

# Fires, Ecological Effects of<sup>☆</sup>

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## Glossary

**Fire ecology** The interactions between fire and the abiotic and biotic components of an ecosystem.

**Fire regime** The expression of multiple fire events within a spatial and temporal domain; the type of fire, mean and variance in fire frequency, intensity, severity, season, and areal extent of a burn in an ecosystem.

**Fire-stimulated recruitment** Seedling recruitment in the first one or two growing seasons after a burn.

**General circulation model (GCM)** Computer models developed to simulate global climate and widely used for global climate change predictions.

**Prescribed burning** Fires intentionally lit for management purposes.

**Serotiny** Seeds stored on the plant with dispersal triggered by fire.

**Wildfires** Uncontrolled wildland fires.

## Fire in Earth History

Fire is an enormously influential disturbance over large areas of land in the modern world. Vegetation burns because the Earth's atmosphere contains sufficient oxygen (>15%) to support combustion (Pyne, 2001). Oxygen started to accumulate in the atmosphere about 2 billion years ago and, since the appearance of plants in the Devonian (~400 million years ago) to provide fuel, there is an almost continuous record of fossil charcoal over the past 350 million years indicating that the atmosphere supported combustion for most of terrestrial plant evolution (Scott, 2000). Oxygen levels reached maxima in the Upper Carboniferous, about 300 million years ago (Ma), when abundant fossil charcoal indicates frequent fires. Fires were also common during the Cretaceous (135–165 Ma) when flowering plants (angiosperms) first began to spread. Fossil flowers, with fine structure beautifully preserved as charcoal, are common and widespread in Cretaceous deposits (Nixon and Crepet, 1993). At these and other times, frequent fires may have played a significant part in the ecology and evolution of paleo-ecosystems (Bowman *et al.*, 2009).

Broadleaved forest, analogous to present-day tropical and temperate forests, first became globally widespread in the Eocene (55–35 Ma) a warm wet period. Fossil evidence for fire is rare during this time but dated molecular phylogenies indicate that fires were continuing to burn in Eocene landscapes (Scott, 2000). Grasslands are the most flammable vegetation that has existed in earth history. Tropical (C4) grasslands and savannas are the most extensive flammable biomes today occupying one-fifth of the world's land surface. Though C4 grasses are ancient (30 Ma BP), the savanna biome first began to spread from the late Miocene (8 Ma). Charcoal from marine sediments increased dramatically during the past 10 Ma as fire-promoting ecosystems, including savannas, began to spread (Bowman *et al.*, 2009).

Hominids have used lightning-ignited fire for perhaps as long as 1–1.5 My but first began to ignite their own fires from 200 to 400 ka BP (Pyne, 2001). Fire was used for many reasons, such as clearing vegetation to facilitate transportation; promoting growth of edible plants in hunter-gatherer communities; and attracting animals to hunting grounds (Vale, 2002; Fig. 1). Fire was (and is) a tool used by farmers to clear new lands and to prepare sites for swidden-type farming. However, the historical impacts of human use of fire on the environment are greatly dependent on geographic area. Increases in charcoal in south-east Asia (50 ka) and Australia (60–45 ka) are coincident with the arrival of fire-using modern humans, however, charcoal records from Europe reveal that climate change, rather than changes in human use of fire, best correlates with fire activity from 70 to 10 ka (Daniau *et al.*, 2010). Charcoal records from around the world for the past two millennia indicate little impact of humans on biomass burning until as late as the mid 1700s with an abrupt decline in burning after 1870 (Marlon *et al.*, 2008). Thus, the area burnt by vegetation fires may be at its lowest level for the past few millennia.

## World Biomes and Fire Incidence

Satellite imagery is beginning to reveal the vast global extent of fires. Between 1997 and 2008, the average global burnt area was 3.7 million km<sup>2</sup> or 2.8% of the total unglaciated land area (Giglio *et al.*, 2010). Nearly one-third of the land surface experienced

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**Fig. 1** A Charles M. Russell painting of Native Americans lighting fires on the Great Plains of North America.

fire activity between 2001 and 2006. Africa accounts for about 70% of annual burnt area with the remaining 30% primarily in Australia, followed by South America and Central Asia. Fires are rare only at the extremes of the climatic continuum. The most humid tropical and temperate forests and the driest deserts have the smallest proportion of burnt area annually (Cochrane and Ryan, 2009). However, between these two extremes, fire has influenced the extent and composition of a great diversity of ecosystems, including tropical grasslands and savannas, temperate grasslands and steppe, boreal forests, dry conifer forests, temperate woodlands, Mediterranean-type shrublands, heathlands, and eucalypt woodlands (Scott *et al.*, 2014). Forests with mast-flowering bamboo understories are also prone to burning after the bamboos flower and die, creating massive fuel loads. Humans have changed landscape patterns of burning. Even humid tropical forests are being burned as a result of logging and deforestation fires. All these biomes experience fires of widely differing frequency and severity which help shape ecosystem structure and function.

