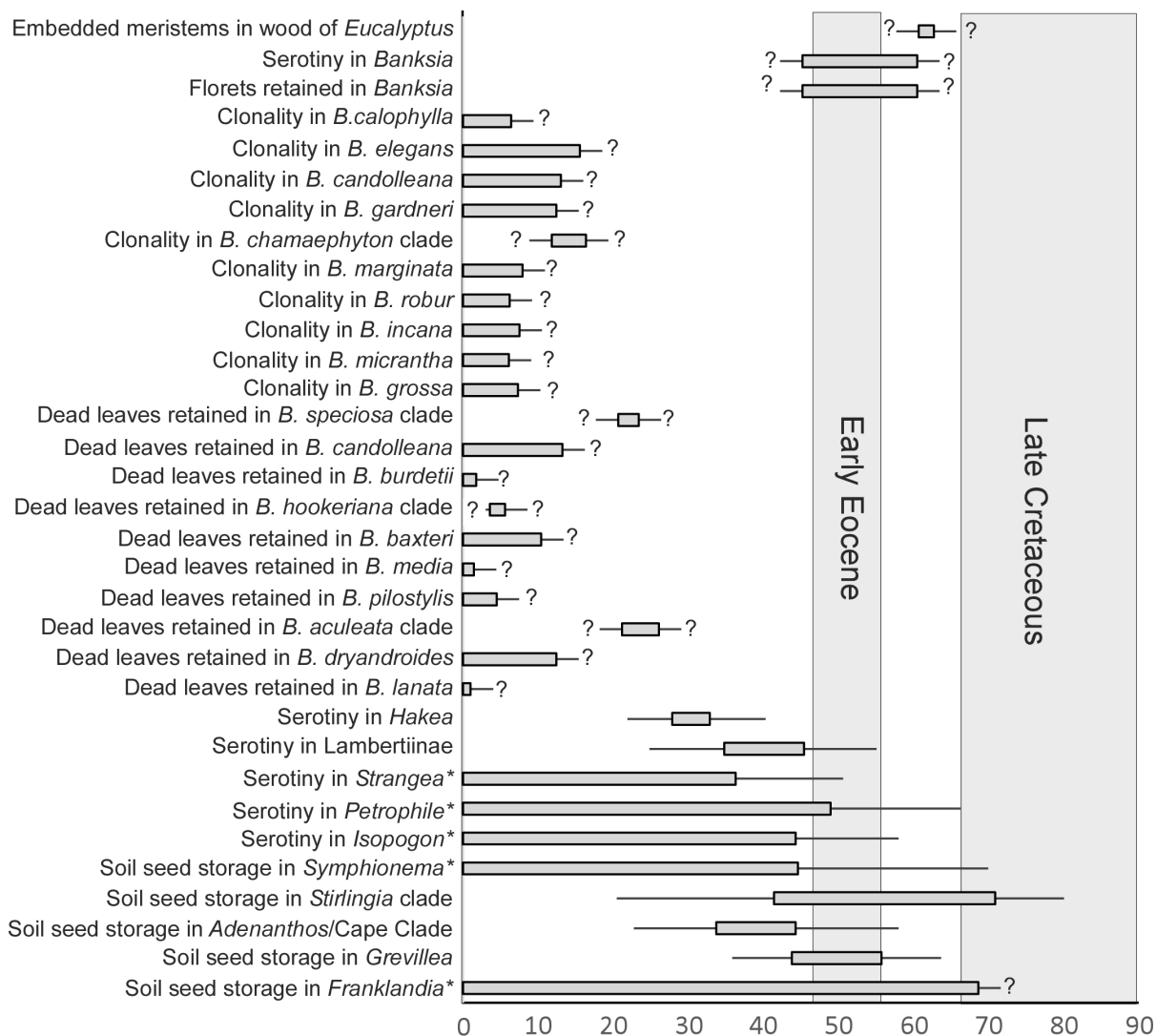
Figure 3. Estimated ages of evolution of fire related traits in the Australian flora. These ranges follow the procedure used by Crisp *et al.* (2011), with solid bars representing the range between the age of the oldest node at which ancestral state reconstruction infers the trait was present and age of the preceding node (at which the trait was reconstructed as being absent). The narrow bars represent 95% confidence intervals on the ages; a question mark indicates nodes for which confidence intervals were not given. The reconstruction for *Eucalyptus* is from Crisp *et al.* (2011), those for *Banksia* are from He *et al.* (2011), the other reconstructions are from Lamont and He (2012) and are for other traits in Proteaceae. The node ages for *Hakea* and *Grevillea* are from Mast *et al.* (2015). The minimum ages of traits in *Strangea*, *Petrophile*, *Isopogon*, *Symphionema* and *Franklandia* are likely to be substantial underestimates – these traits are likely to have arisen with the crown of these clades which may be any age younger than the maximum age for that trait. The reconstructions of soil seed storage and serotiny deep in the Proteoideae (Lamont and He 2012) are not included because of the problems with homology discussed in the main text.

