

Fire regimes and the evolution of the Australian biota

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Introduction

Imagine that a fire-tolerant lineage of plants evolved a specialised structure allowing them to spontaneously combust under hot dry conditions, thereby causing fires that eliminate less fire-tolerant competitors, as well as providing regeneration opportunities for the establishment of the next generation of these ‘pyrogenic’ plants. Such a lineage would be expected to restructure ecosystems radically and alter biogeographic patterns. Although no such plant group actually exists, it has been claimed that some plants have developed specialised features to tolerate and promote fires, thereby fundamentally reorganising regional biotas (e.g. Bond and Van Wilgen 1996). Such a view is based on a synthesis of various traits and syndromes apparent in plants. For example, thick bark and heavily insulated regenerative tissues are thought to be adaptations to enable trees to survive fires, and vigorous resprouting from the base of burnt stems is a common vegetative regeneration strategy for plants in fire-prone environments. Further, some plants have reproductive cycles correlated with fire activity, including fire-stimulated flowering and smoke- and heat-stimulated seed germination (Bell *et al.* 1993; Dixon *et al.* 1995). Some workers suggest that exposure to a long history of fire activity has acted as a selective factor on plant morphology that has increased the occurrence of fires, such as open crown architecture, which allows trees to co-exist with flammable grass (Bond and Keeley 2005). Likewise, some phenological syndromes are thought to favour fire activity such as the production of large quantities of oil-rich and decay-resistant leaves and bark (e.g. Ashton 1981). Finally, it has been claimed that the collective effect of such specialised traits that both tolerate and encourage fire activity has resulted in plant communities with characteristic fire regimes – a particular template of fire intensity, type, frequency and seasonality – to which plants and animals have co-evolved (e.g. Pausas and Keeley 2009). Building on these ideas, it has been argued that a marked excursion from a given fire regime is a threatening ecological process that can cause species loss and ecosystem dysfunction (Bradstock and Kenny 2003). This ‘co-evolutionary’ view of fire regimes and ecosystems has profound theoretical and practical implications. However, it must be acknowledged that much evolutionary thinking remains poorly grounded in both theory or empirical observations, being based on various loose assumptions, and chains of reasoning, often resulting in ‘just so stories’. The purpose of this chapter is to explore the role that fire has played in the evolution of the modern Australian biota.

Australia holds a special place in theories about the evolution of fire tolerance and flammability. The famous ‘Mutch hypothesis’ (Mutch 1970), which first articulated the idea that fire and plants may have co-evolved, drew heavily on research that highlighted the interdependence of Tasmanian forests with fire (Mount 1964; Jackson 1968). Further, Australian taxa such as grass trees, *Xanthorrhoea*, were some of the first examples demonstrating the nexus between fire and flowering (Gill and Ingwersen 1976). Likewise, research has highlighted the importance of smoke in breaking seed dormancy in a range of Australian plant communities (Dixon *et al.* 1995; Enright *et al.* 1997; Morris 2000). Finally, it has been argued that the cause of the dominance of eucalypts and other quintessentially Australian plant groups and the fragmentary, highly restricted distribution of rainforest is due to a long history of landscape burning (Bowman 2000). There are more than 800 eucalypt species (including *Eucalyptus*, *Corymbia* and *Angophora*), plus several other large genera (e.g. *Melaleuca* s.l. >350 species, *Leptospermum* 77 species) forming part of a massive evolutionary radiation of the Myrtaceae (approximately 77 genera and 1600 species in Australia, out of 5500 species worldwide) that stems from Gondwanan rainforest lineages (Bowman 2000; Ladiges *et al.* 2003; Crisp *et al.* 2004).

Thinking about the evolutionary relationship between fire and biota has been frustrated by a lack of a good fossil record to provide a coherent framework to chart the process of how plants adapt to fire, with far more attention given to the evolutionary processes in the nonflammable Paleogene rainforest floras, particularly *Nothofagus*, for which there is a good fossil record (Hill 1994). In any case, there are no unambiguous plant features in the fossil record that can be interpreted as fire-related adaptations, as opposed to ‘exaptations’ – features that confer fire-resistance but evolved in response to a different selective regime (e.g. Bradshaw *et al.* 2011). One feature that is unambiguously related to fire is charcoal, yet interpreting this record is highly problematic (Bowman 2000; Lynch *et al.* 2007). A key example, which we will discuss later, concerns the ecological and evolutionary significance of a spike in charcoal abundance in the pollen record from Lynch’s Crater on the Atherton Tablelands, coinciding with the human colonisation of Australia (Kershaw 1986). This pollen record has spawned a number of ideas, largely speculative, about the drastic impacts of Aboriginal fire use on Australian ecosystems, including the idea that the geographic extent of eucalypt forests increased sharply following colonisation and more speculatively that this stimulated speciation and radiation of fire-tolerant taxa (Kershaw 1981; Singh *et al.* 1981; Gillison 1983; Kershaw 1984;

Janzen 1988; Beard 1990; Hill 1994). As we shall show, much of this speculation is now dismissed, given the availability of two important streams of evidence: molecular phylogenies and direct observation of Aboriginal fire usage.

In this chapter, we will: (a) provide a brief overview of theories of fire–plant evolutionary interactions, (b) present phylogenetic case studies that illuminate thinking about the evolution of eucalypt epicormic bud regeneration, (c) consider the impacts of changed fire regimes following Aboriginal colonisation, and (d) review the consequences of the shift to European fire regimes.

Evolution and fire

In a physicochemical sense, fire is the rapid release of energy via the oxidation of chemical compounds, typically rich in carbon. This process is often summarised in a classic ‘fire triangle’ made up of the three key factors to cause combustion: oxygen, fuel and sufficient heat for ignition (Whelan 1995; Pyne 2007). Fire has a long history that began about 420 million years ago (Ma) when there was sufficient oxygen in the atmosphere and terrestrial biomass available to burn. Atmospheric oxygen concentration creates a ‘window’ that controls fire activity because, when concentration falls below 13%, combustion cannot occur. Above this level, fire activity is limited by fuel moisture, although at 35% oxygen even moist fuels will burn (Scott and Glasspool 2006). Fire activity is thought to have changed significantly through geological time in large part due to the substantial fluctuations in atmospheric oxygen. It has been suggested that increased oxygen levels favoured fire activity that stimulated the radiation of flowering plants (Bond and Scott 2010).

