

CHAPTER 9

Fire and biodiversity

David M.J.S Bowman and Brett P. Murphy

In a famous passage in the concluding chapter of *The Origin of Species*, Darwin (1859, 1964) invites the reader to “contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth” and “reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.” Likewise, let us consider a tropical savanna ablaze with hovering raptors catching insects fleeing the fire-front, where flames sweep past tree trunks arising from dry crackling grass. Within weeks the blackened savanna trees are covered in green shoots emerging from thick bark, woody juveniles are resprouting from root stocks, and herbivores are drawn to grass shooting from grow-

ing tips buried beneath the surface soil (Figure 9.1). In this chapter we will show that the very same evolutionary and ecological principles that Darwin espoused in that brilliant passage relate to landscape fire. This is so because fire is enmeshed in the evolution and ecology of terrestrial life, including our own species. This perspective is deeply challenging to the classical view of the “Balance of Nature” that is still held by a broad cross-section of ecologists, naturalists and conservationists, most of who have trained or live in environments where landscape fire is a rare event, and typically catastrophic (Bond and Van Wilgen 1996; Bond and Archibald 2003). Only in the past decade have books been published outlining the general principles of fire ecology (Whelan 1995; Bond and Van Wilgen 1996) and journals established to communicate the latest findings in fire ecology and



Figure 9.1 A eucalypt savanna recovering from a fire that has occurred in the early dry season in Kakadu National Park, northern Australia. Note the flowering *Livistona* palm and the strong resprouting response of juvenile woody plants on the still bare ground surface. Photograph by David Bowman.

wildfire management (see <http://www.fireecology.net> and <http://www.iawfonline.org>).

9.1 What is fire?

At the most basic level fire can be considered a physiochemical process that rapidly releases energy via the oxidation of organic compounds, and can be loosely considered as “anti-photosynthesis”. This physiochemical process is often summarized in a classic “fire triangle” made up of the three key factors to cause combustion: oxygen, fuel and ignitions (Whelan 1995; Pyne 2007). Atmospheric oxygen levels create a “window” that controls fire activity because ignitions are constrained by atmospheric oxygen (Scott and Glasspool 2006). Fire cannot occur when levels fall below 13% of the atmosphere at sea level, and under the current oxygen levels (21%) fire activity is limited by fuel moisture, yet at 35% even moist fuels will burn. Because of substantial fluctuations in atmospheric oxygen, fire risk has changed significantly through geological time. In the Permian Period (between 290 and 250 million years ago) for example, oxygen levels were substantially higher than at present and even moist giant moss (lycophod) forests would have been periodically burnt (Scott and Glasspool 2006). However, fire in the biosphere should not be considered merely a physicochemical process but rather a fundamental biogeochemical process. Fires instantaneously link biomass with the atmosphere by releasing heat, gases (notably water vapor), and the geosphere by releasing nutrients and making soils more erodible and thus changing the nutrient content of streams and rivers (hydrosphere). Fire is therefore quite unlike other natural disturbances, such as floods and cyclones, given the complex web of interactions and numerous short and long-range feedbacks. 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). Such tight coupling between fire and life bedevils simple attribution of cause and effect, and raises fascinating questions about the potential coevolution of fire and life.

9.2 Evolution and fire in geological time

There is evidence from the fossil record that wildfires started to occur soon after vegetation established on the land surface (about 420 million years ago) (Scott and Glasspool 2006). The long history of exposure of terrestrial life to fire leads to the idea that fire is an important evolutionary factor, and more controversially, that fire and life have coevolved (Mutch 1970). While gaining some support from modeling (Bond and Midgley 1995), this is difficult to prove because adaptations to fire cannot be unambiguously identified in the fossil record. For example, in many fire-prone environments, seeds are often contained in woody fruits that only open after a fire event, a feature known as serotiny. However, woody fruits may also be a defense against seed predators such as parrots, and seeds are released once mature, irrespective of fire (Bowman 2000). In most cases it is impossible to know if fossilized woody fruits are truly serotinous, thus woody fruit occurrence is not clear evidence of an adaptation to fire. Much care is required in the attribution of fire adaptations. For example, microevolution can result in switching from possible fire-adaptations, such as the serotinous state. More problematic for understanding the evolution of flammability, Schwillk and Kerr (2002) have proposed a hypothesis they call “genetic niche-hiking” that flammable traits may spread without any “direct fitness benefit of the flammable trait”.

Insights into the evolution of flammability have been gained by tracking the emergence of highly fire-adapted lineages such as *Eucalyptus*. Eucalypts are renowned for their extraordinarily prolific vegetative recovery of burnt trunks via epicormic buds (Figure 9.2). Recently, Burrows (2002) has shown that eucalypt epicormics are anatomically unique. Unlike other plant lineages, which have fully developed dormant buds on the trunks, eucalypts, have strips of “precursor” cells that span the cambium layer that, given the right cues, develop rapidly into epicormic buds. The advantage of this system is that should the trunk be severely burnt the tree retains the capacity to develop epicormic buds from cells protected in the cambium. The molecular phylogeny of



Figure 9.2 Prolific epicormic sprouts on a recently burnt tall eucalypt forest in eastern Tasmania. Photograph by David Bowman.

eucalypts, dated using the fossil record, suggests that this trait existed before the “bloodwood” eucalypt clade split off from other eucalypts some 30 million years ago, given that it occurs in both these lineages. Such an ancient feature to the lineage suggests that eucalypts had developed a vegetative response to landscape fire, which appears to have become more common in the Australian environment associated with a dry climate and nutrient impoverished soils. This interpretation is concordant with the fresh insights about the evolution of the Australian biota derived from numerous molecular phylogenies of quintessentially Australian plants and animals (Bowman and Yeates 2006).