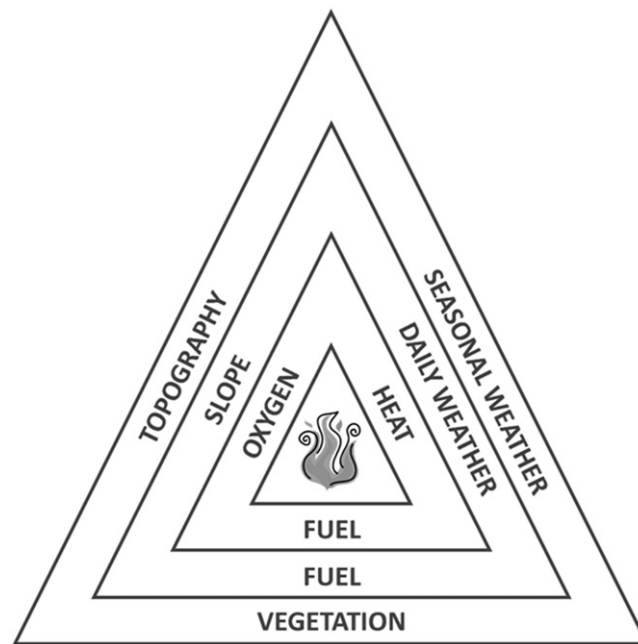
Given its wide geographic extent, fire inevitably influences the distribution and abundance of many plant and animal species. Some ecosystems are dominated by species that depend on fire to complete their life cycles. Others are dominated by species that tolerate burning but have no direct dependence on fire. Ecosystems that seldom or never burn, except when disturbed by human activity, may contain mixtures of species that fortuitously tolerate burning and species extremely intolerant of fire. The impact of burning on biodiversity varies greatly among these different types of ecosystems and species-response patterns.

## Determinants of Fire

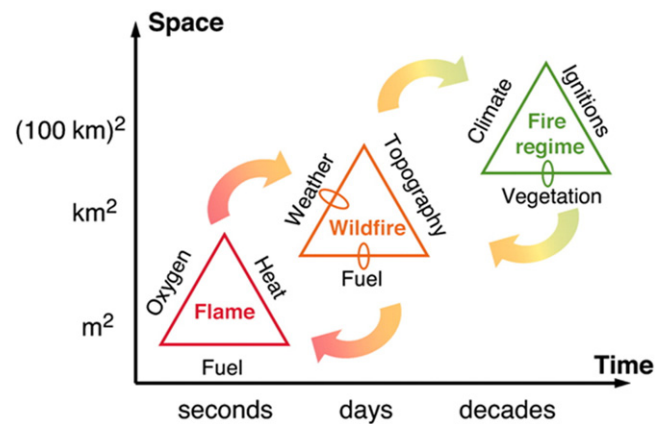
The incidence of wildland fires depends on three simple things – oxygen, fuel, and ignition – often referred to as the fire triangle (Fig. 2). Fuel, defined as live and dead biomass, must be dry enough to burn, so hot, dry, and windy weather conditions are the key driving factors influencing fuel moisture. The flammability of vegetation varies with the moisture content of live plant biomass. Dead matter has the lowest moisture content, whereas live leaves will burn more easily if their moisture content is low. The shape, size, and arrangement of plant parts influence moisture content and flammability. Plants with narrow leaves or thin branches dry rapidly and burn readily. Ecosystems that accumulate slow-decomposing litter are highly flammable. Leaves with large amounts of oils, fats, waxes, and terpenes also burn readily. Volatile substances enhance burning because they are released from leaves, burn fiercely, and thus dry and heat adjacent material.

Because fire depends on moisture content of dead and live biomass, the antecedent climate and ambient weather conditions exert marked influences on the timing of burns. The length of a warm, dry period needed for ignition depends greatly on vegetation properties. A few days of hot, dry weather are sufficient to dry tall grasslands enough to sustain a fire, whereas months of extreme hot and dry conditions are needed for fire to burn pristine humid tropical forests. Therefore, most fires, and especially large fires, in woody ecosystems are generally associated with rare prolonged drought events, such as those produced by El Niño conditions. In contrast, large fires in arid grassy ecosystems are limited by the availability of fuel and are more common after high rainfall years. Fires generate their own heat that, under hot, dry, and windy conditions, creates a positive feedback, increasing the area burnt and the intensity of the fire by drying the vegetation before the fire front.

A source of ignition is needed to start fires. Today, most fires are ignited by humans, except in sparsely populated regions. Lightning fires are still common in many uninhabited landscapes. Lightning often accounts for large numbers of fires but small areas burnt because many are doused by subsequent rain or controlled by fire crews. Rockfalls also ignite fires, accounting for the spate of burns often triggered by earthquakes. Volcanic activity is of local significance, especially on islands in which lightning is rare. The contingent requirements of ignition, suitable weather conditions, and contiguous flammable vegetation make for a high degree of uncertainty in predicting landscape fire patterns.



**Fig. 2** The fire triangle expressed at multiple scales, from the flame, to the stand, to the landscape level (Keane, 2015).