identifies otherwise. However, there is a major violation of this underlying assumption of homology: the reconstructions of Lamont and He (2012) show that the species use different fire traits to function in fire-prone environments, and further that these traits have evolved convergently many times. This reconstruction of ancient fire prone habitats can arise by the coincidence of related clades being adapted independently (and much later) to fire. Such a reconstruction could indicate

the presence of some unknown genetically-determined characteristic of the ancestor that allows the later evolution of fire adaptations, but because such a characteristic has not been recognised as a fire adaptation, it is a prime candidate for being an exaptation. The reconstruction can also arise from geographic coincidence – if the related clades happen to occur preferentially in a region which becomes fire prone, then independent evolution of fire traits in these clades will result in a false reconstruction that fire-prone habitat is ancestral.

Similar problems of lack of homology extend to reconstructions of serotiny and soil seed storage (Lamont and He 2012). The infructescences that provide serotiny (canopy seed storage) in *Petrophile*, *Isopogon*, *Franklandia* and *Aulax* are different, so reconstructing the evolution of this trait as a single character state gives a misleading inference that it is ancestral. Similar problems relate to soil seed storage in this group, and this is made more complex by a lack of understanding of what structures or functions permit this behaviour.

Post-Cretaceous Fire Responses

Glasspool and Scott (2010) estimated very significant changes in atmospheric composition at about the end of the Cretaceous. Their model predicts that the oxygen percentage dropped to something approaching the modern level, and soon afterwards atmospheric carbon dioxide increased to high levels (Anagnostou *et al.* 2016), even taking account of the high variability in reconstructions. These changes led to a super-greenhouse effect and warm and wet conditions over much of the planet through the early and middle Paleogene (~65 to ~33 million years ago). During this long-lasting period, the Earth is characterised as being very warm and wet, mostly because of elevated CO_2 levels and the configuration of the continents at the time, which meant that ocean circulation patterns were favourably disposed to increase the amount of evaporation and rainfall across the latitudes. Plant fossil records are available for many parts of Australia in this period, but in striking contrast to preceding (Late Cretaceous) and the following (Neogene) times, there is effectively no fossil evidence of fire (Martin 1996). In the absence of the recently published Cretaceous data, it was therefore long held that Australia's modern fire-prone flora evolved during the Neogene.

However, it is now apparent that some of the extant taxa that are strongly fire-adapted probably had their genesis in the fire-prone environments of the Late Cretaceous (e.g. some Proteaceae, Casuarinaceae and possibly eucalypts, Restionaceae and Ericaceae). This poses the question of how these now largely fire tolerant taxa survived the prolonged warm and wet period of the Early Paleogene. One option is that fire tolerance evolved later. Another alternative is that there were refugia in which fires were frequent enough to allow fire-tolerant plants to survive in the long term (Crisp *et al.* 2011). Hill *et al.* (in press) propose that this may have been possible in the centre of Australia,

where the developing macrofossil evidence suggests that monsoon-like forests occurred, and included taxa such as the early eucalypts, that almost certainly evolved primarily in response to natural high fire frequencies. Another possibility is the west coast of Australia, where the fossil evidence demonstrates evidence for xeromorphic adaptations in the Middle Eocene (47.8-41.2 million years ago), considerably earlier than established views of the first appearance of dry climates in Australia (Carpenter *et al.* 2014). The dry climate that this implies is another possible "refuge" for taxa that were adapted to fire.

Late in the Paleogene (after about 33 million years ago), Australia began to move away from Antarctica, opening the Southern Ocean, and allowing for a major change in ocean currents. Also at about this time, atmospheric CO_2 levels dropped to near-modern levels (Anagnostou *et al.* 2016), and the climate began to dry and temperature extremes began to develop. Eventually this was to lead to the characteristic modern southern Australian climate, with mild, wet winters, and hot, dry summers, which meant that a summer fire season became an important feature of the environment and fire frequency and intensity began to increase once again. The evolution of most modern fire adaptations suggested in figure 3 is certainly consistent with this, suggesting that as modern climates evolved, a set of plant species were in place to take advantage of the new fire regime that accompanied these hotter and drier climates, and even though the original drivers for fire may have changed (from high atmospheric O_2 levels, to a hot, dry summer period), the adaptations that the species had positioned them well.

There must have been many changes in community make-up and species dominance through time, as Australia continued to dry and then went into a series of glacial and interglacial cycles. This culminated, at least 50,000 years ago, with the arrival of the first humans onto the continent. These first Australians must have brought the capacity to make fire with them, and they soon adapted to (and arguably created) a fire regime designed to make nutritional food readily available to them. This in turn led to the concept of a highly managed native vegetation (most recently summarised by Gammage, 2011), However, there are critics who point out that this view can be taken too far. For example, Low (2014) notes that Aborigines "appeared to wield enormous power only because Australia carries so many flammable plants". That is, the human fire management of the vegetation was only possible because the vegetation was already so well adapted to fire, which was the outcome of tens of millions of years of evolution.