9.3 Pyrogeography

Satellite sensors have revolutionized our understanding of fire activity from landscape to global scales. Global compilations of satellite data have demonstrated the occurrence of landscape fire on every vegetated continent, yet the incidence of fire is not random across the globe (Justice *et al.* 2003). Fire has predictable features regarding how it spreads across landscapes and the frequency and season of occurrence. Such predictability has led to the idea of the “fire regime”.

Key aspects of the fire regime include types of fuels consumed (e.g. grass vs. canopies), spatial pattern (area burnt and shape), and consequences (severity relative to impacts on the vegetation and/or soils) (Gill 1975; Bond and Keeley 2005). For example, savanna fires are often of low intensity and high frequency (often annual), while forest fires are often of low frequency (once every few centuries) and very high intensity. Fire regimes are part of the habitat template that organizes the geographic distribution of biodiversity, and, in turn, species distributions influence the spread of fire. Some authors have even applied “habitat suitability modeling” to predict where fire is most likely to occur at the global to local level.

Fire activity is strongly influenced by climate variability. Fire managers have developed empirical relationships that combine climate data, such as the intensity of antecedent moisture deficit, wind speed, relative humidity, and air temperature, to calculate fire danger (see <http://www.firenorth.org.au>). Mathematical models combining such climate data with fuel loads and topography have been developed to predict how a fire may behave as it spreads across a landscape (Cary *et al.* 2006). The spread of fire is also strongly influenced by vegetation type (Figure 9.3). For example, grassy environments carry fire frequently because of the rapid accumulation of fuel while rainforests burn

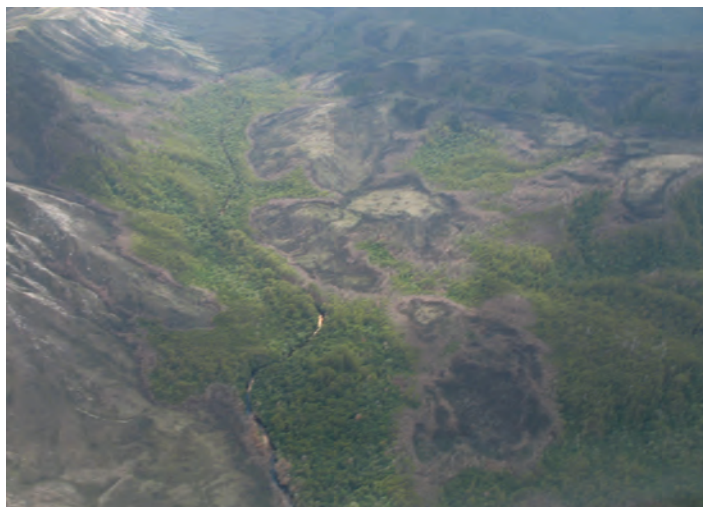


Figure 9.3 Landscape scale patterns of fire spread in southwestern Tasmania. Fire spread is controlled by topography, vegetation, and the meteorological conditions that prevailed at the time of the fire creating strongly non-random patterns of burnt and unburnt areas. Photograph by David Bowman.

infrequently because of microclimates that keep fuels moist under all but drought conditions. Climate cycles such as the El Niño Southern Oscillation (ENSO) also strongly influence fire activity. For example, fire activity typically increases in arid environments after a wet period because of the build-up of fine fuels. Conversely, fire activity increases after a long drought period in moist forests.

The satellite record has been extraordinarily useful in understanding fire activity in highly fire prone environments (see http://www.cfa4wd.org/information/Forest_FDI.htm). Yet the limited time-depth of this record may mask the occurrence of infrequent fire events that occur in long-lived fire-prone vegetation such as the boreal forests of Canada and Siberia. Understanding the “fire regimes” of long-lived forests like those of the boreal zone demands historical reconstruction such as dendrochronology (tree-ring analysis) to determine the timing of “stand replacing fires” which initiate a cohort of regeneration to replace the burnt forest. Statistical analysis of forest stand-age structures can be used to determine the inter-fire intervals (Johnson and Gutsell 1994). Dendrochronology has also been used to date precisely past fire events by identifying injuries to growth rings (fire scars) on the trunks on long-lived trees (Swetnam 1993).

The study by Sibold *et al.* (2006) captures many of the above complexities in understanding fire extent and occurrence. They combined tree ring analyses and geographic information systems (GIS) techniques to identify the influence of vegetation type and structure, elevation and aspect, and regional climate influences on fire activity in the Rocky Mountains National Park, Colorado, USA. Their analysis identified the primary importance of ENSO for fire activity, yet this climatic effect was modulated by landscape setting and vegetation type. Over the 400-year record, fire activity was common in the dry, low elevation slopes that support fire-prone lodgepole pine (*Pinus contorta*) forests but at higher elevation there were large areas of long unburnt mesic spruce-fir (*Picea engelmannii*) forest. On the moist western side of the mountain range were fewer, but larger, fires compared to the drier eastern sides of the mountain range. This example shows that while climate is a driver of fire risk, the linkage between fire, climate and vegetation is complex, frustrating simple attribution of “cause and effect”. Finally, human fire usage has a profound effect on fire activity, disturbing “natural” fire regimes. For example, tropical rainforests are currently being transformed to pasture by burning (see Box 9.1) yet in some environments, like

the forests of the western USA, fire managers have effectively eliminated fire from some fire prone landscapes.