**Fig. 3** The scaling of the combustion process over time and space to create fire regimes (Moritz *et al.*, 2005).

## The Fire Regime

The ecological effects of fire depend on both the fire regime and the occurrence of single fires. The fire regime is the spatiotemporal expression of multiple fires that is governed by the combined effects of climate, fuel properties, and ignition frequency (Fig. 3). It is often described by the type of fire, mean and variance in fire frequency, intensity, severity, season, pattern, and areal extent of a burn. Types of fire include ground fires that burn the organic layers of the soil, surface fires that burn just above the ground, crown fires that burn in the canopies of trees, and mixed fire regimes where fires vary in severity with both surface and crown fire patches. Ground fires occur mostly in organic soils in which they can be extremely damaging, destroying roots and completely altering soil properties. Crown fires are high severity fires typical of low productivity sites including Mediterranean-type shrublands, and North American boreal forests. Surface fires are common in many woodlands and forests where litter is a major fuel. Surface fires with herbaceous fuels predominate in grasslands and savannas and can burn at annual or even subannual intervals where productivity is high. When crown fires do occur in forests, they produce massive stand-replacing fires. The exclusion of fires through active suppression in many areas of the world has led to an increase in young trees and an accumulation of surface fuels that now act as bridging fuels turning surface to crown fires with damaging consequences (Keane *et al.*, 2002).

Fire frequency is estimated from maps of fires, records of fire scars on trees, or patterns of charcoal deposition in sediments. Changes in fire frequency often result in changes in ecosystem structure and function. Fire intensity is measured as energy released per meter of fire front. It is widely used in firefighting operations. Fire severity is the impact of a fire on the ecosystem that is usually estimated from the amount of plant biomass consumed (Keeley, 2009). A fast-moving fire that consumes little biomass and a slow-moving fire that consumes more can have the same fireline intensity but different severities. Fire severity is highly variable, depending on the weather during a burn, wind conditions, and, most importantly, the pre-burn condition of the vegetation. Fire season is largely dictated by the moisture content of flammable biomass. Where the vegetation dries out quickly, fires can burn in almost any season. Seasonal timing of burns can cause significant changes in species composition and ecosystem structure. Continuity of flammable vegetation, especially at the landscape scale, strongly influences the spread of fires (Scott *et al.*, 2014). Habitat fragmentation can lead to a reduction in fire frequency of isolated fire-prone ecosystems or an increase in fire-excluding forests surrounded by flammable vegetation. Land abandonment in some countries has led to successional changes producing large, contiguous, highly flammable vegetation. In the Mediterranean region, reduction of pastoral activities has led to the conversion of grasslands to highly flammable shrublands. This process has contributed to an increase in the area burnt annually from a few 1000 ha in the 1960s to hundreds of thousands of hectares in recent years (Pausas and Vallejo, 1999).

## **Fire Regimes and Phytogeography**

Flammable ecosystems differ greatly from one another in the mix of growth forms and their fire-adaptive traits (Bradstock *et al.*, 2012). This diversity is often linked to differences in fire regime, which are in turn linked to climate. In the absence of humans, key physical preconditions for wildfires were climatic conditions conducive to lightning strikes, periods dry enough for ignition to occur, and enough oxygen in the atmosphere to sustain burning. Where fire influences the geography of plant communities, another physical precondition are the major barriers to fire spread, including rivers, lakes, ice and snow, gravel beds, and other areas with sparse plant growth. Within these physical constraints, the vegetation itself is the major contributor to the fire regime in that it provides the fuel for fire spread.

The way in which the plants themselves contribute to a fire regime is most apparent where contrasting ecosystems, with entirely different fire regimes, occur in the same landscape. These have been described as alternative stable states with each ecosystem state maintained by a different set of positive feedbacks. Examples include mosaics of fire-resistant tropical forests and flammable savannas occupying extensive areas of Africa, South America, and Australia. In some instances, mosaics of alternative ecosystem states occur where both states are flammable but with contrasting fire regimes. In western North America, for example, chaparral shrublands with crown fire regimes occur in landscape mosaics with conifer forests with litter-fueled low intensity surface fire regimes (Agee, 1998). Changes in the fire regime can be brought about by changes in external conditions, such as climate and land use, but also by changes in the growth form mix in vegetation, producing changes in flammability or productivity. The shortest interval between successive fires is constrained by the time taken to build sufficient, continuous flammable biomass for fires to spread. This depends on the plant species present, their abundance, and site productivity. Changes in plant growth form dominance can have major impacts on fire regimes such as those caused by introduction of highly flammable invasive grasses into shrublands and woodlands.

## **Response to Burning**

### **Plants**

Ecosystems subjected to similar fire regimes have convergent vegetative and reproductive traits (Keeley *et al.*, 2011b). There are clear distinctions, for example, between fire-adaptive traits characteristic of crown fire regimes fueled by woody plants as opposed to surface fire regimes fueled by litter or herbaceous plants (Keeley *et al.*, 2011a). In crown fire regimes, a fire event triggers flowering, seed dispersal, or seed germination in fire-dependent plant species. Fire-stimulated flowering is common among perennial grasses and herbs, including orchids, lilies, and other bulb plants. These species flower prolifically after they have been burnt with some species showing a facultative response (continuing low levels of flowering in unburnt vegetation) and others an obligate response with flowering cued by smoke (eg, *Cyrtanthus* spp. in Africa, *Xanthorrhoea* in Australia). Fire-stimulated recruitment also occurs when fires stimulate seed release from woody species with serotinous cone-like structures which store seeds on the plant for years between fires. Serotiny is common in conifers of North American boreal forests and Mediterranean-climate regions and also among diverse groups of flowering plants in Australia and South Africa (Keeley *et al.*, 2011b). Some species are polymorphic for the trait, with serotinous forms increasing in populations that regularly experience large severe crown fires. Fire-stimulated seed germination from soil seedbanks is also common in mixed and crown fire regimes. Dormant seeds in the soil show heat-stimulated seed germination, especially in legumes and other clades with hard seed coats (eg, members of Rhamnaceae). Thick seed coats prevent imbibition of water until cracked by the heat of a fire. Smoke-stimulated seed germination has been reported for many species in fire-prone shrublands of South Africa, Australia, and California. However, smoke-stimulated

germination has also been reported for plants that do not come from fire-prone ecosystems. Regardless of the nature of the germination cue, the appearance of numerous seedlings after a fire event is characteristic of fire-dependent species in ecosystems with an evolutionary history of crown fire regimes.