Fire in the biosphere is not simply a physicochemical process but rather a fundamental biogeochemical process (Bowman *et al.* 2009). For example, fires instantaneously link biomass with the atmosphere by releasing heat, particulates, gases (notably water vapour and CO₂) and changing the surface albedo, thus influencing climate. Likewise, fire also influences the

geo-sphere by releasing nutrients and making soils more erodible and, in the long term, forming large deposits of biologically recalcitrant black carbon. Such complex interactions, including numerous short- and long-range feedbacks, render fire unlike other natural disturbances, such as floods or cyclones. For this reason, some ecologists have suggested that landscape fires should be considered as being ‘biologically constructed’, and have drawn parallels with herbivory (Bond and Keeley 2005) or decomposition (Pyne 2007). The tight coupling between fire and life (and the long history of fire on Earth) raises questions about their potential co-evolution and implications for land management. For example, the refined interdependence of fire and tall eucalypt forests is presented as an exemplar of co-evolution of plants with fire. Tall forest eucalypts retain seeds in woody capsules and the seeds are released *en masse* following fire, with seedling establishment on unburnt sites being extremely rare (Gilbert 1959; Mount 1979; Ashton 1981). It has been claimed that, without periodic burning, somewhere in the order of every 100–400 years, these systems would be replaced by rainforest trees that can continuously regenerate (e.g. Jackson 1968; Bowman 2000). Indeed, foresters argue that they must use high-intensity fires to regenerate logged eucalypt stands, despite growing public opposition to the smoke pollution and release of greenhouse gases.

Mutch (1970) was the first author to clearly articulate the hypothesis that some vegetation types have evolved characteristics to increase the risk of fire. Mutch (1970) argued ‘fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favoured development of characteristics to make them more flammable’. A number of authors have pointed out that, when stated in this way, this evolutionary conjecture is flawed for several reasons. First, flammable vegetation is not necessarily flammable because of direct selection for flammable characteristics, so it is a circular argument to claim that flammable vegetation necessarily evolved to burn (Snyder 1984; Bowman and Wilson 1988; Trabaud 1989; Bradshaw *et al.* 2011). Second, traits that cause flammability may arise in response to other selective forces such as herbivory, drought or low soil fertility (Snyder 1984; Trabaud 1989; Bradshaw *et al.* 2011): a process known as ‘exaptation’. Third, to avoid a ‘group selection’ argument (where evolutionary advantages are provided to unrelated genotypes), there needs to be a clear linkage showing how an individual’s flammability increases its reproductive fitness (Zedler 1995).

To overcome these problems, some authors have argued that fire should be seen as an agent of inter-specific competition, where burning damages competitors but can increase the reproductive success of a flammable species (Bond and Midgley 1995; Possingham *et al.* 1995). For example, Bond and Midgley (1995) theorise that flammable genotypes that interfere with nonflammable competitors would have an evolutionary advantage. However, their modelling showed that the spread of a trait promoting flammability through a population could only occur if the trait increased reproductive fitness and they suggested that this might occur if the flammability trait also conferred other evolutionary advantages, such as providing chemical defences against herbivory. This idea of flammable traits simultaneously providing other benefits has been elaborated on by Schwilk and Kerr (2002) who proposed a hypothesis called ‘genetic niche-hiking’ where flammable traits may spread without any ‘direct fitness benefit of the flammable trait’. For example, the Myrtaceae have foliar glands that produce aromatic oils, which probably evolved as a toxic defence against herbivores, but also promoted flammability (Steinbauer 2010).

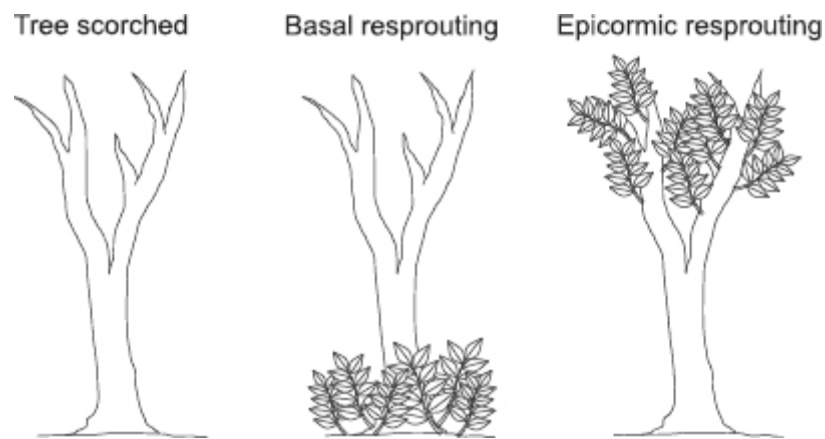


Figure 2.1. Epicormic resprouting allows individuals to rapidly recover pre-fire height, overtopping basal resprouters. Prolific epicormic resprouting following fire is typical of most eucalypts. Epicormic resprouting appears to be one of the features of eucalypts that has allowed them to dominate many of Australia's most fire-prone landscapes.

Clearly, it is difficult to confidently attribute plant traits that promote flammability as fire adaptations. A range of hypotheses have been proposed to explain how flammability may confer a selective advantage, including the recent 'pyrogenicity as protection' hypothesis of Gagnon *et al.* (2010). These authors argue that in fire-prone habitats, natural selection would favour plants that burn rapidly and retain fuels off the ground, thereby avoiding high soil temperatures that can damage underground tissues. Yet, this hypothesis runs counter to the well established 'ashbed effect', critical for the regeneration of wet eucalypt forest species. The ashbed effect occurs when soils are heated to temperatures of around 400–600 °C during high-intensity surface fires, resulting in the partial sterilisation of the soil and an increase in nutrient availability, and enhanced growth of seedlings (Chambers and Attiwill 1994; Launonen *et al.* 1999). Based on this effect, it has been argued that natural selection has resulted in traits that ensure high-intensity surface fires, such as foliage and wood that resist decomposition, thereby creating heavy fuel loads (Mount 1979). Given the diversity of plant life forms, traits and regeneration strategies, it is implausible that broad evolutionary hypotheses such as 'pyrogenicity as protection' or the 'ashbed effect' can be generalised across all flammable plant communities, confounding progress in understanding the evolution of flammability because of the inevitable exceptions. Keeley *et al.* (2011) argue the key to understanding the evolutionary relationships between plants and fire is the nexus between fire regimes and plant traits, yet discerning fire regimes independently from plant traits (in order to avoid circular reasoning) from the palaeo-ecological record is extraordinarily difficult, if not impossible. We argue that a far more powerful route to grappling with this question of the evolution of fire adaptations is to focus on more clearly defined traits in given clades and use molecular phylogenetics to chart their development. This is illustrated for the case of the evolution of epicormic buds in eucalypts – a trait that allows these trees to vigorously resprout from their trunks and branches following wildfire (Figures 2.1 and 2.2).