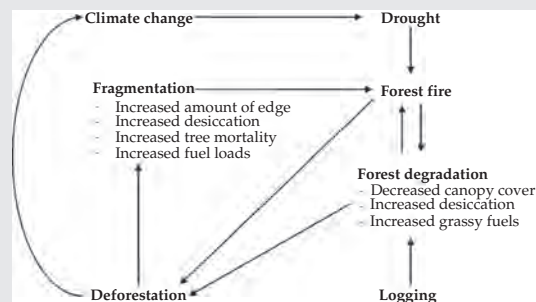
9.4 Vegetation–climate patterns decoupled by fire

A classic view of plant geography is that vegetation and climate are closely coupled. Recently Bond *et al.* (2005) challenged this view by asking

the question of whether the vegetation of the Earth is significantly influenced by landscape fire. The approach they took was via dynamic global vegetation models (DGVMs), which are computer simulations of vegetation based on physiological principles. The effect of landscape fire on global vegetation patterns is implicit in DGVMs because they include “fire modules” that introduce frequent disturbances to modeled vegetation patterns and processes. Such modules are necessary in order to recreate actual

Box 9.1 Fire and the destruction of tropical forests David M. J. S. Bowman and Brett P. Murphy

Each year, extensive areas of tropical forest are unintentionally burnt by anthropogenic fires, and are severely degraded or destroyed as a result (see Chapter 4). Enormous conflagrations can occur in response to drought events associated with ENSO, most notably the Indonesian fires of 1997–1998, which burnt around 8 million hectares of forest (Cochrane 2003). Until recent decades, most tropical forests experienced fires very infrequently, with fire return intervals in the order of centuries, although it is now clear that fire frequency has increased dramatically in the past few decades. Current human land-use activities promote forest fires by fragmenting (see Chapter 5) and degrading forests and providing ignition sources, which would otherwise be rare. These three factors can act synergistically to initiate a series of positive feedbacks that promote the massive tropical forest fires that have become common in recent decades (see Box 9.1 Figure). Forest edges tend to be much more susceptible to fire than forest cores, because they tend to be more desiccated by wind and sun, have higher rates of tree mortality and hence, woody fuel accumulation and grassy fuel loads tend to be higher. The result is that fire frequency tends to increase with proximity to a forest edge, such that highly fragmented forests have high fire frequencies. Forests degraded by selective logging are also at risk of fire due to their reduced canopy cover, which allows the forest to become desiccated and light to penetrate



Box 9.1 Figure The synergistic effects of habitat fragmentation and degradation on the occurrence of tropical forest fires. Adapted from Cochrane (2003).

and encourage grass growth. The waste biomass from logging operations can also dramatically elevate fuel loads. Similarly, forests degraded by an initial fire tend to be more susceptible to repeat fires, further enhancing the feedback loop.

The negative impacts of frequent, intense fires on tropical forest biodiversity are likely to be enormous, given the existing threats posed by the direct effects of deforestation (Chapter 4) and overharvesting (Chapter 6). Intense fires easily kill a large proportion of tropical forest tree species, and repeated fires can be especially detrimental to species regenerating vegetatively or from seed. Generally, repeated fires lead to a loss of primary forest tree species, with these replaced by an impoverished set of pioneer species (Barlow and Peres 2008). The effects of fire on forest animals are less well

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Box 9.1 (Continued)

understood, although studies following the 1997–1998 Indonesian fires suggest severe impacts on many groups, especially those reliant on fruit-trees and arthropod communities in leaf litter (Kinnaird and O'Brien 1998). On Borneo, endangered orangutan (*Pongo pygmaeus*) populations suffered declines of around 33% following the 1997–1998 fires (Rijksen and Meijaard 1999).

In many tropical regions, climate change is expected to exacerbate forest fires. There is evidence that extreme weather events, such as the ENSO droughts that triggered the 1997–1998 Indonesian fires, and tropical storms, may become more frequent (Timmermann *et al.* 1999; Mann and Emanuel 2006). Additionally, we can expect strong positive feedbacks between forest fire occurrence and climate change, because tropical forest fires result in enormous additions of greenhouse gases to the atmosphere, leading to even more rapid climate change. For example, the 1997–1998 Indonesian fires released 0.8–2.6 Gt of carbon to the atmosphere, equivalent to 13–40% of global emissions due to burning fossil fuels, making a large contribution to the largest recorded annual increase in atmospheric CO₂ concentration (Page *et al.* 2002).

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vegetation patterns. Bond *et al.* (2005) found that a world without fire had very different vegetation zones compared with the actual vegetation geography. For example, when fire was “switched off”, dense (>80%) tree cover increased from 27% to 56% of the vegetated Earth surface and more than half (52%) of the current global distribution of tropical savannas were transformed to angiosperm-dominated forests. The core message of this analysis is that fire causes the “decoupling” of vegetation patterns from climate.

Arguably the most well known decoupling of vegetation and climate concerns the geographic distribution of forest and savanna. Savannas are among the most fire-prone biomes on Earth, and are characterized by varying mixtures of both tree and grass biomass. The question of how both trees

and grasses can coexist in the long-term has long puzzled savanna ecologists. Conventional ecological theory of plant succession suggests that highly productive savannas are unstable and should gradually progress toward closed canopy forest. While it seems that in less productive savannas, such as in low rainfall areas, tree biomass is indeed constrained by the limitation of resources, such as water, recent research suggests that in more productive savannas, recurrent disturbance plays an important role in maintaining a tree–grass balance (Sankaran *et al.* 2005). Given the high flammability of savannas, it seems that disturbance due to fire is of particular importance.

