Fire ecology

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Introduction

This course explores the role of fire as an agent of natural disturbance in ecosystems. Many terrestrial ecosystems around the world are fire-prone and fire, or more specifically, the fire regime, controls their composition and structure. Factors such as climate, vegetation type and the source of ignition differ among ecosystems and affect aspects of the fire regime such as its extent (size), frequency and intensity. Because plants and fire share a long evolutionary history, many plants have evolved adaptive traits that not only allow them to persist in flammable environments but to depend on fire for reproduction and growth.

One important consequence of natural fires is the creation of spatial and temporal variation within a landscape, which generates and maintains biodiversity. Many animals exploit the consequences of fire and the mosaic of habitats generated by fire supports a wide diversity of animals and plants. The course also briefly addresses some of the effects and consequences of climate change and global warming on the intensity and frequency of fires.

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Learning Outcomes

After studying this course, you should be able to:

- explain why fire is an important component of healthy ecosystems
- explain what is meant by a ‘fire regime’ and how changes in fire regimes can lead to changes in ecosystems
- describe some adaptive features of plants that have evolved in response to fire
- describe how some animals avoid fires and/or benefit from the aftermath of natural fires
- explain how global warming may result in an increase in both the frequency and intensity of fires.

1 Fire as a natural disturbance

Fire is a natural agent of disturbance. The origin of fire is tied to the origin of plants, which are responsible for two of the three elements essential for fire to exist: oxygen and fuel. The third element – a heat source – has probably been available throughout the history of the planet. Before the appearance of photosynthetic organisms, the atmosphere lacked sufficient oxygen to support burning and before the existence of terrestrial plants, it lacked fuel. Evidence of low-temperature surface fires dates back 440 million years and fire appears to have been continuous since plants invaded the land.

The first evidence that fire actually altered, and had major impacts on ecosystem functioning dates back to the late Tertiary, about 10 million years ago. The spread of C_4 grasses during this period was due to increased fire activity which opened up woodlands and created environments more favourable to C_4 grasslands. The high flammability of such grasslands produced a feedback process that further increased fire activity.

Hominids have used lightning-ignited fire for perhaps as long as 1.5 million years, but first began to ignite fires between 200 000 and 400 000 years ago. Over recent millennia the occurrence of fire has been increasingly influenced by human activity and is currently a major cause of global atmospheric pollution and contributes significantly to the rise in greenhouse gases: CO_2 (carbon dioxide), CH_4 (methane) and N_2O (nitrous oxide). Fire and fire management are becoming increasingly important issues for ecosystem management.

1.1 The effects of fire on an ecosystem

Given the 2020 wildfires on Australia and the obvious devastation they have caused, the perception of wild fires is often that they are destructive disturbances. However, wildfires are an important part of healthy ecosystems and play a key role in shaping the composition, structure and function of many ecosystems on Earth.

Activity 1 The effects of fire on an ecosystem

Allow 30 minutes for this activity.

Watch Video 1, which is the excerpt ‘Fire as an agent of perturbation’ from the BBC programme *The Living Planet, Northern Forests* to give you an introduction to fires as an agent of ecosystem disturbance. As you watch the video, think in particular about the effects of fire on:

- the dominant kind of vegetation
- the overall biodiversity.

You should also consider what effects the frequency of fire might have on:

- the structural complexity of the habitat
- the resistance and resilience of the habitat to fire, i.e. its susceptibility and the time taken to recover from fire respectively.

You should refer to the following notes and questions as you watch the video. You may like to use the text box below to record your notes.

Video content is not available in this format.

Video 1 Fire as an agent of perturbation, with Sir David Attenborough. Fullscreen mode is recommended (last button on right of video control bar).

Provide your answer...

Sir David Attenborough introduces the excerpt by showing that there are two dominant types of tree in the woodland.

What are the two dominant types of tree in the woodland, and how do they differ in terms of their fire resistance?

Answer

They are *Pinus* spp. (pines) and *Quercus* spp. (oaks). It is pointed out that the *Quercus* seedlings are destroyed by fire, while the *Pinus* seedlings are more resistant to fire because they have a protective thatch of pine needles around the growing tips.

Quercus spp. trees are stronger competitors than *Pinus* spp. trees for light and nutrients.

What would happen to the dominant tree type in the woodland if fire was suppressed over many decades?

Answer

The woodland would come to be dominated by *Quercus* spp. trees.

Video 1 also reveals that litter composed of resin-rich pine needles is more combustible than fallen *Quercus* spp. leaves.

Given this fact, what would you expect to happen to the likelihood of fire starting as the time since the last fire increases?