Evolution of epicormic buds

In fire-prone environments, resprouting after wildfire is common and widespread (Bond and Midgley 2001; Vesk and Westoby 2004) with obligate seeders representing a less common strategy among woody plants (e.g. Russell-Smith *et al.* 1998; Clarke *et al.* 2005; Lloret *et al.* 2005; Keeley *et al.* 2006). Most resprouters regenerate from below ground level, with resprouting from aerial stems or branches (epicormic resprouting) being globally rare (Burrows 2008). This is logical, because most heat from a fire goes upwards rather than downwards and buds only a few centimetres below the soil surface can remain relatively cool (e.g. Choczynska and Johnson 2009). Conversely, keeping the vascular cambium and bud-forming tissues alive in aerial stems and branches requires a considerable investment in insulating bark tissues. However, epicormic resprouters have the strong advantage of being able to use much of their existing above ground framework to rapidly re-establish a photosynthetic surface and consequently shade the basal resprouters and seedlings. It is worth noting that such a strategy is clearly inconsistent with the 'pyrogenicity as protection' hypothesis (Gagnon *et al.* 2010), discussed above.

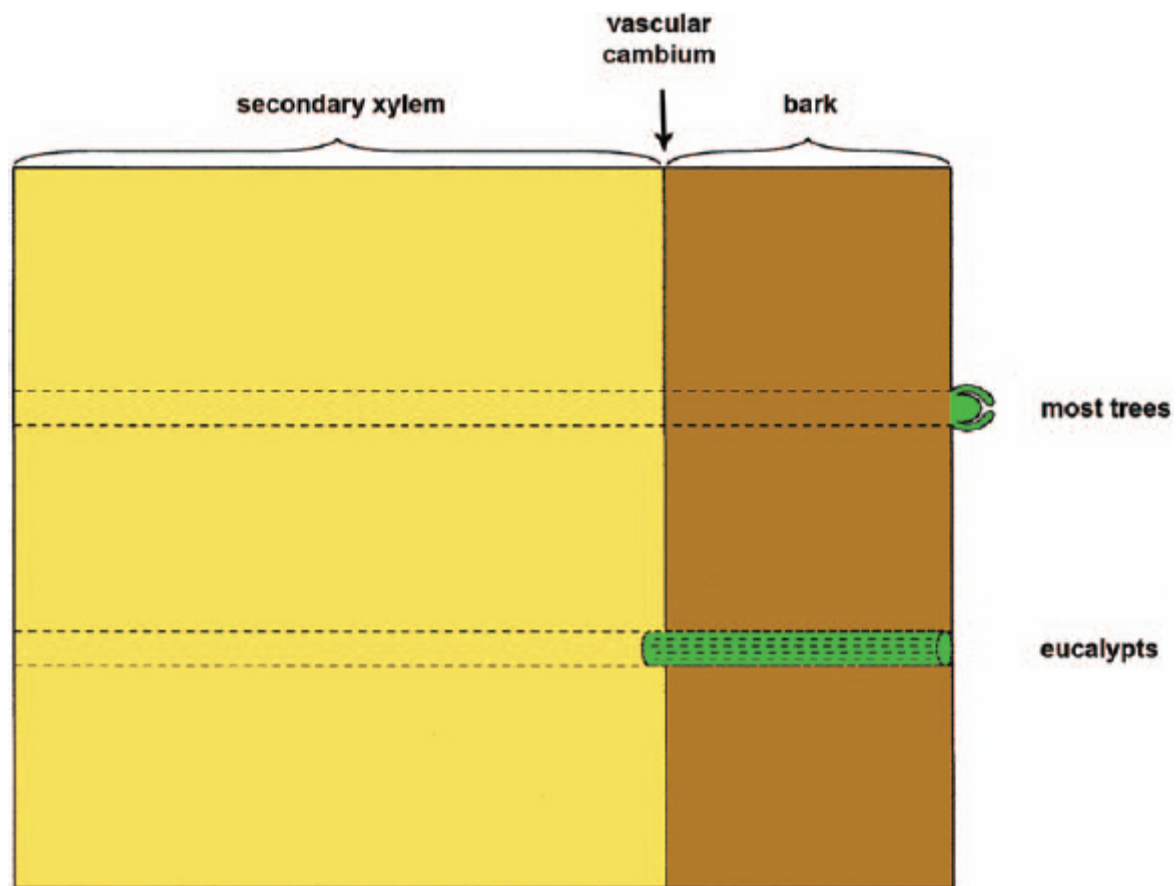


Figure 2.2. In most trees, epicormic buds are located at the surface of the bark (top), a position where they are exposed directly to the heat of a fire. In eucalypts, for each epicormic strand there are several strips of very small cells that run from the bark surface, through the bark and into the wood for a short distance (bottom). These cells can form numerous buds at various depths in the bark after a fire. Thus, even if most of the bark is killed in an intense fire some of the bud-forming cells will still be alive. The dotted lines indicate the epicormic strands, while the light green colour indicates that part of the strand where bud regeneration is possible. The dotted lines within the eucalypt strand surrounded by the bark represent the meristem strips.