The most widely accepted explanation of how frequent fires limit tree biomass in savannas assumes that a “tree demographic-bottleneck”

occurs. It is accepted that fire frequency controls the recruitment of savanna trees, particularly the growth of saplings into the tree layer. Unlike mature trees, saplings are too short in stature to avoid fire-damage and unlike juveniles, if they are damaged they cannot rapidly return to their previous size from root stocks (Hoffman and Solbrig 2003). Thus saplings must have the ability to tolerate recurrent disturbance until they have sufficient reserves to escape through a disturbance-free “recruitment window” into the canopy layer where they suffer less fire damage. Recurrent disturbance by fire can stop savanna tree populations from attaining maximal tree biomass by creating bottlenecks in the transition of the relatively fire-sensitive sapling stage to the fire tolerant tree stage (Sankaran *et al.* 2004). In the extreme case, a sufficient frequency of burning can result in the loss of all trees and the complete dominance of grass. Conversely, fire protection can ultimately result in the recruitment of sufficient saplings to result in a closed canopy forest.

Large herbivores may also interact with fire activity because high levels of grazing typically reduce fire frequency, and this can enable woody

plants to escape the “fire trap”, and increase in dominance (Sankaran *et al.* 2004; Werner 2005). For example, extensive woody plant encroachment has occurred in mesic grassland and savanna in Queensland, Australia, and has been attributed to cattle grazing and changed fire regimes (Crowley and Garnett 1998). This trend can be reversed by reduced herbivory coupled with sustained burning—a methodology used by pastoralists to eliminate so called “woody weeds” from overgrazed savannas. Bond and Archibald (2003) suggest that in southern African savannas there is a complex interplay between fire frequency and herbivory. Heavily grazed savannas support short grass “lawns”, dominated by species in the sub-family Chloridoideae, which do not burn. These lawns support a diversity of large grazers including white rhino (*Ceratotherium simum*), wildebeest (*Connochaetes* spp.), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*), and zebra (*Equus* spp.) (Figure 9.4). Under less intense grazing, these lawns can switch to supporting bunch grass, in the sub-family Andropogoneae, which support a less diverse mammal assemblage adapted to grazing tall grasses, such as African buffalo (*Syncerus caffer*).



Figure 9.4 Zebra and wildebeest grazing on a ‘lawn’ in a humid savanna in Hluhluwe-Umfolozi Park, South Africa. Bond and Archibald (2003) suggest that intense grazing by African mammals may render savannas less flammable by creating mosaics of lawns that increase the diversity of the large mammal assemblage. Large frequent fires are thought to switch the savannas to more flammable, tall grasses with a lower diversity of large mammals. Photograph by David Bowman. See similar Figure 4.6.

The high biomass of the bunch grasslands render these systems highly flammable. Bond and Archibald (2003) propose a model where frequent large fires can result in a loss of lawns from a landscape with corresponding declines in mammal diversity. The mechanism for this is that resprouting by grasses following fire causes a lowering in overall grazing pressure across the landscape. Fully understanding the drivers of the expansion of woody vegetation into rangelands, including the role of fire and herbivory, remains a major ecological challenge (see <http://ag.arizona.edu/research/archer/research/biblio1.html>).

How savanna vegetation evolved is unclear. Some authors suggest that falling atmospheric carbon dioxide (CO₂) concentrations may have stimulated the development of grasses that now dominate tropical savannas (Bond *et al.* 2003). Tropical savanna grasses have the C₄ photosynthetic pathway that is highly productive in hot, wet climates, and under low CO₂ concentrations these grasses have a physiological advantage over woody vegetation that has the C₃ photosynthetic pathway. The production of large quantities of fine and well-aerated fuels may have greatly increased the frequency of landscape fire disadvantaging woody plants and promoting further grassland expansion. The development of monsoon climates might have also been as important a driver as low atmospheric concentrations of CO₂ (Keeley and Rundel 2003). The monsoon climate is particularly fire-prone because of the characteristic alternation of wet and dry seasons. The wet season allows rapid accumulation of grass fuels, while the dry season allows these fuels to dry out and become highly flammable. Furthermore, the dry season tends to be concluded by intense convective storm activity that produces high densities of lightning strikes (Bowman 2005).

9.5 Humans and their use of fire

Our ancestors evolved in tropical savannas and this probably contributed to our own species' mastery of fire. Indeed, humans can be truly described as a fire keystone species given our dependence on fire; there is no known culture that does not rou-

tinely use fire. For example, the Tasmanian Aborigines always carried fire with them, as it was an indispensable tool to survive the cold wet environment (Bowman 1998). The expansion of humans throughout the world must have significantly changed the pattern of landscape burning by either intentionally setting fire to forests to clear them or accidentally starting fires. How prehistoric human fire usage changed landscape fire activity and ecosystem processes remains controversial and this issue has become entangled in a larger debate about the relative importance of humans vs. climate change in driving the late Pleistocene megafaunal extinctions (Barnosky *et al.* 2004; Burney and Flannery 2005). Central to this debate is the Aboriginal colonization of Australia that occurred some 40 000 years ago. Some researchers believe that human colonization caused such substantial changes to fire regimes and vegetation distribution patterns that the marsupial megafauna were driven to extinction. This idea has recently been supported by the analysis of stable carbon isotopes ($\delta^{13}\text{C}$) in fossil eggshells of emus and the extinct giant flightless bird *Genyornis newtoni* in the Lake Eyre Basin of central Australia. Miller *et al.* (2005a) interpreted these results as indicating that sustained Aboriginal landscape burning during colonization in the late Pleistocene caused the transformation of the central Australian landscape from a drought-adapted mosaic of trees, shrubs, and nutritious grasslands to the modern fire-adapted desert scrub. Further, climate modeling suggests that the switch from high to low leaf-area-index vegetation may explain the weak penetration of the Australian summer monsoon in the present, relative to previous periods with similar climates (known as "interglacials") (Miller *et al.* 2005b).