Answer

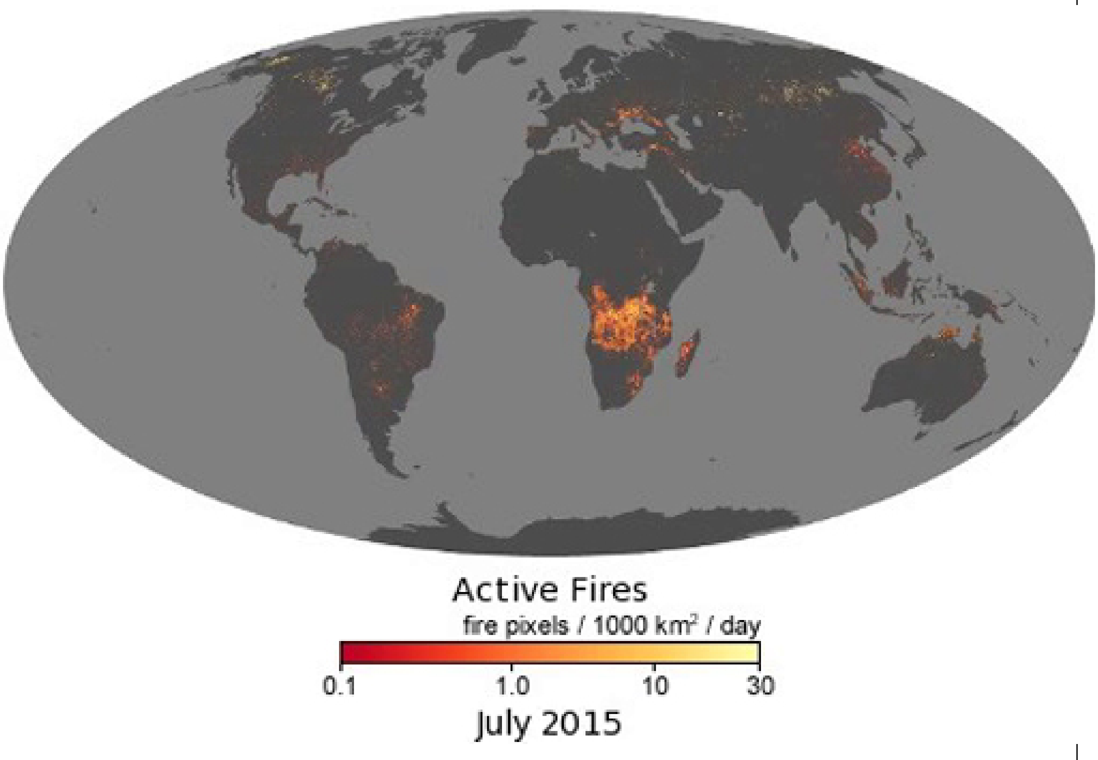
The probability of fire starting would fall as the proportion of *Quercus* spp. leaves in the litter layer increased.

Conversely, in a pine-dominated woodland, the litter layer is dominated by pine needles, and the more pines there are, the more needles there are, and so the more likely it is that fires will start.

Satellite imagery now makes it possible to view the vast areas of the Earth that have been, and are currently, subjected to fire:

Video content is not available in this format.

Video 2 The locations of actively burning fires around the world *(Please note this video has no audio.)*



The map shows the locations of actively burning fires around the world on a monthly basis, based on observations from the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Terra satellite. The colours are based on a count of the number (not size) of fires observed within a 1,000-square-kilometer area. White pixels show the high end of the count — as many as 30 fires in a 1,000-square-kilometer area per day. Orange pixels show as many as 10 fires, while red areas show as few as 1 fire per day.

Many of these fires have, in recent times, been catastrophic, destroying lives, properties and infrastructure. In 2016 and 2017, large areas of Canada, the western United States, southern Europe, Greenland, Indonesia, Chile, Australia and South Africa were affected by wildfires and this trend is set to continue with rising global temperatures, something that will be returned to later in the course.

Although in some cases, the economic and social effects of wildfires can be devastating, as you saw in the previous video, fire is also an important natural ecological phenomenon, regulating and influencing community composition and ecosystem function in many parts of the world. At present, the type of community (e.g. whether grassland or forest) and the relative abundance of species present on over half the land's surface is believed to be determined largely by the interaction of fire and climate.

1.2 Fire dependant ecosystems

Using dynamic global vegetation models, ecologists have compared the present global vegetation distribution which is subjected to fire with the potential vegetation distribution in the absence of fire. They estimated that if fire were 'switched off' dense tree cover would increase from 27% to 56% of the vegetated earth surface and more than half (52%) of tropical savannahs would become tropical angiosperm-dominated forests. This suggests that the presence of savannah and grasslands in climates wet enough to support forests is due largely to fire.

For the past few thousand years, fires have been started deliberately by humans. However, well before the emergence of humans, earth fires were started naturally by lightning, and the close association between fires and the emergence of plants suggests that fires played a key role in the origins of adaptive morphological characters of many plants that evolved in fire-prone areas. There are now many species and whole communities of plants that cannot persist unless fires occur with a certain minimum frequency. One example of such a community is the Fynbos (meaning 'fine bush' in Afrikaans) of South Africa – a natural shrubland/heathland vegetation occurring mainly in the winter rainfall Mediterranean climate areas of the Western Cape, South Africa.

Activity 2 Fynbos on fire

Allow 5 minutes for this activity.

Watch Video 3, which describes the effect of fire on the Fynbos in the Cape region of South Africa.

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Video 3 Fynbos on fire.

The commentator mentions that fire is important in maintaining the health of Fynbos for two reasons. What are these?

Answer

Fire releases important minerals into the soil.

Fire is important for the release of seeds.

Communities such as Fynbos are known as **fire climax communities** and are typical of areas with a Mediterranean climate (hot, dry summers and warm, wet winters). However, in virtually all regions with a definite dry season, fire has become an essential part of cyclic change in ecosystems. It is now clear that in order to sustainably manage ecosystems both for conservation and timber production it is necessary to understand both the ecological role of fire and a central aspect of fire ecology, which is the concept of a fire regime.

1.3 Fire regimes

Fire has predictable features regarding how it spreads across landscapes and the frequency and season of occurrence. Such predictability has led to the concept of a **fire regime**: the temporal and spatial characteristics of the fire and the impact it has on the landscape (Table 1).

Table 1 Characteristics used to describe fire regimes

Fire characteristic	Description
Type	There are 3 basic types of fire: crown fires, surface fires and ground fires.
Frequency	How often a fire occurs in an area/ecosystem or the return time of a fire to an area/ecosystem.

Intensity	Refers to the energy release and is measured by flame length or rate of spread.
Severity	A measure of the impact of fire on an ecosystem. In forested ecosystems tree mortality is often used as measure of severity; in shrublands the metric is the mortality of above-ground plants.
Size	Spatial extent of the fire.
Pattern	Patch size distribution of fire; spatial heterogeneity of fire effects.
Season	Time of year that fire occurs. Fire season is determined by the coincidence of ignitions and low moisture in the fuel. This is usually the driest time of the year.
Duration	Length of time the fire persists.

The ecological effects of fire depend largely on the fire regime but the concept of a fire regime is far from simple. The variability in the characteristics listed in Table 1 coupled with the interaction of these characteristics with other disturbances as well as climate, make fire regimes one of the most complex processes governing landscape dynamics and controlling biodiversity.