Eucalypts are the most accomplished post-fire epicormic resprouters in the world (Burrows 2002; Burrows 2008) and this trait is vigorously expressed by nearly all eucalypts (Nicolle 2006) (Figure 2.1). For example, of 82 eucalypt taxa in the Sydney region (about 400 × 400 km), 80% were post-fire epicormic resprouters, 19% were basal-only resprouters and 1% were killed (Benson and McDougall 1998). In contrast, 30% of 72 species of non-eucalypt Myrtaceae were killed, 40% were basal-only resprouters, 20% were epicormic resprouters and 10% were classified as resprouters of unspecified type. This relatively small sample illustrates both the wide diversity of post-fire resprouting responses in the family and the outstanding resilience of the eucalypts.

Epicormic buds of most species studied to date, except eucalypts, are located close to the bark surface (Fink 1983; Fink 1999), where they are often killed by fire. The epicormic structures of eucalypts have narrow, radially-orientated strips of cells of meristematic appearance (Cremer 1972), which are best developed within the innermost bark or even the outermost wood (Burrows 2000; Burrows 2002; Burrows *et al.* 2010) (Figure 2.2). 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 (e.g. Clarke 2002; Burrows and Wardell-Johnson 2003). This specialised structure has been found in all major eucalypt taxonomic groups, growth forms and Australian regions. This basic structure also occurs in *Syncarpia* and *Tristaniopsis* (Myrtaceae), which are also known to be post-fire epicormic resprouters (Burrows 2008).

It has been argued that the evolution of fire-tolerance in the Myrtaceae was directly linked to the origins and expansion of flammable biomes in Australia (Bowman 2000; Orians and Milewski 2007; Bradstock 2010). However, the Australian fossil record has provided little direct evidence of fire, indicated by the presence of fusain (fossil charcoal), before the mid-Miocene when the climate aridified and charcoal levels increased dramatically (Hill 1994; Bowman 2000; Kershaw *et al.* 2002). Some of the best evidence of pre-Miocene fire-adapted swamp flora is from the Gippsland brown coals that make up a pyric succession given the occurrence of charcoal (Blackburn and Sluiter 1994). These fire-prone communities have no modern analogue and included *Banksia*, *Callitris* and Casuarinaceae, but no Myrtaceae, species.

Dated phylogenies using relaxed molecular clocks can provide indirect evidence on the timing of evolutionary transitions in organismal traits, including their habitat tolerances, and can be used as a framework for testing hypotheses about historical relationships (Ackerly *et al.* 2006). Using this approach, Crisp *et al.* (2011) have recently shown that this unique epicormic

anatomy has been strictly conserved until the present in eucalypts, despite changes in habitat and response to fire. For example, *Eucalyptus regnans*, which dominates wet sclerophyll forest in south-eastern Australia, is readily killed by fire and regenerates primarily from seed, yet still possesses specialised protected meristem strips (Waters *et al.* 2010). This species is nested deeply within the eucalypts (Ladiges *et al.* 2010), whose shared ancestor was a resprouter (Crisp *et al.* 2011), supporting the inference that its obligate seeding fire response is a derived feature. Melaleuceae (Wilson *et al.* 2005) is another diverse Myrtaceae clade that has evolved a different structure allowing epicormic resprouting. Some *Melaleuca* species have buds at the level of the vascular cambium protected by numerous layers of dead phellem (Burrows *et al.* 2010). The Melaleuceae clade warrants further investigation because it shows less conservative epicormic evolution, having four of the five known types that have been identified by Burrows *et al.* (2010).

The molecular phylogenetic analysis of Crisp *et al.* (2011) suggests that both epicormic resprouting in the Myrtaceae and flammable sclerophyll biomes originated in the earliest Cenozoic (Paleocene, 55–60 Ma) and their evolution is significantly linked. He *et al.* (2011) have also reported recently that a suite of inferred fire adaptations, such as serotiny, emerged in the Australian genus *Banksia* at about this time. In other parts of the world, there is charcoal evidence that fire frequency increased in the lead-up to the Paleocene–Eocene ‘greenhouse world’ (Collinson *et al.* 2007; Collinson *et al.* 2009; Bond and Scott 2010) and that seasonally dry climates occurred during this period (Schmitz and Pujalte 2007; Raigemborn *et al.* 2009). Although scleromorphy in the Australian flora dates back to the Late Cretaceous (Hill 1998), this leaf morphology is not necessarily an indicator of arid climates in general or fire-prone vegetation in particular (Hill 1998; Haworth and McElwain 2008). Consequently, it has been widely assumed that fire-dominated Australian biomes only became extensive when the global climate aridified and became more seasonal after 15 Ma (Cowling *et al.* 1996; Bowman 2000; Bond and Keeley 2005) and charcoal become a more constant feature of the sedimentary record (Kershaw *et al.* 2002).