Yet despite the above evidence for catastrophic impacts following human colonization of Australia, it is widely accepted that at the time of European colonization Aboriginal fire management was skilful and maintained stable vegetation patterns (Bowman 1998). For example, recent studies in the savannas of Arnhem Land, northern Australia, show that areas under Aboriginal fire management are burnt in patches to increase kangaroo densities (Figure 9.5; Murphy and Bowman

2007). Further, there is evidence that the cessation of Aboriginal fire management in the savannas has resulted in an increase in flammable grass biomass and associated high levels of fire activity consistent with a “grass–fire cycle” (see Box 9.2). It is unrealistic to assume that there should only be one uniform ecological impact from indigenous fire usage. Clearly working out how indigenous people have influenced landscapes

demands numerous studies, in order to detect local-scale effects and understand the underlying “logic” of their landscape burning practices (e.g. Murphy and Bowman 2007). Also of prime importance is study of the consequences of prehistoric human colonization of islands such as New Zealand. In this case, there is clear evidence of dramatic loss of forest cover and replacement with grasslands (McGlone 2001).

Box 9.2 The grass–fire cycle

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D’Antonio and Vitousek (1992) described a feedback between fire and invasive grasses that has the capacity to radically transform woodland ecosystems, a process they described as the “grass–fire cycle”. The cycle begins with invasive grasses establishing in native vegetation, increasing the abundance of quick-drying and well-aerated fine fuels that promote frequent, intense fires. While the invasive grasses recover rapidly from these fires via regeneration from underground buds or seeds, woody plants tend to decrease in abundance. In turn, this increases the abundance of the invasive grasses, further increasing fire frequency and intensity. The loss of woody biomass can also result in drier microclimates, further adding momentum to the grass–fire cycle. Eventually the grass–fire cycle can convert a diverse habitat with many different species to grassland dominated by a few exotics.

The consequences of a grass–fire cycle for ecosystem function can be enormous. The increase in fire frequency and intensity can result in massive losses of carbon, both directly, via combustion of live and dead biomass, and indirectly, via the death of woody plants and their subsequent decomposition or combustion. For example, invasion of cheatgrass (*Bromus tectorum*) in the Great Basin of the United States and the establishment of a grass–fire cycle has led to a loss of 8 Mt of carbon to the atmosphere and is likely to result in a further 50 Mt loss in coming decades (Bradley *et al.* 2006). During fires, nitrogen is also volatilized and lost in smoke,

while other nutrients, such as phosphorus, are made more chemically mobile and thus susceptible to leaching. Thus, nutrient cycles are disrupted, with a consequent decline in overall stored nutrients for plants. This change can further reinforce the grass–fire cycle because the fire-loving grasses thrive on the temporary increase in the availability of nutrients.

An example of an emerging grass–fire cycle is provided by the tropical savannas of northern Australia, where a number of African grasses continue to be deliberately spread as improved pasture for cattle. Most notably, gamba grass (*Andropogon gayanus*) rapidly invades savanna vegetation, resulting in fuel loads more than four times that observed in non-invaded savannas (Rossiter *et al.* 2003). Such fuel loads allow extremely intense savanna fires, resulting in rapid reductions in tree biomass (see Box 9.2 Figure). The conversion of a savanna woodland, with a diverse assemblage of native grasses, to a grassland monoculture is likely to have enormous impacts on savanna biodiversity as gamba grass becomes established over large tracts of northern Australia. Despite the widely acknowledged threat posed by gamba grass, it is still actively planted as a pasture species in many areas. Preventing further spread of gamba grass must be a management priority, given that, once established, reversing a grass fire–cycle is extraordinarily difficult. This is because woody juveniles have little chance of reaching maturity given the high frequency of intense fires and intense competition from grasses.

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Box 9.2 (Continued)



Box 9.2 Figure An example of a grass-fire cycle becoming established in northern Australian savannas. African gamba grass is highly invasive and promotes enormously elevated fuel loads and high intensity fires, resulting in a rapid decline in woody species. Photograph by Samantha Setterfield.

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Agricultural expansion is often enabled by using fire as a tool to clear forests, a pattern that has occurred since the rise of civilization. Currently, this process is occurring most in the tropics. The fire-driven destruction of forests has been studied in close detail in the Amazon Basin, and is char-

acterized by an ensemble of positive feedbacks greatly increasing the risk of fires above the extremely low background rate (Cochrane *et al.* 1999; Cochrane 2003; see Box 9.1). Recurrent burning can therefore trigger a landscape-level transformation of tropical rainforests into flammable



Figure 9.5 Traditional land management using fire is still practiced by indigenous people in many parts of northern and central Australia. Recent work in Arnhem Land suggests that skilful fire management results in a fine-scale mosaic of burnt patches of varying age, which is thought to be critically important for maintaining populations of many small mammals and granivorous birds. Photograph by Brett Murphy.

scrub and savanna, exacerbated by the establishment of a “grass–fire cycle” (see Box 9.2).