Although there are several characteristics that define a fire regime, they are most often described in terms of severity and frequency because these two factors are the most important to land management.

1.4 Fire severity

What determines **fire severity** is mainly the temperatures reached and the speed at which the fire spreads. These in turn are a function of climate, vegetation, topography and soil. A source of fuel is the first prerequisite for fire and must be dry enough to burn. Hot dry and windy weather conditions are key driving factors influencing fuel moisture, which is why primary rainforests virtually never burn naturally. A few days of hot dry weather is sufficient for dry tall grasslands to sustain a fire whereas months of extremely hot and dry conditions are needed to burn tropical forest. This means that fires in tropical forests are associated with rare prolonged drought events such as those produced by El Niño conditions. Grasslands on the other hand, burn frequently and tend to burn after high rainfall years when long grass and hence fuel is abundant.

The type of vegetation is also an important determinant of fire severity. Dead litter has the lower moisture content compared to live vegetation and so will burn more easily but the shape and size of plant parts also influence moisture content and hence flammability. Species such as *Pinus* spp. with narrow leaves and thin branches burn readily. Also, the high wax or oil content of these species mean that they burn at especially high temperatures.

The rate of fire spread, and to some extent its severity, are influenced by wind speed. Fires also move faster up slopes than over level ground. The rate of spread approximately doubles for every 10° increase in slope (Figure 1).

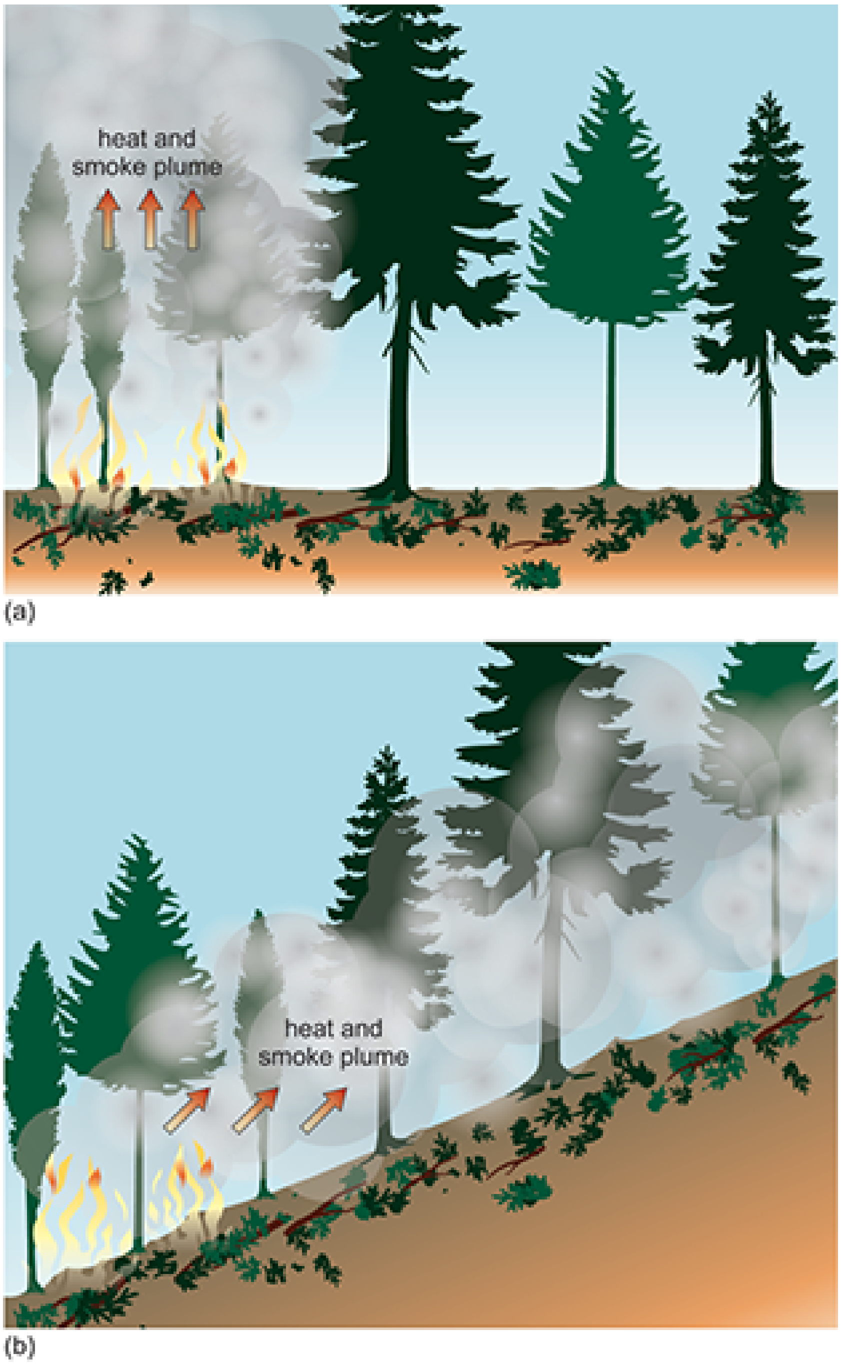

Figure 1 Fire spreads more rapidly uphill than over level ground. The heat in (b) rises in front of the fire more effectively than in (a), so it preheats and dries up-slope fuels, making for more rapid spread.

Finally, the amount of organic matter in the soil can affect fire severity. Where the soil has a high content of organic matter (e.g. peat or landfill sites), a severe fire can cause the soil itself to smoulder, sometimes for weeks and in the case of peat fires, even years. Peatlands store a large amount of CO_2 which is released into the atmosphere when peat burns. Peat fires in south-east Asia (1997, 1998, 2002, 2013, 2014 and 2015) are believed to have accounted for up to 40% of global CO_2 emissions in each of those years.

In general, there are three categories of fire severity:

- low severity surface fires

- high severity stand replacement fires
- mixed severity fires.