Vegetative features of plants also vary with fire regime reflecting the plant's ability to survive fire and/or to quickly revegetate after the fire (Keeley *et al.*, 2011b). Three morphological characteristics may allow woody plants to survive fire: thick bark, open crowns, and deep roots (Kolstrom and Kellomaki, 1993; Fig. 4). Sprouting from insulated buds is another common fire survival mechanism, either from the root stock or from branches above the ground. Some species possess large swollen burls or lignotubers which are thought to act as bud banks or storage reserves. Paradoxically, many woody species in crown fire regimes cannot resprout and are often killed by fire. These nonsprouting plants often have higher seed production and higher seedling growth than related sprouting species. In some lineages, sprouting is the ancestral feature and loss of sprouting is viewed as an adaptive response to fire. Nonsprouting shrubs are particularly common in chaparral and similar shrublands and require fire to release seeds from serotinous cones or to stimulate germination. Among trees in fire-prone forests, many conifers do not sprout and a few eucalypts are also killed by fire. Nonsprouting species are particularly prone to local extinction if recruitment fails after burning.

The occurrence of species with flammable morphologies in crown fire regimes has led to the suggestion that flammability has evolved to promote burning (Mutch, 1970). However, vegetative traits that promote flammability may also serve other functions. Some woody plants accumulate highly flammable fuel by retaining dead branches while also requiring fire for recruitment. In western North America, serotinous pine species retain dead branches and recruit seedlings only after crown fires have destroyed the trees. These species appear to both promote the spread of crown fires and benefit from fire-stimulated reproduction. This strategy contrasts strongly with self-pruning, thick-barked pines (eg, *Pinus ponderosa*) which tolerate frequent surface fires and do not require fire for seedling recruitment.

Surface fire regimes fueled by herbaceous plants select for a different suite of plant traits. Grasses are among the most fire resistant of all plant growth forms. The buds of new shoots are insulated by either layers of leaf sheaths or the soil where species have underground rhizomes. Grasslands recover from burning more rapidly than woody plants and can survive very frequent fires (1–3 years) in productive sites. Although many grasslands burn readily, few species have an obligate dependence on burning. Fire-stimulated flowering is rare but has been reported in many mostly temperate tussock grass species, including species of *Chionochloa* in New Zealand. Several widespread warm-climate (C4) grasses (eg, *Themeda triandra* and *Andropogon gerardi*) decline rapidly in the absence of burning. These species become locally extinct if fires are suppressed for more than a decade since litter accumulates, shades, and kills the grass plants. Unlike crown fire systems, all woody plants in savannas resprout after fire and seedling recruitment is not fire dependent. Instead, savanna trees have developed a remarkable ability to tolerate very frequent grassland fires (Dantas *et al.*, 2013). These create a particularly hostile environment for juvenile stages. Tree seedlings survive by rapidly acquiring the ability to sprout, and juveniles slowly develop food reserves in swollen roots and eventually produce bolting stems that place foliage above flame height. This peculiar life history occurs in several pine species (eg, *Pinus palustris*) growing in grassy habitats and also in many savanna trees. Juvenile stages of savanna trees can tolerate repeated burning, suffering repeated killing of the stem parts, for decades before they die or escape the flame zone to become adults.

## Animals

The direct effects of fire on wildlife are often surprisingly small. Agile animals flee to refugia within the fire, such as termite mounds, or moving across the fireline to places of safety. Soil is an effective insulator so that many animals survive in crevices and cracks or in burrows in the soil. Mortalities of large mobile vertebrates, including humans, occur only in the most severe fires. Reptiles and slow-moving invertebrates can suffer higher mortalities and their carcasses provide a food source to scavenging birds and other



**Fig. 4** Ponderosa pine trees have thick bark, high and thin crowns, and deep roots to better survive fire.



creatures in the first few days after a burn. The threatened bald ibis of South Africa makes extensive use of recently burnt grasslands, as does the endangered whooping crane in its Texan winter feeding grounds.

The indirect effects of burning are generally far more important than fireline mortality, especially changes in habitat attributes as vegetation recovers from a fire. A large crown fire in a forest causes drastic structural change and local extirpation of all faunal elements that depend on unburnt forest habitat. Post-burn stages are colonized by a new suite of species. Different successional stages support different suites of animals. Even frequently burnt grasslands, such as those of the South African highveld, have distinct bird assemblages which turn over with successive years of regrowth after burning.