9.6 Fire and the maintenance of biodiversity

9.6.1 Fire-reliant and fire-sensitive species

Many species in fire-prone landscapes are not only fire tolerant, but depend on fire to complete their life-cycles and to retain a competitive edge in their environment. Such species typically benefit from the conditions that prevail following a fire, such as increased resource availability associated with the destruction of both living and dead biomass, nutrient-rich ash, and high

light conditions (see Box 9.3). For example, fire is critically important for the regeneration of many plant species of the fire-prone heath communities typical of the world’s Mediterranean climates (e.g. South African fynbos, southwestern Australian kwongan, Californian chaparral). Many species in these communities have deeply dormant seeds that only germinate following fire, when normally limited resources, such as light and nutrients, are abundant. Many hard-seeded heath species, especially *Acacia* species and other legumes, are stimulated to germinate by heat, while many others are stimulated by chemicals in smoke (Bell *et al.* 1993; Brown 1993). Other species in these communities typically only flower following a fire (e.g. Denham and Whelan 2000).

Box 9.3 Australia’s giant fireweeds David M.J.S Bowman and Brett P. Murphy

Australian botanists have been remarkably unsuccessful in reaching agreement as to what constitutes an Australian rainforest (Bowman 2000). The root of this definitional problem lies with the refusal to use the term “rainforest” in the literal sense, which would involve including the tall eucalypt forests that occur in Australia’s high rainfall zones (see Box 9.3 Figure). This is despite the fact that the originator of the term, German botanist Schimper, explicitly included eucalypts in his conception of rainforest. The reason why eucalypt forests are excluded from the term “rainforest” by Australians is that these forests require fire disturbance to regenerate, in contrast to true rainforests that are comparatively fire-sensitive. Typically, infrequent very intense fires kill all individual eucalypts, allowing prolific regeneration from seed to occur, facilitated by the removal of the canopy and creation of a nutrient-rich bed of ash. Without fire, regeneration from seed does not occur, resulting in very even-aged stands of mature eucalypts.

The gigantic (50–90 m tall) karri (*Eucalyptus diversicolor*) forests of southwestern Australia underscore the complexity of the term

“rainforest” in Australia. These forests grow in a relatively high rainfall environment (>1100 mm per annum) with a limited summer drought of less than three months duration. Elsewhere in Australia, such a climate would support rainforest if protected from fire. However, in southwestern Australia there are no continuously regenerating and fire intolerant rainforest species to compete with karri, although geological and biogeographic evidence point to the existence of rainforest in the distant past. The cause of this disappearance appears to be Tertiary aridification and the accompanying increased occurrence of landscape fire. For example, a pollen core from 200 km north of Perth shows that by 2.5 million years ago the modern character of the vegetation, including charcoal evidence of recurrent landscape fires, had established in this region, although some rainforest pollen (such as *Nothofagus* and *Phyllocladus*) indicates that rainforest pockets persisted in the landscape at this time (Dodson and Ramrath 2001).

continues

Box 9.3 (Continued)

The gigantic size of karri and a regeneration strategy dependent upon fire disturbance, including mass shedding of tiny seeds with



Box 9.3 Figure Giant *Eucalyptus regnans* tree in southern Tasmania. The life-cycle of these trees depends upon infrequent fire to enable seedling establishment. Without fire a dense temperate *Nothofagus* rainforest develops because of the higher tolerance of rainforest seedlings to low light conditions. Photograph by David Bowman.

limited reserves onto ashbeds, suggests convergent evolution with other, distantly related, eucalypts such as mountain ash (*E. regnans*) in southeastern Australian and *E. grandis* in northeastern and eastern Australia. Such convergence suggests that all have been exposed to similar natural selection pressures and have evolved to compete with rainforest species by using fire as an agent of inter-specific competition (e.g. Bond and Midgley 1995). The extraordinary diversity of the genus *Eucalyptus* and convergent evolution of traits such as gigantism in different lineages in this clade, and similar patterns of diversification in numerous other taxonomic groups, leads to the inescapable conclusion that fire had been an integral part of the Australian environment for millions of years before human colonization. Aborigines, therefore, learnt to live with an inherently flammable environment.

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Even within fire-prone landscapes, there may be species and indeed whole communities that are fire-sensitive. Typically these occur in parts of the landscape where fire frequency or severity is low, possibly due to topographic protection. For example, when fire sensitive rainforest communities occur within a flammable matrix of grassland and savanna, as throughout much of the tropics, they are often associated with rocky gorges, incised gullies (often called “gallery for-

ests”), and slopes on the lee-side of “fire-bearing” winds (Bowman 2000). Several factors lead to this association: fires burn more intensely up hill, especially if driven by wind; rocks tend to limit the amount of grassy fuel that can accumulate; deep gorges are more humid, reducing the flammability of fuels; and high soil moisture may lead to higher growth rates of the canopy trees, increasing their chances of reaching maturity, or a fire-resistant size, between fires.