Low severity **surface fires** (Figure 2) are usually frequent and burn surface fuels at low intensities, causing low understory vegetation mortality. They are commonly used for land management (as on heather moors); soil surface temperatures rarely exceed 200 °C and litter is scorched but not always consumed. They predominate in grassland and savannahs and burn naturally at annual intervals or in some cases even more frequently than that.

Forest ecosystems surface fires that burn only the lowest vegetation layer and may be composed of grasses, low shrubs, herbs, mosses and lichens (surface fuels), are often called understory fires.

Figure 2 Surface fire

High severity stand replacement fires reduce or kill the majority of the dominant vegetation, they contain both surface fires and active **crown fires** that burn most of the crown of dominant plants, usually trees, and usually ascend from the ground into the forest canopy. They are influenced by wind topography (the way the terrain influences wind speed and direction) and tree density and are the hottest and most devastating: temperatures at the soil surface may reach 800 °C and all litter is consumed, leaving bare earth.

Finally, **mixed severity fires** contain elements of both surface and passive and active crown fires mixed in time and space. Passive crown fires (in which only the crowns of individual or small groups of trees burn), patchy stand replacement fires and low intensity understory/surface fires are common in mixed severity burns.

1.5 Fire frequency

How often a fire re-burns an area, the **fire frequency**, has significant effects on ecosystem structure and function. The essential nature of many ecosystems – the species present, their size, age and density – depends on the frequency of fire. If an area burns before plants have developed fire resistance or before they have started producing seeds, these species may be lost from the ecosystem. Conversely if fire becomes rare, those species that require fire to reproduce or persist, for example, the Fynbos of South Africa, will be lost.

One way of looking at the effects of fire frequency on ecosystems is to look at how an ecosystem would change if fire frequency is altered. For example, savannahs are amongst the most fire-prone biomes on Earth and are characterised by varying mixtures of both tree and grass biomass (Figure 3).

Figure 3 Tarangire National Park, Tanzania (East Africa) showing an ecosystem with a mixture of trees and grassland.

How trees and grasses can coexist in the long term has puzzled ecologists for years. This is because conventional plant succession theory would suggest that highly productive savannahs (with adequate rainfall) are unstable and should progress towards closed canopy forest. The reason why this doesn't happen is because fire frequency controls the recruitment of savannah trees, particularly the growth of saplings into the tree layer. Unlike mature trees, saplings cannot withstand or avoid fire damage because they are too short. Recurrent disturbance by fire therefore stops saplings from reaching a size where they escape through a disturbance-free 'recruitment window' into the canopy layer where they suffer less fire damage and survive.

- What would happen to a savannah biome if fire frequency was drastically increased?
- A high frequency of burning can result in the loss of all trees and the complete dominance of grass.

Conversely if fire is suppressed, for example due to intervention by humans, the increased recruitment of saplings can result in an increase in closed canopy forest at the expense of grass. In some places in Southern Africa, forests have replaced savannah (in areas where water is sufficient) 10–30 years after fire suppression.

The following section looks at the effect of fire on plants. Many plants have fire-adaptive traits that have either arisen in response to different fire regimes (i.e. are adaptations) or have arisen in response to some other environmental factor and persist because of their survival value in fire-prone landscapes. There are some plant species that are dependent on fire for survival.

2 Adaptation of plants in fire-prone ecosystems

Wildfires underpin the dynamics and diversity of many ecosystems worldwide to the extent that some species are dependent on recurrent fires for their existence. This is particularly true of many species of plants that show a diverse array of fire-adaptive traits that allow them to persist in ecosystems subjected to recurrent fires, and are often dependent on fires – or more specifically a fire regime – for successful reproduction.

- What are these types of plant communities called?
- Fire climax communities – a climax community of vegetation that is maintained by periodic fires.

- Recall a fire climax community that you have already come across.
- South African Fynbos.

Flammable ecosystems differ greatly from one another in the mix of plants they support and also in the fire-adaptive traits of the plants present. This diversity is linked to differences in the fire regime. For example, plants in ecosystems that are subjected to crown fire regimes have very different vegetative and adaptive traits from those of plants found in ecosystems that are subjected to low intensity surface fire regimes. Conversely, plants in ecosystems subjected to similar fire regimes have similar vegetative and reproductive traits. Some of the adaptive traits characteristic of plant species subjected to different fire regimes are outlined in the next section.

2.1 Thick bark

Thick bark is a good insulator and protects the sensitive living tissue inside a tree (Figure 4). Some barks are better insulators than others. For example, the cork produced by the Mediterranean cork oak (*Quercus suber*) has air-filled sacs that insulate the tree, keeping the heat out.

Figure 4 Thick bark protects the tree from damage.

Other species that have thick highly insulating bark include the Douglas fir (*Pseudotsuga menziesii*) of North America, some eucalyptus (*Eucalyptus* spp.) from Australia and the giant sequoia (*Sequoiadendron giganteum*) of the Sierra Nevada mountains of California (Figure 5).

Figure 5 The giant sequoia (*Sequoiadendron giganteum*) can grow to over 10 m in width and has spongy air-filled bark between 30 and 80 cm thick. These trees experience fire every 3–35 years and can live in excess of 2000 years; scars from earlier fires are visible on both specimens in this photo.

Thick basal bark as well as self-pruning lower branches are characteristic of trees that live in ecosystems with regular surface or understory fires.

- In what way would these two features be adaptive in ecosystems where surface or understory fires are common?
- Thick bark around the base of the trunk would protect the inner part of the tree (cambium) from damage. The self-pruning of lower branches would ensure that the fire does not reach the live canopy (because there is little or no fuel to burn between the ground and the canopy) and result in a high intensity crown fire.

- Would pine needles that produce a highly flammable litter also be considered an advantage in understory fire ecosystems?
- Yes, because resin-rich pine needle litter increases the probability of fire and so prevents the build-up of understory fuel which could generate a high intensity crown fire.

2.2 Sprouting from insulated buds

Buds may be protected beneath bark, by moist, densely packed leaf bases in aerial organs (as in some palms), by dense tussocks at ground level, or on underground organs such as tubers and rhizomes (soil being an effective insulator against heat).