The pattern of fires across a landscape imposes a mosaic of patches of different successional ages. The size and configuration of patches influence animal metapopulation structure and composition through local extinction and patch recolonization of animal species (Pons and Clavero, 2010). For example, nectar-feeding birds in shrublands of Australia and South Africa lose their food source (shrubby members of the Protea family) after a burn and have to seek unburnt stands for food. The landscape configuration of old stands with flowering proteas, and young stands with immature shrubs, necessitates a highly mobile bird assemblage. Changes in the spatial pattern of fires may change extinction risks in different faunal elements. Some species of Australian honeyeaters are threatened with extinction because changes in the fire regime no longer produce the right mix of mature and immature populations of nectar plants. The decline of many bird species in Australian savannas has been attributed to the development of homogeneous landscapes through the systematic burning of large tracts of land. Smaller, patchier burns are thought to have prevailed under aboriginal burning practices. The extinction of many Australian small to medium-sized (50 g to 5 kg) mammals since European settlement (23 species) has been attributed to similar changes in the fire regime, but predation by feral animals is also a major factor.

Fires in tropical rain forests, caused by human impacts on forest structure, have had devastating effects on the forest fauna. In Sumatra, for example, primary forest specialists, including squirrels, hornbills, and other fruit-eating and frugivorous birds, and some primate species disappear altogether from burnt and adjacent forests. The increasing risk of fire in humid tropical forests poses serious threats to survival of the forest fauna in addition to those caused by direct forest clearing.

## **Ecological Effects of Fire**

### **Ecosystem Structure**

The consequences of increasing fire frequency and severity for ecosystem structure are to reduce vegetation height (tall forests to shorter ones and woodlands to shrublands); reduce woody vegetation to be replaced by grasslands; promote flammable species or communities (low litter decomposition rates, more xeromorphic leaves, and finer twigs/branches); and to reduce biomass (Scott *et al.*, 2014). Both tropical and temperate landscapes contain mixtures of fire-prone grassland or shrubland communities and closed forests which tend to exclude fire. Savannas and closed forest are well-studied examples of such alternative ecosystem states; relative proportions of flammable savannas and fire-resistant forests, for example, vary across precipitation gradients and, locally, with soil type. Boundaries between states are typically abrupt with fires excluded from forests, which shade out grasses. In some instances, paleoecological studies have shown that these sharp boundaries have remained stable for millennia. Simulations using physiologically based global vegetation models suggest that forests would at least double in extent in the absence of fire, particularly in the flammable savanna biome. Replacement of flammable communities by fire-resistant forest elements frequently occurs when fires are suppressed. In southern Africa, forests have replaced savannas after 10–30 years of fire suppression in some places. Stable boundaries often coincide with different soil types, with forests occurring on the better drained or more fertile soils.

Changes from fire-resistant to flammable ecosystems may also be rapid. In the Brazilian Amazon, fires in closed-canopy forests spread as a “thin, slowly creeping ribbon of flames a few tens of centimeters in height.” Despite the low severity of an initial fire, burning causes structural changes, opens up the forest canopy, dries out the understory and contributes to an increase in flammable understory biomass, increasing the risk of a second fire. Weedy vines and grasses quickly colonize twice-burned forests, further adding to the flammable biomass. Positive feedbacks of this kind are estimated to reduce a forest to scrubby vegetation resembling recently abandoned farmland in 20–30 years.

The parade of fires that occur on a landscape to create a fire regime also creates a shifting mosaic of plant and animal communities and structures (McKenzie *et al.*, 2011). The rate and magnitude of vegetation development after the burn, coupled with the direct effects of the fire during the burn (eg, fuel consumption, mortality), will dictate the availability of fuels to foster future fires. In many landscapes, the low fuels left after a fire are insufficient to support the spread of future fires, and as a result, the burn acts as a “firebreak” that impedes fire spread. This property of fire regimes is an example of a self-organized process in which the structure of future landscapes is controlled by the historical footprint of fires and their effects, and the growth of fuel after a burn (Peterson, 2002).

### **Ecosystem Function**

The immediate effect of fire is gaseous loss of carbon and nitrogen from burned dead and live biomass. Nutrient losses are greatest when the greatest biomass is burn, which is often during the most severe fires. Strong winds accompanying fire often lead to losses

of phosphorus and cations blown away in ash. Cation nutrients in ash tend to be mobile and in a plant-available form and can be washed away in runoff from post-burn rain. Their presence leads to increases in soil pH – large increases in acid forest soils and smaller increases in neutral or alkaline soils in grasslands or savannas. Increased solar radiation, decreased evaporation, and higher pH lead to increased microbial activity, increased rates of mineralization, and increased availability of nutrients after a burn. After a chaparral burn, for example, nitrate increased more than 20-fold relative to unburnt controls. Short-term increases in nutrient availability can be offset by long-term decreases where fire frequencies are high and inputs to the system between fires are not high enough to replace losses. Severe fires can lead to nitrogen shortages. Many ecosystems have nitrogen-fixing organisms as major components of post-burn vegetation which replace nitrogen losses in a few years.

Fire can lead to changes in ecosystem processes at landscape scales. The reduction in biomass caused by burning and changes in soil properties lead to temporary hydrological changes in patterns of stream flow. Severe fires can lead to increased soil erosion. In the United States, the Yellowstone fire of 1988 led to significant increases in sediment loads and altered the geomorphology of river systems. Debris spread over a distance of 12 km in one valley bottom.