Somewhat counter-intuitively, many fire-sensitive species in fire-prone landscapes are favored by moderate frequencies of low intensity fires, especially if they are patchy. Such fires greatly reduce fuel loads and thus the likelihood of large, intense fires. In addition, because low intensity fires are typically more patchy than high intensity fires, they tend to leave populations of fire-sensitive species undamaged providing a seed source for regeneration. Such an example is provided by the decline of the fire-sensitive endemic Tasmanian conifer King Billy pine (*Athrotaxis selaginoides*) following the cessation of Aboriginal landscape burning (Brown 1988; http://www.anbg.gov.au/fire_ecology/fire-and-biodiversity.html). The relatively high frequency of low-intensity fires under the Aboriginal regime appears to have limited the occurrence of spatially extensive, high intensity fires. Under the European regime, no deliberate burning took place, so that when wildfires inevitably occurred, often started by lightning, they were large, intense, and rapidly destroyed vast tracts of King Billy pine. Over the last century, about 30% of the total coverage of King Billy pine has been lost.

A similar situation has resulted in the decline of the cypress pine (*Callitris intratropica*) in northern Australian savannas (Bowman and Panton 1993). Cypress pine is a fire-sensitive conifer found across much of tropical Australia. Mature trees have thick bark and can survive mild but not intense fires, and if stems are killed it has very limited vegetative recovery. Seedlings cannot survive even the coolest fires. Thus, it is aptly described as an “obligate seeder”. Populations of cypress pine can survive mild fires occurring every 2–8 years, but not frequent or more intense fires because of the delay in seedlings reaching maturity and the cumulative damage of fires to adults. Cessation of Aboriginal land management has led to a decline of cypress pine in much of its former range, and it currently persists only in rain-forest margins and savanna micro-sites such as in rocky crevasses or among boulders or drainage lines that protect seedlings from fire (Figure 9.6). Fire sensitive species such as King Billy pine and cypress pine are powerful bio-indicators of altered fire regimes because changes in their distribution,



Figure 9.6 Recently killed individuals of cypress pine (*Callitris intratropica*), a conifer that is an obligate seeder. Changes in fire regime following the breakdown of traditional Aboriginal fire management have seen a population crash of this species throughout its range in northern Australia. Photograph by David Bowman.

density, and stand structure signal departure from historical fire regimes.

9.6.2 Fire and habitat complexity

A complex fire regime can create habitat complexity for wildlife by establishing mosaics of different patch size of regenerating vegetation following fires. Such habitat complexity provides a diversity of microclimates, resources, and shelter from predators. It is widely believed that the catastrophic decline of mammal species in central Australia, where clearing of native vegetation for agriculture has not occurred, is a direct consequence of the homogenization of fine-scale habitat mosaics created by Aboriginal landscape burning. This interpretation has been supported by analysis of “fire scars” from historical aerial photography and satellite imagery. For example, Burrows and Christensen (1991) compared fire scars present in Australia’s Western Desert in 1953, when traditional Aboriginal people still occupied the region, with those present in 1986, when the area had become depopulated of its

original inhabitants. In 1953, the study area contained 372 fire scars with a mean area of 34 ha, while in 1986, the same area contained a single fire scar, covering an area of 32 000 ha. Clearly, the present regime of large, intense and infrequent fires associated with lightning strikes has obliterated the fine-grained mosaic of burnt patches of varying ages that Aboriginal people had once maintained (Burrows *et al.* 2006). The cessation of Aboriginal landscape burning in central Australia has been linked to the range contraction of some mammals such as the rufous hare-wallaby (*Lagorchestes hirsutus*) (Lundie-jenkins 1993). Recent research in northern Australia's tropical savannas, where small mammals and granivorous birds are in decline, also points to the importance of unfavorable fire regimes that followed European colonization (Woinarski *et al.* 2001). A prime example is the decline of the partridge pigeon (*Geophaps smithii*). This bird is particularly vulnerable to changes in fire regime because it feeds and nests on the ground and has territories of less than 10 ha. Their preferred habitat is a fine-grained mosaic of burnt and unburnt savanna, where it feeds on seeds on burnt ground but nests and roosts in unburnt areas (Fraser *et al.* 2003). Aboriginal landscape burning has been shown to produce such a fine-grained mosaic (Bowman *et al.* 2004).

9.6.3 Managing fire regimes for biodiversity

The contrasting requirements of different species and communities within fire-prone landscapes highlights the difficulties faced by those managing fire regimes for biodiversity conservation. How does one manage for fire-reliant and fire-sensitive species at the same time? Lessons can clearly be learnt from traditional hunter-gatherer societies that extensively used, and in some cases still use, fire as a land management tool. While it is unlikely that the enormous complexity of traditional fire use can ever be fully encapsulated in fire regimes imposed by conservation managers, it is clear that spatial and temporal complexity of the regime must be maximized to ensure the maximum benefits to biodiversity. Clearly, in the case of fire regimes designed for biodiversity conser-

vation, one size can't fit all. The quest for sustainable fire regimes demands trialing approaches and monitoring outcomes while balancing biodiversity outcomes against other priorities such as protection of life and property. This quest for continuous improvement in land management has been formalized in a process known as "adaptive management". This iterative process is most applicable when faced with high levels of uncertainty, and involves continually monitoring and evaluating the outcomes of management actions, and modifying subsequent actions accordingly.

9.7 Climate change and fire regimes

There is mounting concern that the frequency and intensity of wildfires may increase in response to global climate change (see Chapter 8), due to the greater incidence of extreme fire weather. While the effect is likely to vary substantially on a global scale, regions that are likely to experience substantial increases in temperature and reductions in rainfall are also likely to experience more extreme fire weather. Indeed, such a trend is already apparent in southeastern Australia (Lucas *et al.* 2007) and the western United States (Westerling *et al.* 2006).