Regrowth from these protected buds is the key mechanism by which many fire-resistant plants recover. Trees such as *Q. suber* and some Australian eucalyptus sprout rapidly after fire because dormant buds on the stem, protected by bark, are stimulated to grow by loss of foliage; this is called **epicormic sprouting** (Figure 6).

Resprouting from the stem is an advantage in ecosystems with frequent crown fires because it enables quick regeneration of vegetative and reproductive structures.

Figure 6 Epicormic growth on a eucalyptus tree after fire.

Many shrubs sprout from buds on roots or at the stem base and some have **lignotubers** – large woody swellings which hold a mass of buds (Figure 7). They are found on many trees in dry tropical savannahs that are prone to frequent ground fires. A number of South African plants of the genus *Protea*, that occur mainly in the Cape, resprout from lignotubers.

Figure 7 Resprouting lignotuber of the Greek strawberry tree *Arbutus andrachne* (family Ericaceae) from southern Turkey in the eastern Mediterranean Basin (photo by J. Keeley)

Growing points can be protected by plant parts other than bark. For example, some cycads (primitive distant relatives of conifers) and grass trees (*Xanthorrhoea* spp.) of Australia have a growing tip protected by dense rigid leaf bases that cluster round the tip and are glued together with gum exuded by the trees (Figure 8).

Figure 8 Grass tree (genus *Xanthorrhoea*) regrowth after fire.

Grasses are among the most fire-resistant of all plants. The buds of new shoots are insulated by layers of leaf sheaths, or by the soil in species that have underground rhizomes. Grasses are subjected mainly to surface fires and although they burn readily, and can survive frequent fires, few species have an obligate dependence on burning.

2.3 Fire-stimulated seed release

Many pines and hardwood trees are frequently burnt in intense crown fires. They retain either all or a substantial proportion of the seeds on the mature plant. Seeds are held in long-lived woody fruits or cones, which are often attached to trunks or large branches in the canopy and open to release seeds only after fire. This phenomenon is called **serotiny** ('late appearance'). At least 500 different woody trees and shrubs around the world are serotinous. Most occur in the Southern Hemisphere. In the Northern Hemisphere, serotiny is most common among pines. Jack pine (*Pinus banksiana*) in North America has serotinous cones held in the canopy that can withstand temperatures of up to 360 °C for one minute before igniting; heating to above 140 °C melts the resin that keeps the cones closed and liberates the protected seeds inside after the fire has passed (Figure 9). The trees have thin bark and retain their lower branches.

- What would the advantage be to trees in having thin bark and retaining their lower branches?
- Thin bark and the retention of lower branches would facilitate crown fires which are required for seeds to be released from cones which are held in the canopy.

Figure 9 The appearance of Jack pine requires fire to open their cones and release seeds. The trees retain their lower branches and have thin bark, facilitating crown fires

Activity 3 Serotiny and fire

Allow 5 minutes for this activity.

Watch Video 4, which describes how the serotinous North American giant sequoia depends on fire for reproduction.

Video content is not available in this format.

Video 4 Giant sequoias and fire.

Mediterranean pines such as *Pinus halepensis* (Aleppo pine), Australian eucalyptus and many members of the family Proteaceae such as *Banksia* (Figure 10) and *Hakea* spp. (from South Africa and Australia respectively) show serotiny. The Aleppo pine seems to adopt a double strategy; trees simultaneously produce two types of cones: regular mature brown cones that open seasonally during hot dry days and serotinous cones that remain closed after maturation and only open in response to fire (Figure 11).

Figure 10 *Banksia* rely on fire to germinate. Cones open after fires, releasing seeds.

Figure 11 Serotinous pine cones of the Aleppo pine (*Pinus halepensis*) before and after seed release.

Serotiny is advantageous in areas that have high-intensity, fairly frequent fires. However, the degree of serotiny (i.e. the extent to which cones or fruits remain closed) may vary among populations of the same species depending on the fire regime. If fires are too frequent, there is insufficient time to accumulate the next crop of seeds. Conversely, if fires are not frequent or intense enough, seeds will not be released often enough.

2.4 Fire-stimulated seed germination from seed banks

Many plants shed seeds as normal but these do not germinate immediately. They are incorporated into the litter and humus to form a soil seed bank. Some seeds remain in the soil only during the inhospitable time of the year but others can be stored for a few years or even decades. Storage of seeds in the soil is a useful strategy in areas where the interval between fires is longer than the lifespan of the plant. Fire stimulates seeds in seed banks to germinate, the trigger being direct stimulation by heat. This is most common in plants with seeds that have thick, hard seed coats that prevent germination by keeping oxygen and water away from the seed inside (Figure 12). The heat from the fire results in rapid expansion of the seed coat causing it to crack, allowing water and oxygen in and triggering germination.

Figure 12 Seeds of the black wattle (*Acacia mearnsii*) from Australia. The seeds form seed banks in the soil and germinate rapidly after fire.

Often seeds of the same species show variation in the amount of heat they need to trigger germination. This ensures that some seeds (with a low heat threshold) will germinate between fires but if these fail to mature, there is still a seed bank available. The chemical products of fire are also implicated in triggering germination, the most common being smoke. In almost 50% of 301 South African Fynbos species (Figure 13) tested, seed germination was improved after exposure to smoke (Brown et al., 2003).

Figure 13 Mountain Fynbos of the Cape Peninsula in South Africa. Many of the species typical of the Fynbos have seeds that are triggered to germinate by smoke.

2.5 Fire-stimulated flowering

Among fire-resistant grasses, lilies and orchids, fire often stimulates flowering. The result is higher seed production (with fewer seed predators around to eat them) and more seedlings, with a fine open seedbed in which to grow. This strategy is especially common in the Fynbos of South Africa with spectacular post-fire displays in some species; for example, fire lily (*Cyrtanthus ventricosus*) flowering is stimulated by smoke (Figure 14).

Figure 14 The fire lily (*Cyrtanthus ventricosus*) five days after a fire. Flowering can be initiated at any time of the year, being initiated entirely by fire.