### Species and Populations

At the local scale, and within flammable ecosystems, species respond to differences in fire frequency, season, and severity. Variation in the fire interval is an important determinant of population trends. In crown fire regimes characteristic of woody fuels, the effect of fire on population growth depend on key demographic attributes of the species. Population size of nonsprouting species fluctuates more than that of sprouting species, and local extinction is not uncommon after a single fire. Species that are slow to mature are particularly vulnerable where populations are burnt before they have first flowered and set seed. Populations are also negatively affected where intervals between fires exceed the life span of a species or its seedbank. C4 grasses are also sensitive to variation in fire frequency with the dominant species in some grasslands disappearing after a decade or more of fire exclusion. The rich forb diversity in upland grasslands in Africa and South America is also dependent on frequent fires and fire exclusion has been shown to lead to loss of long-lived perennial species, especially those with large underground storage organs. This contrasts with North American prairies where fire exclusion promotes forb diversity. Manipulation of the fire interval is a key tool for influencing biodiversity of vegetation stands. In flammable woody ecosystems, information on the reproductive status of plants, especially the size of the viable seedbank, at different post-burn stages has been extensively used to help determine optimum fire frequencies to maintain particular species.

Post-burn recovery of plant populations also depends on the unique combination of circumstances on the day a fire burns. These “event-dependent” effects can be as important as fire frequency in influencing biodiversity in some ecosystems. Fire season has a marked influence on recruitment of serotinous members of the Proteaceae in Western Australia and South African fynbos. Spring burns can reduce protea populations to less than one-tenth of their pre-burn density, whereas autumn burns can result in a 10-fold or greater increase in plant densities. Fire season also influences recovery of sprouting plants where the size of root reserves varies seasonally, affecting the vigor of resprouting. Manipulation of fire season is sometimes the only effective tool for managing densities of sprouting shrubs. Stem density of clonal species of hazel (*Corylus* spp.) in the understory of temperate forests increased fivefold with four successive spring burns but was halved by successive summer burns. In Zambian woodlands, annual burns in the early dry season caused a 10-fold increase in tree seedlings and halved the adult mortality rate over a decade. Grassland composition can also be very sensitive to fire season. In a long-term burning experiment in the Kansas prairies, late-spring burns caused a halving of *Andropogon scoparius* biomass relative to fires burnt a few weeks earlier. The effects of fire season on species and ecosystem recovery are poorly known in many ecosystems. They may be unimportant where the fire season is short because of climate constraints.

By definition, severe fires cause the most extreme biomass losses in some ecosystems. In many conifer and some eucalyptus forests, intense crown fires kill all aboveground plant growth. Where trees are incapable of sprouting, these fires cause complete replacement of canopy trees. Sprouting plants, especially shallow-rooted species, can be killed by high severity burns. The effects of fire severity on recruitment from seeds vary among species. Legumes and other plants with hard, dormant seeds in fire-prone shrublands do not germinate unless a burn heats the soil sufficiently. For example, the Australian shrub, *Acacia suaveolens*, will not germinate unless soils are heated to more than 50°C. Variation in fire intensity can directly affect species composition in fire-prone shrublands, incinerating some seeds and stimulating germination in others. Key species, such as legumes, may fail to germinate after low-intensity fires that are applied for safety reasons.

Fire intensity is an important factor in savanna ecology. Where grass growth is sufficient to carry fires at frequent intervals, burning kills the aboveground parts of juvenile trees and shrubs. The amount of dieback depends on the intensity of the burn. In mesic savannas, fires are so frequent and so intense that juvenile trees may spend decades trapped in the grass layer. The frequency and intensity of fire are also important determinants of tree biomass (and habitat structure) in savanna ecosystems.

The relative sensitivity of plants to fire season and fire severity varies among species. This makes general prediction of population trends under different fire cycles difficult without species-specific information. In Mediterranean shrublands, species with diverse responses to frequency, season, and intensity of burn occur in the same community suggesting a history of fires that vary in these factors. It is a considerable conservation challenge to incorporate variability into fire regimes to maintain the full diversity of species.

## Interactions Between Fire and Other Ecological Processes

### Fire and Herbivory

Fire interacts with, and is influenced by, other agents of disturbance that can also influence ecosystem structure on a large scale. Herbivores influence the distribution and biomass of plants and therefore the attributes of fire regimes (White *et al.*, 1998). Heavily grazed savanna grasslands often do not burn because animals capable of grazing grasses too short to burn, such as wildebeest, white rhino and prairie dogs, can reduce landscape fire activity. Extirpation of short-grass grazers can, in turn, promote more frequent larger fires reducing landscape heterogeneity. Persistent heavy grazing by cattle often leads to an increase in tree densities because of the reduction in fire frequency. In Africa, elephants open up woodlands, enhancing grass growth which promotes more frequent and more severe fires. The combination of elephants and grass fires can cause a marked reduction in tree densities. In miombo woodlands of Zimbabwe, changes in woodland structure under the combined influence of elephants and fire markedly reduced bird diversity and led to local extinction of four endemic woodland bird species.

Insect herbivory also influences fire regimes, especially in northern ecosystems. In balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) forests of eastern North America, fires are rare, but large-scale tree mortality is caused by spruce budworm outbreaks may inhibit the spread of fire by changing vegetation structure and fuel properties. In general, however, plants that provide fuel for burning make poor food for herbivores and vice versa. Fires burn readily where decomposition is slow, causing dead matter to accumulate. Slow decomposition is associated with high C:N ratios, high fiber contents, and high leaf-specific weight, all of which inhibit herbivore food intake. Thus, the most fire-prone vegetation tends to be least edible and vice versa.