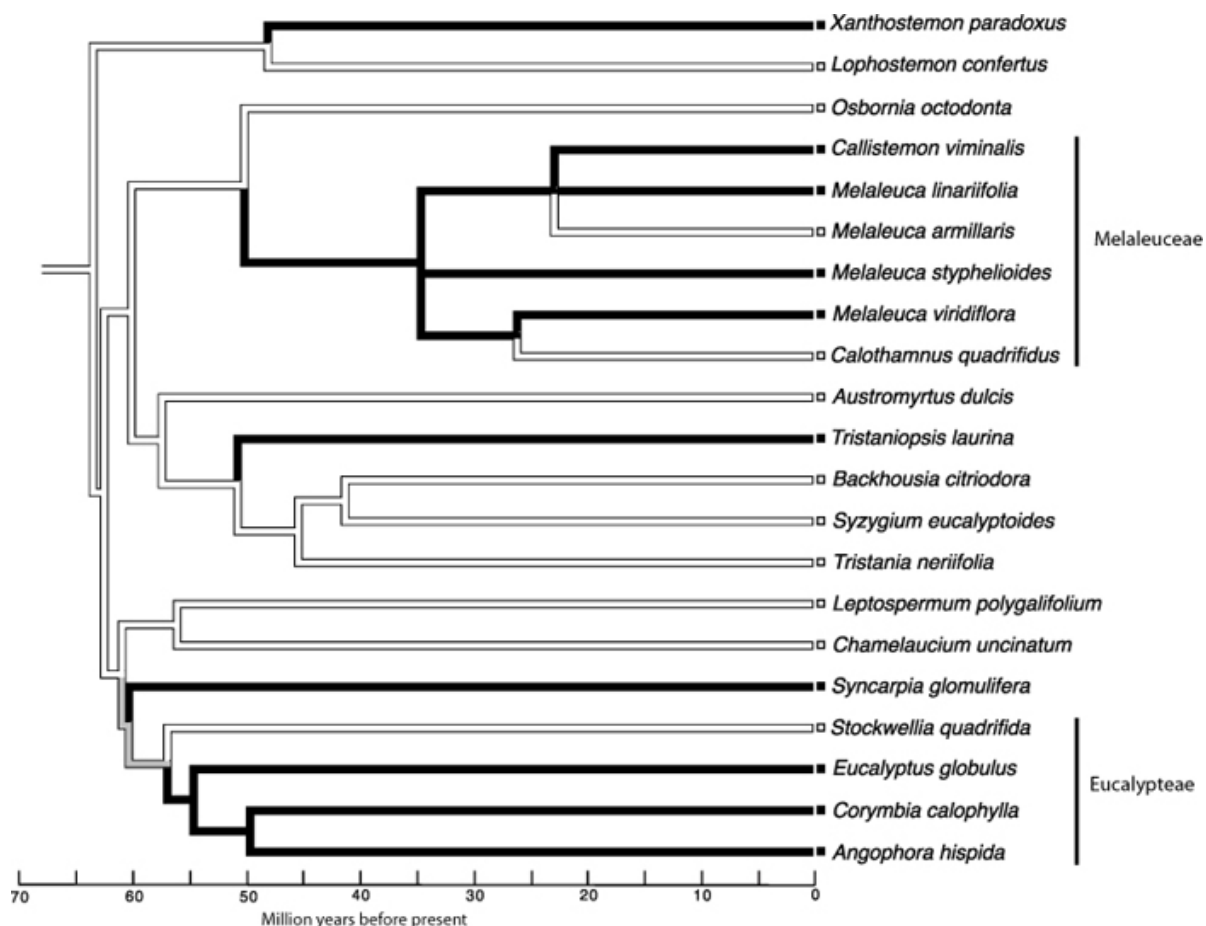


Figure 2.3. Dated molecular phylogeny of the Myrtaceae showing inferred transitions to specialised, fire-adapted epicormic resprouting, shown in black. White indicates lineages that do not resprout epicormically. Grey indicates ambiguous reconstruction. (Source: simplified from Crisp *et al.* 2011)

The analysis of Crisp *et al.* (2011) shows multiple origins of resprouting in the Myrtaceae: once in each of Melaleuceae, *Tristaniopsis* and *Xanthostemon* and once or twice in the eucalypt–*Syncarpia* lineage (Figure 2.3), favouring the hypothesis that flammable biomes originated first and thereby drove the evolution of traits adapted to fire-prone landscapes. Alternatively, fire-promoting Myrtaceae could have risen to dominance first, favouring more frequent fire regimes, thus

initiating a feedback loop that maintained or increased the dominance of the Myrtaceae and driving further specialisation to promote and withstand fire.

Crisp *et al.* (2011) found that Myrtaceae species' biome preferences were significantly conserved phylogenetically and that when transitions from one biome to another did occur they were strictly directional – all sclerophyll lineages originated from a rainforest ancestor and all monsoonal savanna lineages arose later, from sclerophyll or rainforest ancestors. Most of the biome shifts were into savanna, confirming that this biome is a sink relative to the other biomes (Crisp *et al.* 2009). This is consistent with the emerging view that the advent of the monsoonal climate opened a major ecological opportunity that the pre-adapted species could exploit effectively (Bowman *et al.* 2010a). For example, a molecular phylogenetic analysis of the Australian palm *Livistona* revealed that the closest relative of the extant fire-adapted savanna species was a South-East Asian ancestor that colonised the Australian monsoon tropics some 10 Ma (Crisp *et al.* 2009).

It is clear from the study of Crisp *et al.* (2011) that flammable biomes, and strongly conserved adaptations to them, evolved in Australia tens of millions of years earlier than previously thought. Indeed, the growing number of molecular phylogenies of quintessentially Australian plants and animals have fundamentally framed the debates about the impacts of Aboriginal fire use (Bowman and Yeates 2006). There is no doubt that phylogenetic analyses of fire traits and fire-tolerant biota will revolutionise thinking about the evolution of flammability worldwide.

Evolutionary impacts of Aboriginal fire management

In the late 20th century, the debate about Aboriginal fire impacts was dominated by the significance of the apparent coincidence of charcoal spikes and associated vegetation transitions at around the time humans were thought to have colonised Australia in the Late Pleistocene (Bowman 1998; Bowman 2000). For example, from a pollen core taken from Lynch's Crater in Australia's humid tropics, Kershaw (1986) noted that a spike in microscopic charcoal concentrations was associated with the transition from rainforest to sclerophyll vegetation. There has been considerable difficulty in reliably dating this charcoal spike and there remains uncertainty as to when humans colonised Australia, placing a question mark over Kershaw's (1986) bold interpretation (Bowman 1998). Re-dating of the Lynch's Crater pollen core by Turney *et al.* (2001b) suggested that the charcoal spike occurred around 45 000 years ago (ka) (7000 years earlier than the original estimate), close to the lower confidence limit for the broadly accepted arrival date for humans in Australia (45–55 ka; Roberts *et al.* 1990; Turney *et al.* 2001a).

As noted, the ecological and archaeological interpretation of charcoal in sedimentary records is fraught with difficulties (Bowman 1998). Indeed, in a recent review of charcoal proxy data, Lynch *et al.* (2007) highlighted the complexity in using charcoal records to partition human fire effects from background climatic variation operating from geological to interannual time-scales. For example, several recent studies have highlighted the strong control of climate over fire activity in the Late Pleistocene and Holocene, with humans having relatively limited impact (Haberle and Ledru 2001; Black *et al.* 2008).