Much controversy continues to exist over the way that interaction between people and fire developed over the millennia, how it impacted on the extinction of the megafauna, and how that in turn led to changes in the vegetation. For example, Mooney *et al.* (2011), in their synthesis of the fossil

pollen record, noted that "There is no distinct change in fire regime corresponding to the arrival of humans in Australia at 50 ± 10 ka and no correlation between archaeological evidence of increased human activity during the past 40 ka and the history of biomass burning". It is interesting to speculate that if there had been an even earlier human occupation of Australia than the one widely recognised at about 50,000 years ago, this anomaly would disappear. The long presence of early humans in the Indonesian archipelago means we should not dismiss that possibility. It was into this possibly deeply managed ecosystem that European settlers established themselves, in an environment that was so foreign that they often misunderstood, and therefore mismanaged it. This is the legacy we have inherited and the imperative to understand the long geological history that led to this modern situation, with all the management challenges that it brings, remains strong.

Acknowledgements

References

Anagnostou E, John EH, Edgar KM, Foster GL, Ridgwell A, Inglis GN, Pancost RD, Lunt DJ, Pearson PN (2016) Changing atmospheric CO_2 concentration was the primary driver of early Cenozoic climate. *Nature* **533**, 380-384.

Arvidson RS, Mackenzie FT, Guidry M (2006) MAGic: A Phanerozoic model for the geochemical cycling of major rock-forming components. *American Journal of Science* **306,** 135-190.

Belcher CM (2009) Re-igniting the Cretaceous-Palaeogene firestorm debate. *Geology* **37,** 1147-1148.

Belcher CM, Yearsley JM, Hadden RM, McElwain JC, Rein G (2010) Baseline intrinsic flammability of Earth's ecosystems estimated from paleoatmospheric oxygen over the past 350 million years. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 22448-22453.

Bergman NM, Lenton TM, Watson AJ (2004) COPSE: a new model of biogeochemical cycling over Phanerozoic time. *American Journal of Science* **304,** 397-437.

Berner RA (2006) GEOCARBSULF: A combined model for Phanerozoic atmospheric O_2 and CO_2. *Geochimica et Cosmochimica Acta* **70,** 5653-5664.

Blackburn DT, Sluiter IRK (1994) The Oligo–Miocene coal floras of southeastern Australia. In 'History of the Australian vegetation: Cretaceous to Recent'. (Ed. RS Hill) pp. 328–367. (Cambridge University Press: Cambridge).

Bond WJ, Scott AC (2010) Fire and the spread of flowering plants in the Cretaceous. *New Phytologist* **188,** 1137-1150.

Bowman DMJS, Murphy BP, Burrows GE, Crisp MD (2012) Fire regimes and the evolution of the Australian biota. In 'Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world. (Eds AM Gill, RJ Williams and RA Bradstock). (CSIRO Publishing: Melbourne)

Bowman DMJS, French BJ, Prior LD (2014) Have plants evolved to self-immolate? *Frontiers in Plant Science* **5**, 590.

Bradshaw SD, Dixon KW, Hopper SD, Lambers H, Turner SR (2011a) Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends in Plant Science* **16**, 69-76.

Bradshaw SD, Dixon KW, Hopper SD, Lambers H, Turner SR (2011b) Response to Keeley *et al*.: Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**, 405.

Brown SAE, Scott AC, Glasspool IJ, Collinson ME (2012) Cretaceous wildfires and their impact on the Earth system. *Cretaceous Research* **36**, 162-190.

Carpenter RJ, McLoughlin S, Hill RS, McNamara KJ, Jordan GJ (2014) Early evidence of xero-morphy in angiosperms: Stomatal encryption in a new Eocene species of *Banksia* (Proteaceae) from Western Australia. *American Journal of Botany* **101,** 1486-1497.

Carpenter RJ, Macphail MK, Jordan GJ, Hill RS (2015) Fossil evidence for open, Proteaceae-dominated heathlands and fire in the Late Cretaceous of Australia. *American Journal of Botany* **102,** 2092-2107.

Carpenter RJ (in press) Cretaceous fire in Australia: a review with new geochemical evidence, and relevance to the rise of the angiosperms. *Australian Journal of Botany.*

Crisp MD, Burrows GE, Cook LG, Thornhill AH, Bowman DMJS (2011) Flammable biomes dominated by eucalypts originated at the Cretaceous-Palaeogene boundary. *Nature Communications* **2**.