In addition to the effects of climate change, an increase in atmospheric CO₂ concentration is likely to affect the abundance and composition of fuel loads, and hence the frequency and intensity of fires. Elevated CO₂ concentration is likely to increase plant productivity, especially that of species utilizing the C3 photosynthetic pathway (mainly woody plants and temperate grasses), such that there have been suggestions that fuel production will increase in the future (Ziska *et al.* 2005). Further, elevated CO₂ concentration may lower the nitrogen content of foliage, slowing decomposition and resulting in heavier fuel build up (Walker 1991). However, to state that an increase in CO₂ concentration will increase fuel loads, and hence fire frequency and intensity, is likely to be a gross over-generalization; the effects of elevated CO₂ are in fact likely to vary substantially between biomes. For example, in tropical savannas, it is likely that increases in CO₂

concentration will strongly favor woody plants, especially trees, at the expense of grasses and other herbaceous plants (Bond and Midgley 2000). A shift from highly flammable grassy fuels to fuels based on woody plants is likely to reduce fire frequency and intensity in savannas. Indeed, Bond and Archibald (2003) have argued that managers should consider increasing fire frequencies to counteract the increase in growth rates of savanna trees that would result in higher tree densities due to a weakening of the "tree demographic bottle-neck". In contrast, in more arid biomes where fire occurrence is strongly limited by antecedent rainfall (Allan and Southgate 2002), an increase in productivity is indeed likely to increase the frequency with which fires can occur with a corresponding decrease in woody cover.

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 summarizes 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."

Again this demands an adaptive management approach, the key ingredients of which include: (i) clear stated objectives; (ii) comprehensive fire mapping programs to track fire activity across the landscape; (iii) monitoring the population of biodiversity indicator species and/or condition and

extent of habitats; and (iv) rigorous evaluation of the costs and benefits of management interventions.

An important concept is "thresholds of potential concern" which predefines acceptable changes in the landscape in response to different fire regimes (Bond and Archibald 2003). Bradstock and Kenny (2003) provided an example of this approach for assessing the effect of inter-fire interval on species diverse sclerophyll vegetation in the Sydney region of southeastern Australia. This vegetation supports a suite of species that are obligate seeders whose survival is held in a delicate balance by fire-frequency. Fire intervals that are shorter than the time required for maturation of plant species result in local extinction because of the absence of seeds while longer fire intervals also ultimately result in regeneration failure because adults die and seed-banks become exhausted. Bradstock and Kenny (2003) found that to sustain the biodiversity of sclerophyll vegetation, fire intervals between 7 and 30 years are required. Monitoring is required to ensure that the majority of the landscape does not move outside these "thresholds of potential concern".

Fire management is set to remain a thorny issue for conservation biologists given the need to devise fire regimes to achieve multiple outcomes that on the one hand protect life and property and on the other maintain biodiversity and ecosystem services. The accelerating pace of global environmental change, of which climate change is but one component, makes the quest for sustainable fire management both more critical and more complex. The current quest for ecologically sustainable fire management can draw inspiration from indigenous societies that learnt to coexist with fire to create ecologically sustainable and biodiverse landscapes (also see Box 1.1). Modern solutions will undoubtedly be science based and use space-age technologies such as satellites, global positioning systems, computer models and the web.

Summary

- The Earth has a long history of landscape fire given: (i) the evolution of terrestrial carbon based vegetation; (ii) levels of atmospheric oxygen that are sufficient to

support the combustion of both living and dead organic material; and (iii) abundant and widespread ignitions from lightning, volcanoes and humans.

- There is a clear geographic pattern of fire activity across the planet reflecting the combined effects of climate, vegetation type and human activities. Most fire activity is concentrated in the tropical savanna biome.

- Fire activity shows distinct spatial and temporal patterns that collectively can be grouped into “fire regimes”. Species show preferences for different fire regimes and an abrupt switch in fire regime can have a deleterious effect on species and in extreme situations, entire ecosystems. A classic example of this is the establishment of invasive grasses, which dramatically increase fire frequency and intensity with a cascade of negative ecological consequences.

- Climate change presents a new level of complexity for fire management and biodiversity conservation because of abrupt changes in fire risk due to climate change and simultaneous stress on species. Further, elevated atmospheric CO₂ concentration may result in changes in growth and fuel production due to changes in growth patterns, water use efficiency and allocation of nutrients.

- Numerous research challenges remain in understanding the ecology and evolution of fire including: (i) whether flammability changes in response to natural selection; (ii) how life-history traits of both plants and animals are shaped by fire regimes; and (iii) how to manage landscape fire in order to conserve biodiversity.

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Relevant websites

- Online journal of the Association for Fire Ecology: <http://www.fireecology.net>.
- International Journal of Wildland Fire, journal of the International Association of Wildland Fire: <http://www.iawfonline.org>.
- North Australian Fire Information: <http://www.fire-north.org.au>.
- Forest Fire Danger Meter: http://www.cfa4wd.org/information/Forest_FDI.htm.
- Proliferation of woody plants in grasslands and savannas – a bibliography: <http://ag.arizona.edu/research/archer/research/biblio1.html>.
- How fires affect biodiversity: http://www.anbg.gov.au/fire_ecology/fire-and-biodiversity.html.
- Kavli Institute of Theoretical Physics Miniconference: Pyrogeography and Climate Change (May 27–30, 2008): http://online.itp.ucsb.edu/online/pyrogeo_c08.

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