Charcoal evidence does, however, reliably demonstrate the long history of fire in the Australian environment. This, coupled with the insights provided from calibrated molecular phylogenies (e.g. Crisp *et al.* 2009), has demolished the once widespread view that Aboriginal landscape burning triggered the evolutionary diversification of fire-adapted species (Kershaw 1981; Singh *et al.* 1981; Gillison 1983; Kershaw 1984; Janzen 1988; Beard 1990; Flannery 1994; Hill 1994). This idea appears to have grown out of confusion regarding two separate issues: the geographic extent of eucalypt vegetation and the diversification of flammable vegetation. An example of the conflation of these two ideas is provided by Kershaw (1981): 'the recent increased impact of fire is probably related to an increase in importance of fire-promoting species – particularly the eucalypts – within the flora. Although it is very unlikely that eucalypts evolved as recently as this, it is possible that the ecology of the genus has changed through time. The great variation shown within species and species groups would support a relatively recent radiation and massive extension of range which may have been linked with the development of open eucalypt communities as we see them today'. Kershaw concluded that 'the most tenable explanation of why [these] changes occurred at this particular time is that aboriginal man encouraged fire and its effects'. There remains much debate about the actual impact of Aboriginal burning in changing vegetation distribution patterns and species ranges, but there is little support for the view that Aboriginal burning was a driver of plant *speciation*. The more profound evolutionary effect may have been causing of the *extinction* of the Pleistocene megafauna, with potential knock-on effects on ecosystems and fire regimes.

Flannery (1994), in his successful and influential book *The Future Eaters*, clearly articulated the hypothesis that Aboriginal fire usage had a significant evolutionary impact on Australian ecosystems following the extinction by over-hunting of a diverse assemblage of large reptiles, birds and marsupials, collectively known as the megafauna. Flannery contended that, following the extinction of the megafauna through over-hunting and dramatic relaxation of grazing and browsing pressure, fire became a much more prominent feature of Australian landscapes. The Australian Pleistocene extinctions were particularly pervasive, with the loss of 21 out of 23 genera of land animals (reptiles, birds and marsupials) that included species with body mass exceeding 44 kg (Koch and Barnosky 2006). The timing of the megafaunal extinctions

remains controversial, although there now appears to be widespread acceptance that they were tightly clustered around 45–50 ka (Miller *et al.* 1999; Roberts *et al.* 2001; Brook and Bowman 2002; Brook *et al.* 2007), shortly following the arrival of humans sometime between 45 and 55 ka (Roberts *et al.* 1990; Turney *et al.* 2001a). With some important exceptions (e.g. Wroe and Field 2006), there is now widespread agreement in the literature that human colonisation was pivotal in causing these extinctions (Brook *et al.* 2007), with many authors citing climatic stability at the time of the extinctions as evidence (e.g. Miller *et al.* 1999; Johnson 2005; Gillespie *et al.* 2006; Brook *et al.* 2007). Although the mechanism of the extinctions remains elusive, recent research suggests a fundamental change to the feeding niches of Australian ecosystems, given that browsers are overrepresented among the extinct marsupial megafauna (Bowman *et al.* 2010c).

Miller *et al.* (2005a) provide very robust evidence for the changed diets of two large flightless herbivorous birds around 45–50 ka in the Lake Eyre Basin: one now extinct (*Genyornis newtoni*) and one extant (emu, *Dromaius novaehollandiae*). These researchers assembled a large dataset of the carbon isotopic composition of eggshells, spanning the last 140 000 years. These isotopic data suggest that both birds consumed a mixture of C₃ (woody plants and herbs) and C₄ (tropical grasses)

plants, although the emu had substantially greater dietary breadth than *Genyornis*. These inferences could be made because the ratio of the rare, heavy stable isotope of carbon ¹³C relative to the abundant, lighter ¹²C (expressed as an index $\delta S_{13}C$) differs between plants with C₃ and C₄ photosynthetic pathways. Most importantly, the data suggest a major switch in emu diet $\delta^{13}C$ away from a C₄ and towards a C₃ dominated diet, coincident with the extinction of *Genyornis* at Lake Eyre about

45–50 ka. Miller *et al.* (2005a) suggest that this dietary shift was due to sustained landscape burning by humans, independent of any climate influence. Indeed, they argue that these data demonstrate that Aboriginal landscape burning triggered ‘ecosystem collapse’ in central Australia, leading to megafaunal extinction, widespread changes in vegetation composition and structure and impacts on regional climate. Johnson *et al.* (1999) and a number of other authors (Magee *et al.* 2004; Miller *et al.* 2005b; Miller *et al.* 2007) suggest that a reduction in vegetation cover across the Australian continent, due to burning by humans, led to a reduction in the feedback of moisture to the atmosphere, and consequent failure of the Australian monsoon to reinvigorate in the Holocene.

However, a recent re-analysis of the data of Miller *et al.* (2005a) by Murphy *et al.* (2011) suggests that gradual climate change, rather than ‘abrupt ecosystem collapse’ as postulated by Miller *et al.* (2005a), was responsible for shift in emu diets. Emu diet $\delta^{13}C$ shows a gradual, steady decrease, suggesting consumption of less C₄ plant (tropical grasses) material between

about 80 ka and 30 ka, thus commencing tens of thousands of years before humans arrived in Australia (45–55 ka; Roberts *et al.* 1990; Turney *et al.* 2001a). Murphy *et al.* (2011) show that emu diet $\delta^{13}C$ closely tracks reconstructed water levels for Lake Eyre, thought to reflect the intensity of the Australian monsoon, over the last 140 000 years (Magee *et al.* 2004). Indeed, the extinction of *Genyornis* and other megafauna about 45–50 ka (Miller *et al.* 1999; Roberts *et al.* 2001), occurred when Lake Eyre was in its most prolonged low level phase since that associated with the Penultimate Glacial Maximum, 140 ka.

Because emus are mixed-feeders, consuming both grasses and woody plants, the ecological significance of carbon isotopic signatures in emu eggshells is ambiguous. The large change in emu diet $\delta^{13}C$ may indicate either a change in the abundance of grasses (C₃ and C₄) relative to woody (primarily C₃) plants, a change in the relative abundance of C₃ and C₄ grasses, or both. In contrast, the carbon isotopic signatures of grazers are less ambiguous, because they solely reflect the dietary abundance of C₃ and C₄ grasses. The Late Pleistocene shift in $\delta^{13}C$ of emu eggshell is also detectable in the teeth of

the grazing marsupial wombats collected at Port Augusta and the Murray–Darling Lakes in southern Australia. Thus the wombat tooth enamel $\delta^{13}C$ data provide strong evidence that, at least at those two locations, the shift in $\delta^{13}C$ in emu eggshell was primarily due to a change in the relative abundance of C₃ and C₄ grasses, not a change in the relative abundance of grasses and woody vegetation. Although the relative abundance of C₃ and C₄ grasses is known to be clearly affected by

climate, particularly summer rainfall activity (Winslow *et al.* 2003; Murphy and Bowman 2007b), there is little reason to suspect that landscape burning by humans would affect the mix of these functional types of grasses.