As you have seen, plants have a plethora of fire-adaptive morphological traits that allow them to persist after fire and many are dependent on fire for their persistence in a community.

The next section looks at how fire generates habitat complexity and at a landscape scale, may maintain biodiversity by generating a patchwork of different kinds of habitat suitable for a wide variety of both plant and animal species.

3 The response of animals to fire

Information regarding how animals respond to fire is limited in spite of the fact that many species of animals occur in fire-prone areas. Nonetheless, there are a number of behavioural, structural and phenotypic traits of animals that contribute to their ability to live in habitats subjected to fires and even benefit from it. Some of these are discussed next.

3.1 Avoiding fire

Unlike plants, animals are mobile. Large mobile animals are able to move away from the fire while small agile animals are able to take refuge, for example in termite mounds (Figure 15) within the fire zone, or move to places of safety.

Figure 15 Termite mounds which often serve as a refuge for snakes during a fire.

Soil is a good insulator so many animals take refuge in cracks or crevices or in burrows in the soil during a fire.

- In Video 1 you saw two examples of animals that are likely to take refuge in burrows during a fire. What were these?
- Snakes; Tortoises

There is also evidence that some animals are able to detect fires early and avoid them – a behaviour that is likely to be adaptive given the detrimental effects of fire on animals. Some species of bats and possums, for example, appear able to detect smoke even when in torpor (a temporary reduction in temperature and metabolic rate in response to food availability and ambient temperature) and move to safety (Nowack et al., 2016). Frogs appear to be able to recognise the sound of fire and move away (Grafe et al., 2002) and newts have been observed crossing fire fronts to move to unburned areas (Stromberg, 1977).

3.2 Benefitting from fire

Like plants, some animals benefit from the habitats generated by recurrent fires and may even be reliant on them. The new, high quality vegetation regrowth after fires serves as an important food source for many large mammalian herbivores. For example, sable antelope (*Hippotragus niger*, Figure 16) rely on post-fire regrowth to help cope with limited food availability during the dry season. This regrowth has been shown to be crucial for lactating females, in particular (Parrini and Owen-Smith, 2010).

Figure 16 Male sable antelope. Lactating females are reliant on new growth generated by fires.

Many birds, for example the southern bald ibis (*Geronticus calvis*, Figure 17) depend on fires by making extensive use of recently burned grassland for foraging for insects and other invertebrates.

Figure 17 The southern bald ibis (*Geronticus calvus*).

Migrating hummingbirds in tropical ecosystems rely on post-fire flowers to fuel migration (Contreras-Martinez and Santana, 1995) and the black-backed woodpecker (*Picoides arcticus*, Figure 18) inhabits severely burned coniferous forests in North America where it feeds on beetle larvae and nests in trees recently killed by fire (Collard, 2015).

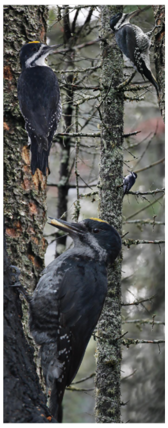

Figure 18 The black-backed woodpecker (*Picoides arcticus*) feeds and nests in recently burned coniferous forests.

The black-backed woodpecker (*Picoides arcticus*) is highly dependent on burned coniferous forests in North America with abundant fire-killed trees. They feed primarily on wood boring beetle larvae which are abundant after the adult beetles have laid their eggs on trees killed by fire. It also nests in trees recently killed by fire (Collard, 2015).

3.3 Morphological traits for detecting fire

An interesting example of a morphological trait in animals that may be adaptive in fire-prone habitats is the presence of fire detectors in a number of insect species. The **pyrophilic insects** are attracted to fires and mate close to fires, lay eggs in killed or weakened trees and their larvae feed on burned wood.

- One species of beetle that is attracted to habitats burned by fire has been mentioned in Video 1. Recall the morphological trait used by these beetles to detect fire.
- They have infrared receptors.

The species shown belongs to the genus *Melanophilia*, also known as fire beetles. They have infrared receptors on the underside of their middle pair of legs, and there is some evidence that they can detect fire at distances of 130 km (Schmitz and Bousack, 2012; Figure 19).

Figure 19 Black fire beetle (*Melanophilia acuminata*) has infrared detectors on the underside of its middle pair of legs.

Other beetles that detect and are attracted to fire, are several species of the longhorn beetles (genus *Monochamus*) which are thought to have smoke receptors on the antennae (Alvarez et al., 2015).

While some animals may benefit from habitats generated by recurrent fires, others benefit from the fire itself. Birds have been seen catching insects fleeing the fire front (e.g. the fork-tailed drongo, *Dicrurus adsimilis*) or walking behind a fire feeding on recently charred invertebrates (some species of egret, genus *Egretta*). A recent study reported that there is even evidence of raptors intentionally spreading fire by picking up and dropping burning branches, thereby increasing the availability of prey (Bonta et al., 2017; Figure 20).

Figure 20 Black kites (*Milvus migrans*) are one species of raptor that have been implicated in intentionally spreading fire.

A substantial impact of fire on fauna is the change in the habitat as the vegetation recovers from fire which can occur over decades. After an intense crown fire for example, all species dependent on unburned forest habitat may disappear and be replaced by a whole new suite of animals that changes as the forest recovers. Across a landscape, the pattern of fire can result in a mosaic of patches where vegetation differs in successional age – some patches being burnt more recently than others. This influences animal population structure and composition as some species go extinct locally and some recolonise older or unburned patches. Nectar-feeding birds, for example, may lose their source of nectar after a fire and move to unburned patches for food. Changes in the spatial pattern of fires may also change extinction risks of birds like Australian honey-eaters that require a specific mix of mature and immature populations of nectar plants. At the landscape scale, fire may therefore increase biodiversity by maintaining a patchwork of habitats suitable for different animal species.