De Lillis M, Bianco PM, Loreto F (2009) The influence of leaf water content and isoprenoids on flammability of some Mediterranean woody species. *International Journal of Wildland Fire* **18**, 203-212.

Dobzhansky T (1956) What is an Adaptive Trait? *The American Naturalist* **90,** 337-347.

Falcon-Lang HJ, Mages V, Collinson M (2016) The oldest *Pinus* and its preswervation by fire. *Geology* **44,** 303-306.

Friis EM, Crane PR, Pedersen KR (2011) 'Early Flowers and Angiosperm Evolution.' (Cambridge University Press: Cambridge).

Gammage B (2011) 'The Biggest Estate on Earth.' (Allen and Unwin: Sydney).

Glasspool IJ, Scott AC (2010) Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. *Nature Geoscience* **3,** 627-630.

Grandcolas P, Nattier R, Legendre F, Pellens R (2011) Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: Does it make sense at all? *Cladistics* **27**, 181-185.

Hansen KW, Wallmann K (2003) Cretaceous and Cenozoic evolution of seawater composition, atmospheric O_2 and CO_2: A model perspective. *American Journal of Science* **303,** 94-148.

He T, Lamont BB, Downes KS (2011) *Banksia* born to burn. *New Phytologist* **191**, 184-196.

Hill RS, Beer YH, K., Maciunas E, Tarran M, Wainman C (in press) Evolution of the eucalypts – an interpretation from the macrofossil record. *Australian Journal of Botany.*

Jordan GJ, Harrison PA, Worth JRP, Williamson GJ, Kirkpatrick JB (2016) Palaeoendemic plants provide evidence for persistence of open, well-watered vegetation since the Cretaceous. *Global Ecology and Biogeography* **25,** 127-140.

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**, 406-411.

Kirkpatrick JB, Bridle KL, Dickinson KJM (2010) Decades-scale vegetation change in burned and unburned alpine coniferous heath. *Australian Journal of Botany* **58**, 453-462.

Lamont BB, He T (2012) Fire-adapted Gondwanan Angiosperm floras evolved in the Cretaceous. *BMC Evolutionary Biology* **12**.

Low T (2014) 'Where Song Began.' (Viking: UK)

Macphail MK (2007) Australian palaeoclimates: Cretaceous to Tertiary. *CRC LEME Special Volume*. 279p.

Martin HA (1996) Wildfire in past ages. *Proceedings of the Linnean Society of New South Wales* **116,** 3-18.

Mast AR, Olde PM, Makinson RO, Jones E, Kubes A, Miller ET, Weston PH (2015) Paraphyly changes understanding of timing and tempo of diversification in subtribe Hakeinae (Proteaceae), a giant Australian plant radiation. *American Journal of Botany* **102**, 1634-1646.

McNamara, K.J. and Scott, J.K. 1983. A new species of *Banksia* (Proteaceae) from the Eocene Merlinleigh Sandstone of the Kennedy Range, Western Australia. Alcheringa 7, 185-93.

Mooney SD, Harrison SP, Bartlein PJ, Daniau A-L, Stevenson J, Brownlie KC, Buckman S, Cupper M, Luly J, Black M, Colhoun E, D'Costa D, Dodson J, Haberle S, Hope GS, Kershaw P, Kenyon C, McKenzie M, Williams N (2011) Late Quaternary fire regimes in Australia. *Quaternary Science Reviews* **30,** 28-46.

Manfroi J, Dutra TL, Gnaedinger S, Uhl D, Jasper A (2015) The first report of a Campanian palaeo-wildfire in the West Antarctic Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology* 418, 12-18.

Orians GH, Milewski AV (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* **82,** 393-423.

Robinson JM (1989) Phanerozoic O_2 variation, fire, and terrestrial ecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **75,** 223-240.

Sluiter IR, Holdgate GR (in press) Fire and south-eastern Australia's Late Oligocene to Mid Miocene age peat mega-swamps: a floristic and palaeoclimatic interpretation. *Australian Journal of Botany*.

Tappert R, McKellar RC, Wolfe AP, Tappert MC, Ortega-Blanco J, Muehlenbachs K (2013) Stable carbon isotopes of C3 plant resins and ambers record changes in atmospheric oxygen since the Triassic. *Geochimica et Cosmochimica Acta* **121**, 240-262.

Tng DYP, Janos DP, Jordan GJ, Weber E, Bowman DMJS (2014) Phosphorus limits eucalyptus grandis seedling growth in an unburnt rain forest soil. *Frontiers in Plant Science* **5**.

Tng DYP, Williamson GJ, Jordan GJ, Bowman DMJS (2012) Giant eucalypts - globally unique fire-adapted rain-forest trees? *New Phytologist* **196**, 1001-1014.

Watson J, Alvin KL (1996) An English Wealden floral list, with comments on possible environmental indicators. *Cretaceous Research* **17,** 5-26.