### Fire and Landscape Fragmentation

The spread of fire in a landscape is sensitive to the continuity of flammable vegetation. Landscape fragmentation can have major impacts on the fire regime, in turn affecting survival of species within fragments. Species losses from North American prairie fragments during a 50-year period were greater among plants of early post-burn environments. Similar patterns of local extinction occur in fynbos fragments surrounded by nonflammable forests in South Africa. The causes of species loss in both prairies and fynbos are attributed to infrequent burning due to isolation of the fragments. Small forest patches in extensive areas of fire-prone shrublands or grasslands are also more likely to suffer local extinction of species intolerant of burning. In the tropical forests of Guyana, fire-tolerant forest tree species with thick, fissured bark, and small seeds are unusually common near savanna boundaries and human settlements.

### Fire and Invasives

The interplay between fire and invasive species can cause alarming ecosystem transformation. Direct effects of invasive plants can be minor relative to the indirect effects on fuel properties and fire regimes. Grass invasion into woody ecosystems has particularly damaging consequences. In Hawaii, invasion of tall nonnative grasses has transformed the unique forests to grasslands entirely alien to the island ecosystem by fueling frequent fires. In South America, invasion of logged-over tropical forests by fire-promoting grasses can cause elimination of the forest ecosystem and its rapid replacement by the alien grass. In southwestern Australia, species-rich heathlands are fire dependent but they have also been invaded by nonnative grasses which burn so frequently that the heathlands are transformed into a species-poor savanna with scattered relictual trees. And in the western United States, invasion of cheatgrass (*Bromus tectorum*) into native sagebrush grasslands has increased fire frequencies and severities (Billings, 1992; Keeley, 2006). The reverse pattern, that of invasion of fire-prone grasslands by plants that do not burn easily, may also be a problem. For example, *Lantana camara* is invading fire-dependent grasslands in South Africa but burns much less readily than the native vegetation.

## Managing Fires

Because fires are such a widespread feature of the world's ecosystems, managing fires for particular objectives, including protection of property and conservation of biodiversity, is a major concern. Attitudes and actions to wildfire are never neutral. Fires are actively suppressed in some ecosystems but purposely ignited in others. Wildfires commonly arouse public and media concern. In the United States, the settlement of wildland areas has exposed more people to potential wildfires, while in Europe, the decline of the urban interface as more people flock to cities has increased threats of wildfire to people and properties. Smoke management has also become an important health and safety issue. Enormous effort and expense are often expended on fire management. Appropriate fire management policies continue to be a central management headache in protected areas as different as Yellowstone National Park in a coniferous ecosystem and Kruger National Park in African savannas. The expense of maintaining firefighting teams consumes conservation agency resources. Litigation, when fires move beyond the borders of protected areas, can



also strain conservation budgets. Arson burns are common, sometimes as a protest against state authority. In summary, active fire management, mostly in the suppression of fires, consumes a great deal of time and is a major expense in fire-prone ecosystems.

### Fire Management Policies

There is no consensus on how to manage fires in protected areas or outside them. For the first half of the 20th century, complete fire suppression was a common policy, and it still is in many parks of the world. Suppression policies have slowly changed, partly because of their cost, partly because they are inefficient, and partly because of changes in ecological thinking. Fire suppression leads to the buildup of dead biomass in fire-prone ecosystems which may produce more severe fires when they do burn. Suppression policies were also relaxed following the discovery of fire-dependent features of plants. In the Cape fynbos, the beautiful marsh rose (*Orothamnus zeyheri*) declined to a handful of plants before managers realized that the species had an obligate dependence on fire to stimulate germination of its seeds. There has also been increasing recognition of disturbance as a natural process in ecosystems. Outside of rain forests, complete fire suppression is rarely the aim of fire management. However, decades of suppression have led to pronounced changes in ecosystem structure that now pose major challenges regarding how to reintroduce fires without causing more problems. Many conifer forests were maintained as open parklands by frequent surface fires. Fire suppression has allowed numerous young trees to establish, creating “fuel ladders” that facilitate a switch from surface to crown fires. In some savannas, fire suppression has led to invasion of grasslands by forest species in a process that is very difficult to reverse except by costly manual clearing of trees to restore large mammal habitat.

Prescribed fires are intentionally lit for management purposes. Safety for the fire crew, and for property, is always an important consideration. Therefore, prescribed burns often cause significant changes to the fire regime, especially to season and intensity but also to fire frequency. Changes to the fire regime can lead to significant population declines in sensitive species such as legumes, which depend on intense heat for seed germination. Prescription burning calls for clear management objectives. Because fire is so influential a force on community structure and composition, decisions have to be made regarding the desirable objective and what kind of burning pattern should be used to achieve it. In the South African savanna parks, fire policy changed from complete fire exclusion to prescribed burning at fixed intervals (promoting large mammals) to fire regimes that “maximize biodiversity.” The intention of the latter is to create and sustain a landscape mosaic of different successional ages or habitat types that can maintain viable populations of most species.