The research of Murphy *et al.* (2011) highlights the importance of climate, rather than Aboriginal landscape burning in driving ecological changes in the Late Pleistocene. It is well known from the Holocene pollen record that, following the end of the Pleistocene, Aboriginal burning did not stop the climatically driven expansion of rainforest (Bowman 2000). Furthermore, theories about initial impacts of Aboriginal colonisation on fire regimes must also be contextualised with the more reliable ecological and anthropological evidence that Aboriginal fire usage in the historical period was important for the maintenance of habitat and wildlife populations and that some European fire regimes have been destructive of biodiversity.

Ecological impacts of European fire management

A growing body of research supports the view that at the time of European colonisation Aboriginal fire use was skilful and important for maintaining the functioning of ecosystems (Bowman 1998). Further, some research has shown that when this tradition of fire management was disrupted there were often significant ecological effects. For example, across large areas of northern Australia's savannas, the cessation of Aboriginal fire management has resulted in the decline of the cypress pine, *Callitris intratropica*: a fire-sensitive obligate seeder (Bowman and Panton 1993; Figure 2.5). Mature trees have thick bark and can survive mild, but not intense, fires and, if the stems are killed, the plants have no capacity for vegetative recovery. Seedlings cannot survive even the coolest fires. It appears that the prehistoric survival of *Callitris* was a consequence of Aboriginal patch burning aimed at creation of grazing for game (Murphy and Bowman 2007a). A by-product of this burning was the creation of habitat patches that remained unburnt for long enough for recruitment of *Callitris* into the canopy layer.

It seems that the creation of habitat heterogeneity, sometimes called pyrodiversity, by Aboriginal fire management was critical for the survival of a range of plants and animals that are currently undergoing precipitous declines following the widespread breakdown of this practice (Burbidge and McKenzie 1989; Russell-Smith and Bowman 1992; Fordyce *et al.* 1997; Russell-Smith *et al.* 1998; Franklin 1999; Woinarski *et al.* 2001; Russell-Smith *et al.* 2002; Fisher *et al.* 2003; Pardon *et al.* 2003; McKenzie *et al.* 2007; Woinarski *et al.* 2010). For example, the decline of the partridge pigeon, *Geophaps smithii*, has been linked to recent changes to fire regimes (Fraser *et al.* 2003). The partridge pigeon is particularly vulnerable to such changes because, within territories of less than 10 ha, it feeds and nests on the ground in unburnt areas but also feeds in burnt areas. Traditional Aboriginal landscape burning creates a fine-grained mosaic of burnt and unburnt savanna (Figure 2.4).

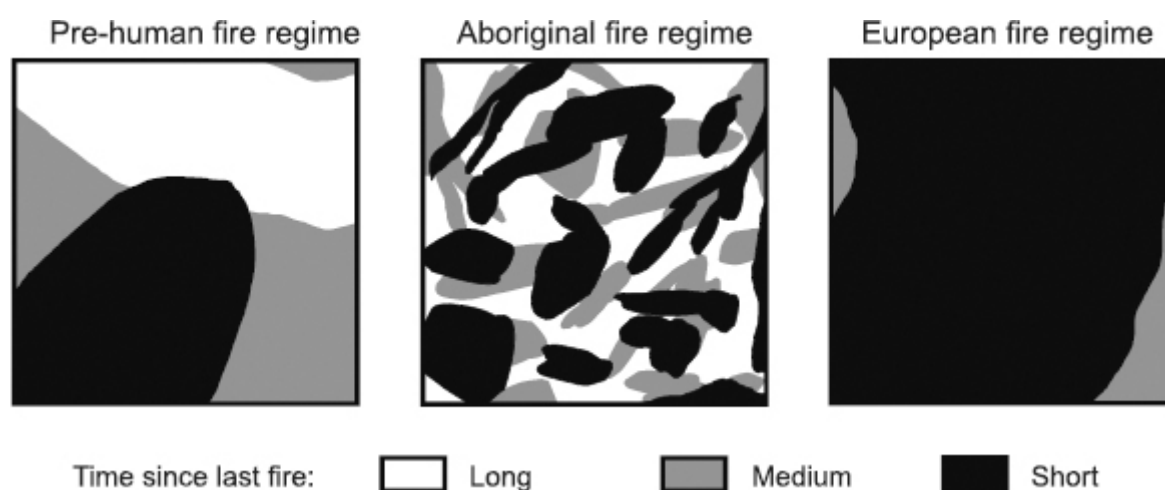


Figure 2.4. Graphical representation of likely changes in the spatial scale and frequency of fires in a hypothetical Australian landscape. (a) In the pre-human period, lightning-started fires would have infrequently burnt large areas, creating a broad-scale habitat mosaic to which various species had become adapted. (b) Aboriginal fire management was characterised by a high frequency of fires that burnt much smaller areas, producing a fine-scale habitat mosaic that supported most of the pre-human wildlife assemblage, with the notable exception of the Pleistocene megafauna. (c) Under European management, fires that had a similar frequency as the earlier Aboriginal period burnt large areas, thereby obliterating the pre-existing habitat mosaic created by Aboriginal fire management. (Source: adapted from Bowman 2003)