4 Fire, habitat complexity and biodiversity

Many communities, populations and ecosystems are subjected to disturbances such as fire which, as you have seen, can play a significant role in shaping ecosystem structure to the extent that some populations may even cease to exist without fire. Fire disrupts the continuity of a biological community by reducing or eliminating species and populations from some areas in the landscape, and creates the conditions required for new species to move in – in other words, fire opens up gaps in a landscape where localised recolonisation of the burnt area can take place. In effect, disturbances such as fire return communities to the early colonising stages of **ecological succession**.

4.1 Fire and ecological succession

Early successional communities establish themselves relatively quickly after a fire (rapid colonisers) while late successional communities establish themselves much later (Figure 21).

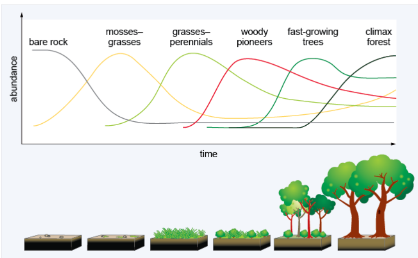

Figure 21 Diagrammatic representation of forest succession over time. There is a steady increase in biodiversity, biomass and thickness of soil layer as succession proceeds, i.e. as time passes.

Although fires open up gaps for early successional communities, community composition – the number and diversity of species present – is profoundly affected by the fire regime, and in particular its frequency and/or intensity.

For example, if fires are frequent the community will be dominated by early-succession, opportunistic, fast-colonising, resistant species because species characterising later successional stages will not be able to become established before the next fire.

- What kind of community would be expected if fires are rare?
- The community tends to be dominated by a few highly competitive, late-succession species. These species outcompete earlier-colonising species and can become established before the next fire.

4.2 The intermediate disturbance hypothesis

The realisation that the frequency of disturbance can influence community structure led to the formulation of the **intermediate disturbance hypothesis** (IDH) (Connell, 1978; Figure 22 below). The IDH proposes that species diversity is generally maximised if disturbance is neither too rare nor too frequent because species that thrive at both early and late successional stages can coexist.

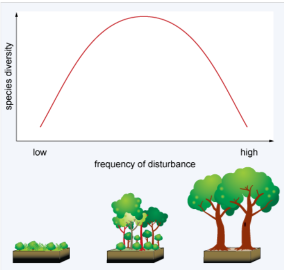

Figure 22 The intermediate disturbance hypothesis. At low disturbance frequency and/or intensity, competitively dominant species exclude competitively inferior species. With high disturbance frequency and/or intensity, only species that quickly colonise and reach maturity survive. At intermediate frequency or intensity both colonisers and competitors coexist.

Connell's original paper has received more than 4000 citations and is still referenced in important scientific papers. Many studies have empirically validated the IDH, particularly for marine systems. However, there are also an increasing number that show little support and this has led to a great deal of controversy regarding its validity in explaining the relationship between disturbance and species diversity. For example, it can be argued that tropical forests show high diversity even though natural disturbance is minimal.

Whether or not the IDH holds appears to depend, to some degree, on scale (whether on a local or geographical scale) and the type of disturbance. For example, at a small local scale species diversity is often maximised at a high frequency of fire rather than at an intermediate or low frequency.

- Give an example where frequent fire is necessary to maintain species diversity.
- The Fynbos in the Cape region of South Africa.

However on a larger scale, disturbances of intermediate frequency and/or intensity may generate diversity. For example, a fire of intermediate or mixed severity could increase diversity by generating spatial heterogeneity within a landscape.

This is because a mixed severity fire will result in a complex of patches in a landscape. Patches differ in severity of burn and include unburned patches, low severity burn patches, moderate severity burn patches where perhaps one-third to two-thirds of the vegetation is killed, and high severity burn patches where almost all the vegetation is killed (Figure 23). In this case, the IDH may not hold on a local scale (within patches) because species richness within a small area may decline (for example, in severely burnt areas). However, on a larger landscape scale a fire of intermediate severity may increase species diversity. This is because areas or patches that differ in burn severity, and that are at different stages of post-fire change, would sustain more species with different disturbance sensitivities.

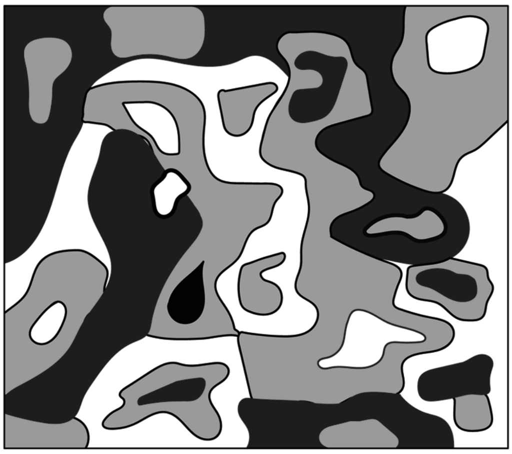

Figure 23 Fire can generate a mosaic of patches within a landscape where patches differ in burn severity thereby generating diversity (white patches -low severity burn; grey patches -moderate severity burn; black patches-high severity burn)

Although the IDH is controversial, the idea that landscapes with greater heterogeneity in size, age, and burn severity of post-fire patches support a greater diversity of species, has led some researchers to propose that a diversity of fire regimes across a landscape (named *pyrodiversity*) is necessary to maintain biodiversity.

4.3 The pyrodiversity-biodiversity hypothesis

Without fire, ecosystems that operate to a predictable seasonal or cyclical pattern can, over time, become uniform in how they look and function. Disturbances such as fire break up this uniformity. The pyrodiversity-biodiversity hypothesis recognises that a complex fire regime (that varies in frequency and intensity across the landscape) can create habitat complexity by establishing shifting mosaics of patches of different size and post-fire age of regenerating vegetation. This promotes and maintains diverse plant functional types and their associated fauna thereby generating diversity.