Another commonly considered policy is to recreate “natural” burning regimes, often called “let burn fires,” “wildland fire use,” or “prescribed natural fires” in the past. This policy permits fires that have been ignited by lightning, rockfalls, or other nonhuman agents within acceptable weather conditions but suppresses fires of human origin. Recreating natural fire regimes has been criticized for not including aboriginal influences on fire regimes which may have significantly influenced landscape patterns over millennia. A variation on natural burning policies is to recreate aboriginal burning practices to try to reproduce pre-agricultural landscapes. Implementation of these policies is constrained by lack of biological knowledge, techniques for fire management, and safety-related considerations.

In practice, future fire management must find the most appropriate integration of fire suppression, prescribed burns, and controlled natural fires depending on safety concerns and conservation objectives in different parts of the landscape.

## Fire and Global Climate Change

### Effects of Climate Change on Fire Ecology

The impact of climate change on fire regimes is likely to be quite different depending on whether fire activity is limited primarily by weather or by sufficient fuel to burn. Weather-dependent fires are characteristic of woody ecosystems such as conifer forests, eucalypt woodlands, and flammable shrublands. Fires in these ecosystems are most severe and burn the largest areas following long hot dry periods. In contrast, fires in grass-fueled ecosystems burn most extensively after unusually wet years. The implication is that climate change will have different effects depending on the nature of the ecosystem. In the boreal forests of Canada, burned area has increased over the past half century. This is attributed to global warming with warmer temperatures generating larger fires (Flannigan *et al.*, 2009). Global warming in the circumboreal region is predicted to cause a doubling of area burned along with a 50% increase in fire occurrence by the end of this century. Similar predictions have been made for the conifer forests of Yellowstone with such frequent and severe fires that the forests may be eliminated and replaced by low biomass ecosystems by midcentury (Westerling *et al.*, 2006). Global warming might also increase the frequency of high severity fires entering tropical forests from adjacent savannas. However savannas, which currently account for more than half the world’s annual burnt area, are also influenced by other global change factors that might cause large reductions in fire activity. Climates are predicted to be drier for much of Africa resulting in less grass biomass to fuel fires. In addition, increasing atmospheric CO<sub>2</sub> may favor the spread of less flammable grasses than those that currently dominate these highly flammable ecosystems. Increasing CO<sub>2</sub> is also thought to be contributing to increased woody cover in savannas, and the expansion of forest into savannas despite frequent fires. Increasing human population densities are leading to fragmentation of fuels and reduction of burnt area through increased livestock

densities, exotic invasions, land conversion to crops, expanded road networks, and growing urbanization. Thus the future of fires, and of ecosystems, is very uncertain. Uncertainties in global change predictions for fire regimes are being addressed by the development of physically based fire spread models coupled with physiologically based global vegetation models that incorporate both climate and CO<sub>2</sub> effects on future vegetation. Ultimately, however, the challenge is to devise innovative fire management options that reduce risks to lives and property while maintaining landcover that meets diverse human needs.

### Fire as a Source of Greenhouse Gases

Vegetation fires contribute significantly to greenhouse gas emissions thereby influencing global climate change (Loehman *et al.*, 2014). Satellite data have greatly improved estimates of global fire emissions but there are still many uncertainties, not least of which is interannual variability in fire activity. Global fire emissions from 1997 to 2009 averaged 2.0 Pg C year<sup>-1</sup> compared with ~7.2 Pg C year<sup>-1</sup> from fossil fuel combustion (van der Werf *et al.*, 2010). Major contributions to global fire emissions are from Africa (52%), South America (15%), Equatorial Asia (10%), the boreal region (8%), and Australia (7%). Savannas and grasslands contributed 60% of C emissions but most of these emissions would be compensated by rapid post-burn regrowth. Annual emissions ranged from lows of 1.5 Pg C to a high of 2.8 Pg C in 1998, following an El Niño, with major fires in Indonesia. About a quarter of fire carbon emissions (0.5 Pg C year<sup>-1</sup>) were attributed to deforestation, burning of tropical peatlands, and degradation in the period 1997–2009 and are probably a net source of CO<sub>2</sub> to the atmosphere. Unlike savanna fires, deforestation fires also emit large quantities of reduced trace gases like CO and CH<sub>4</sub>. Deforestation, degradation and tropical peat fires together account for about half of global CH<sub>4</sub> (methane) emissions. Boreal peatlands are a major C pool storing as much as 270–370 Pg C. Increased fires, and a change from surface to ground fires, in boreal forests could potentially release enormous quantities of C into the atmosphere. The increasing frequency of fire in humid tropical forests is also of concern. Tropical forests are estimated to store one-fifth of the world's carbon. If burning of tropical forests continues, large areas could be converted to flammable secondary scrub or grassland releasing this carbon into the atmosphere.

Fire is also an important source of aerosols. Aerosols decrease regional and global irradiation through backscattering of incoming solar radiation. Smoke aerosols can also increase or decrease cloud cover in complex and nonlinear ways that are not yet adequately quantified. Fire can also influence radiative forcing by altering the albedo. Black soot immediately after a burn heats the surface by reducing albedo. However, fire-induced reduction in tree cover can cause cooling by extending snow cover in boreal forests or replacing dark forests with more reflective vegetation (eg, savanna grasses) elsewhere. The net effects of changing fire regimes on global warming are complex and uncertain. Public concern regarding atmospheric impacts of burning is leading to public pressure regarding the use of fire for conservation purposes. This may have positive effects if it leads to adoption of logging practices that reduce fire hazard in humid forests. Public pressure to suppress fires could have negative impacts on naturally flammable ecosystems and their fire-dependent species.

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