It must be acknowledged that understanding the effects of the cessation of Aboriginal landscape burning is confounded by environmental changes, even in uncleared landscapes. This is well illustrated by the effect of changed fire regimes on small patches of monsoon rainforest that occur throughout the tropical savannas (Russell-Smith 1991). Fire is a key factor in restricting monsoon rainforest distribution, given that this vegetation type occurs on fire-protected sites or sites where high growth rates are possible, allowing juvenile trees to reach fire resistant size classes between fires (Bowman 2000). Early reports from the Northern Territory suggested that monsoon rainforests were declining because of frequent severe fires that typify contemporary fire regimes (e.g. Russell-Smith and Bowman 1992; Russell-Smith *et al.* 1993). However, despite an apparently adverse fire regime, historical aerial photography suggests that closed forests within this savanna landscape have expanded substantially over the last 50 years (Bowman *et al.* 2001; Banfai and Bowman 2006; Bowman and Dingle 2006; Brook and Bowman 2006). The cause of the expansion may be higher rainfall and atmospheric CO₂ concentrations (Bowman *et al.* 2010b). The research of Prior *et al.* (2007) may explain the contrasting response of monsoon rainforest and cypress pine, *Callitris intratropica*, populations in northern Australian savannas (Figure 2.5). These authors found that at a site where *Allosyncarpia ternata* dominated rainforests were expanding, the forest structure changed from large old trees to young, regenerating stems, reflecting this species' capacity to resprout from rootstocks. On the other hand, *C. intra-tropica* was declining because the contemporary fire regime was inhibiting recruitment of seedlings and saplings, creating a demographic bottleneck.

Contemporary fire regimes in the monsoon tropics seem to select for flammable grasses, particularly the tall, annual species of *Sarga* (Bowman *et al.* 2007). In parts of the Darwin region, contemporary fire regimes are also changing due to the deliberate introduction of African pasture grasses. Most notably, gamba grass (*Andropogon gayanus*) rapidly invades savanna vegetation, resulting in fuels loads three to four times that observed in non-invaded savannas (Rossiter *et al.* 2003; Setterfield *et al.* 2010). Such fuel loads allow extremely intense savanna fires, resulting in rapid reductions in tree biomass (Ferdinands *et al.* 2006). This has resulted in the development of a grass–fire cycle that presents a significant evolutionary filter for a flora adapted to less intense fires.



Figure 2.5. A stand of the obligate seeding cypress pine, *Callitris intratropica* (Cupressaceae), entirely killed by fire, surrounding vigorously resprouting individuals of the endemic rainforest tree *Allosyncarpia ternata* (Myrtaceae), on the Arnhem Plateau in Kakadu National Park. Although *C. intratropica* is declining in this area, *A. ternata* populations are more resilient, due primarily to their ability to resprout following fire.

Throughout Australia there is mounting concern that the frequency and intensity of wildfires may increase in response to global climate change. Fire regimes are likely to be affected by changes in both fire weather and fuel characteristics. It is clear that the incidence of extreme fire weather is already increasing in southern Australia and this trend is expected to accelerate in coming decades (Lucas *et al.* 2007; Williams *et al.* 2009). The effects of climate change on fuels are less clear. Decreases in water availability, which are predicted across much of southern Australia, may reduce primary productivity and fuel accumulation, although rising atmospheric CO₂ concentration ([CO₂]) is likely to increase them (Nemani *et al.* 2003; Ziska *et al.* 2005; Wang 2007). Further, it is possible that elevated [CO₂] may lower the nitrogen content of foliage, slowing decomposition and resulting in heavier fuel build up (Walker 1991). Hence, there remains considerable uncertainty about how [CO₂] and climate change will affect fuel loads and thus the frequency and intensity of fire. For example, increases in [CO₂] are expected to strongly favour woody plants, especially trees, at the expense of grasses and other herbaceous plants (Bond and Midgley 2000) and is likely to reduce fire frequency and intensity in savannas by favouring greater woody biomass.

Climate change is set to make fire management even more complicated, given that climate change simultaneously changes fire risk, ecosystem function and the habitat template for most organisms, including invasive species. A recent report by Dunlop and Brown (2008) discussing the impact of climate change on nature reserves in Australia succinctly summarises the problem conservation biologists now face. They write:

The question is how should we respond to the changing fire regimes? Efforts to maintain 'historic' fire regimes through hazard reduction burning and vigorous fire suppression may be resource intensive, of limited success, and have a greater impact on biodiversity than natural changes in regimes. It might therefore be more effective to allow change and manage the consequences. The challenge is to find a way to do this while ensuring some suitable habitat is available for sensitive species, and simultaneously managing the threat to urban areas, infrastructure, and public safety.

Summary

Molecular phylogenetic evidence and the sedimentary charcoal record leave no doubt that fire has been an important evolutionary factor in the Australian environment throughout the Cenozoic. There is increasing recognition that fire activity has been linked to climate change and varies among climate zones, thereby creating complex geographic and historical patterns in both vegetation and fire regimes. It is for this reason that tracts of fire-sensitive vegetation, such as rainforest, have been able to persist in refugia in otherwise highly fire-prone landscapes. Aboriginal colonisation in the Late Pleistocene changed fire regimes by introducing a new ignition source, which changed the pattern of burnt and unburnt vegetation patches from the coarse grain under natural ignitions to a much finer grain (Figure 2.4). A controversial theory is that this change in fire regimes contributed to the extinction of a large diversity of large birds, reptiles and marsupials. An alternative theory is that the extinctions caused fire regimes to change. There is much less evidence of plant extinctions at this time, relative to other periods in the fossil record, although shifts in the extent of vegetation types may have occurred in response to Aboriginal colonisation. This interpretation is consistent with observed impacts following the cessation of Aboriginal fire management over the last 200 years. The homogenisation of habitat 'pyrodiversity' has been linked with declines of some birds, small mammals and fire-sensitive plants. However, European colonisation has also altered fire regimes by land clearance, introduction of large herbivores and flammable plants, especially grasses, and fire suppression, thus complicating our understanding of how fire management has influenced fire regimes. Climate change is set to shift fire regimes further still. It is clear that the adaptation of plants to fire regimes occurs over very long time periods (millions of years) yet changes to fire regimes appear to have had far greater impacts on animals than on plants. The evolutionary consequences of the current rapid changes to fire regimes associated with climate change, invasive organisms, habitat fragmentation and native species extinctions remain uncertain, but the available evidence suggests land managers should be preparing for unanticipated and unparalleled changes, perhaps as dramatic as the Late Pleistocene megafaunal extinctions. Effective monitoring of fire regimes is a prerequisite for any prospect of adaptive management.

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