Patch mosaic burning is often advocated in fire ecology as a way of increasing biodiversity. It is based on the premise that a complex habitat provides a diversity of microclimates, resources and shelters and hence supports a diversity of plant but also animal species. As you have already seen, many animals exploit opportunities presented by fire, and the diversity of conditions that occur during recovery following a fire event would allow a succession of species to exploit these conditions. For example, in the forests of northern Canada, deer, mice, moose and black bear are found exploiting vegetation characteristic of early post-fire stages, while northern red-backed voles and caribou are more typically found in habitats characteristic of later post-fire stages of more than 50 years old. A landscape that includes both early post-fire stages and later stages of post-fire recovery therefore supports more species.

There is some evidence that in the absence of the patch mosaic created by fires, diversity declines significantly. For example, it is believed that the decline in small mammal species in central Australia, where clearing for agriculture has not occurred, is a consequence of the loss of fine-scale habitat mosaics created by Aboriginal landscape burning (e.g. Ziembicki et al., 2014). In the absence of these frequent, less intense fires, large, intense and infrequent fires caused by lightning strikes have obliterated the mosaic of burnt patches of varying ages that the Aboriginal people once maintained, resulting in a largely homogenised landscape supporting fewer species of plants and animals.

However, the ‘pyrodiversity begets biodiversity’ argument has also been criticised for lacking a solid empirical or theoretical basis. Several recent studies suggest that fire management strategies aimed at maximising pyrodiversity may actually threaten some species, e.g. Taylor et al., 2012; Nimmo et al., 2013; Kelly et al., 2012.

5 Climate change and fire ecology

Wildfires are integral in shaping the structure and distribution of fauna and flora in many habitats, giving rise to self-regulating ecosystems. Native species and their interaction have evolved along with fire and are dependent on the conditions created by fire. However, it is becoming increasingly evident, that human activity and the impact of human-induced changes in fire regimes, have caused a shift in this stable state.

Over the last few years there have been an increasing number of devastating wildfires reported in the media. Research is now showing that one of the main causes of these bigger, more frequent fires is global warming. Higher temperatures result in drier forests, longer periods of dry weather, more intense winds, more intense storms and higher incidents of lightning strikes. Added to these more obvious effects of a warming climate, other, less obvious factors, are also playing a role. In the Western United States and Canada, longer periods of warmer temperatures have resulted in large increases in the numbers of bark beetles. Although the beetles are native to the region the hot dry weather has water-stressed trees and beetle numbers have exploded, killing the trees and increasing the amount of fuel available to sustain wildfires. Similarly, insect outbreaks in California resulted in the death of more than 300 million trees between 2010 and 2017, turning them into kindling for catastrophic forest fires.

Possibly of greatest concern is the feedback process generated by a warming climate. Warming causes more fires which release more greenhouse gases which causes more warming.

Although it is difficult to predict the full effects of climate change, it is becoming evident that the fire regimes of many ecosystems are changing with respect to both intensity and frequency - such changes in turn will have significant effects on the type and distribution of fauna and flora that inhabit them. For example, in Africa, drier conditions due to global warming will result in less biomass to fuel savannah fires. This, together with increasing CO_2 levels which favours the spread of less flammable C4 grasses, could result in a reduction in fire frequency in these ecosystems and the expansion of forest into savannahs.

Conclusion

Natural fires occurred long before humans emerged and flammable ecosystems predate anthropogenic burning by millions of years. In fact, we cannot understand ecosystem distribution without including fire as a process in the natural history of our planet. During most of Earth's history fire has been integral to the evolution of fauna and flora and is still a major influence on biodiversity.

Many biodiverse ecosystems are fire-prone and include boreal forests, eucalyptus woodlands, shrublands, grasslands and savannahs. The diversity of form found in these ecosystems is due largely to the diversity of natural fire regimes.

Different fire regimes produce different landscape patterns and select for different plant attributes, so it follows that changes in the fire regime within a given landscape will have significant consequences for species composition, biodiversity and hence ecosystem function.

Humans have had profound impacts on fire regimes by increasing fire frequency in some cases and suppressing fire in others. The impact of this on ecosystems is still unclear but because of the long evolutionary history of fire in many ecosystems, species are adapted to a particular fire regime rather than to fire itself and any departures from that regime can have devastating impacts on the sustainability of many ecosystem components.

This OpenLearn course is an adapted extract from the Open University course S397 *Terrestrial ecosystems*.

Glossary

fire climax communities

: A climax community of vegetation that is maintained by periodic fires.

fire regime

: The temporal and spatial characteristics of the fire and the impact it has on the landscape.

fire severity

: A measure of the impact of a fire on the ecosystem in terms of the degree to which the ecosystem is altered or disrupted by fire.

surface fires

: Fires that burn only the lowest vegetation layer which may be composed of grasses, low shrubs, herbs, mosses and lichens (surface fuels). In forest ecosystems surface fires are often called understory fires.

crown fires

: Fires that burn the upper tree or shrub canopy. In most cases the understory is also burned. Depending on the species, a crown fire may or may not be lethal to all dominant vegetation. A crown fire may be continuous burning the whole canopy (active crown fire) or occur in patches so only the crowns of individual or small groups of trees burn (passive crown fire).

mixed severity fires

Fires that contain elements of both surface and crown fires in time and space so that in some areas there is little damage to overstory vegetation, other areas exhibit considerable overstory damage but not complete stand replacement and in other areas, stand replacement occurs.

fire frequency

The recurrence of fire in a given area (number of fires per unit time).

epicormic sprouting

Resprouting of new shoots from buds beneath the bark on the trunk or branches of trees.

lignotubers

A rounded woody growth at or below ground level on some shrubs and trees that grow in areas subject to fire or drought. They contain a mass of buds from which new stems sprout and food reserves in the form of starch.

serotiny

Delayed seed release by retaining the seeds in a woody structure.

pyrophilic insects

Insects attracted to fire.

ecological succession

(1) Directional change in ecosystem structure and functioning resulting from biotically driven changes in resource supply. (2) The process of change in species structure of an ecological community over time.

intermediate disturbance hypothesis

Proposes that species diversity is maximised if disturbance is neither too rare or too frequent.

patch mosaic burning

Strategy where fire is manipulated to create a mosaic of patches representative of a range of fire histories to generate heterogeneity across space and time.

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