

MULTIDISCIPLINARY

Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth's flora

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ABSTRACT

Fire became a defining feature of the Earth's processes as soon as land plants evolved 420 million years ago and has played a major role in shaping the composition and physiognomy of many ecosystems ever since. However, there remains a general lack of appreciation of the place of fire in the origin, evolution, ecology and conservation of the Earth's biodiversity. We review the literature on the presence of fire throughout the Earth's history following the evolution of land plants and examine the evidence for the origin and evolution of adaptive functional traits, biomes and major plant groups in relation to fire. We show that: (1) fire activities have fluctuated throughout geological time due to variations in climate, and more importantly in atmospheric oxygen, as these affected fuel levels and flammability; (2) fire promoted the early evolution and spread of major terrestrial plant groups; (3) fire has shaped the floristics, structure and function of major global biomes; and (4) fire has initiated and maintained the evolution of a wide array of fire-adapted functional traits since the evolution of land plants. We conclude that fire has been a fundamental agent of natural selection on terrestrial plants throughout the history of life on the Earth's land surface. We suggest that a paradigm shift is required to reassess ecological and evolutionary theories that exclude a role for fire, and also there is a need to review fire-suppression policies on ecosystem management and biodiversity conservation in global fire-prone regions.

Keywords: angiosperms, ecosystems, fossil charcoal, palaeo-atmospheric oxygen, terrestrial floras, wildfire

INTRODUCTION

Wildfires are widespread in the modern world, with much of the Earth subject to periodic fires [1]: about 60% of the Earth's land surface is currently burnt over a given 15-year period [2]. Fire-prone ecosystems have historically been interpreted in terms of climate and other biogeographical factors or recent anthropogenic disturbances [3,4], with little consideration of the evolutionary and ecological role of fire in shaping plant functional types and community assembly. Ecologists have long documented the apparent adaptation of plants to fire in fire-prone ecosystems [5,6], even though knowledge on the ecology and evolution of floras in relation to fire has largely been omitted from textbooks on ecology, conservation biology and biogeography [7]. Despite extensive research on this topic, much scepticism remains. For example, Hopper *et al.* [8] criticized current studies on fire ecology conducted within the 'adaptationist paradigm' and argued that 'we still

lack the evidence ... for a long history of fire as an evolutionary force at local to broad spatial scales'.

Such a view either ignores the relevance of fire in the evolution of plants [9] or rejects the evidence that fire has been a significant ecological and evolutionary force that has shaped past and current terrestrial ecosystems [10]. This is probably a result of reluctance by researchers to accept relevant results outside their particular discipline. For example, paleontologists (Carpenter *et al.* [11]) identified fossil charcoal at 75–70 Ma among Proteoid leaves and pollen, but did not accept the indirect evidence from ancient trait reconstruction for on-plant seed storage then [12] as they were unable to locate burnt cones as well. Another possible impediment is the equivocal results in some studies on whether plants promote or simply tolerate fire [13]. However, the real test is two-fold: whether fire-related traits improve fitness in the presence of fire and whether the evolution of these traits coincided with the presence

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of fire [12]. What support then is there for the fire-adaptationist ‘programme’? We examine the proposition that the history of terrestrial biodiversity may only be understood in the context of fire. We show that the antiquity of fire and fire-adapted traits, and the coincidence of peak fire activities with the diversification of major plant groups, point to a pivotal role for fire as an agent of natural selection in the origin and evolution of terrestrial biota. Pyne [14] concluded that ‘fire is a natural process that is as fundamental to ecosystems as rain and the sun and (thus) we need a theory that rises out of this fact’. This leads to the formulation of a theory that is the subject of this review: fire has been a fundamental agent of natural selection in the evolution of terrestrial plants.

In this review, we first explain the key elements that maintain fire as an ecosystem process. We further examine evidence (a) for the continuous presence of fire since the origin of land plants, (b) support for the hypothesis that fire has shaped the floristics, structure and function of major global biomes and (c) that fire promoted the origin and evolution of terrestrial plants. In support, we examine the origin and evolutionary history of two fire-related functional traits: on-plant seed storage/release and fire-stimulated germination. We briefly consider flammability and the neglected field of plant–animal relations regarding the impact of fire. Relevant future research directions are proposed.

FIRE AS AN ECOSYSTEM PROCESS

Three key elements are required to sustain a fire: fuel, ignition source and oxygen (O_2) to maintain combustion (Fig. 1A). The origin of fire is directly tied to the origin of land plants, as these generate two of the three elements: fuel and O_2 . The most important natural heat source to ignite fuel is lightning strikes that have been present throughout the history of the Earth. Globally, there are currently about 1.4 billion flashes per year (NASA, thunder.msfc.nasa.gov). For example, in the monsoon forests, the most common cause of fires is lightning strikes. Though an immediate spread of fire after lightning strikes can be prevented by rain, fuel may continue to smoulder and lead to fire spread after the storm [15].

Evolution of primary producers as fuel

Fire has been a feature of the Earth’s dynamics since the origin of land plants. The earliest megafossils of land plants were discovered in strata of the Late Silurian age, 420 million years ago (Ma) [16]. Evidence for the earliest wildfires is known from the Late Sil-

urian in the form of charred remains of a rhyniophytoid plant form [17]. Thus, wildfires commenced on the Earth simultaneously with the origin of land plants that provided combustible fuel and released sufficient O_2 to support fire. In the modern world, there are predictable relationships between climate (precipitation, temperature and seasonality) as it interacts with lightning frequency and the fire regime, especially fire frequency, that dictate the type of vegetation present [Figs 1B and 2]. It is likely that this interaction and changes in the fire-proneness of vegetation as a result of evolutionary changes in the terrestrial flora have influenced fire activity on the Earth over the past 420 million years [15,18,19].

The earliest land plants were mainly herbaceous plants that were capable of ignition, except later on when under deep shade in wet forests [20], and could provide a small amount of fuel to carry a surface fire [21]. However, it is unlikely that fires were widespread or intense until the evolution of woody shrubs and forest trees [22]. Fire only became frequent in the Devonian when leaves and woody stems evolved [23]. The evolution of wood in terrestrial vascular plants occurred in the middle Devonian, 370 Ma [24], and the emergence of woody lycopsid forests [25] represents the first extensive and continuous fuel loads able to sustain and carry a fire for a significant period over broad spatial scales. The evolution of cordaitaleans and conifers coincided with widespread acidification beginning in the Carboniferous, 360 Ma [26]. The emergence of seasonally dry woodland provided sufficient fuel for broad-scale fires, evidenced by an increase in the abundance of charcoal [22] (Fig. 2). For the first time, sufficient and continuous fuel allowed large forest fires to develop [15]. More importantly, abundant fuel, high atmospheric O_2 and strong seasonality [27] combined to produce widespread and regular fires conducive to the evolution of fire-tolerant seed plants (Figs 1B and 2).

Fluctuations in atmospheric oxygen as a major determinant of fire activity

O_2 levels in the atmosphere closely determine the probability of biological material burning [28]. An increase in O_2 facilitates ignition of fuel and increases the combustion rate that leads to greater heat flux from burning fuels. Belcher *et al.* [28] estimated that natural plant material requires a minimum concentration of 16% atmospheric O_2 to ignite and sustain combustion. Burn probabilities remain low until atmospheric O_2 levels reach 19%, when they escalate but then they slow again and plateau at 23%. The level of O_2 in the atmosphere is believed to

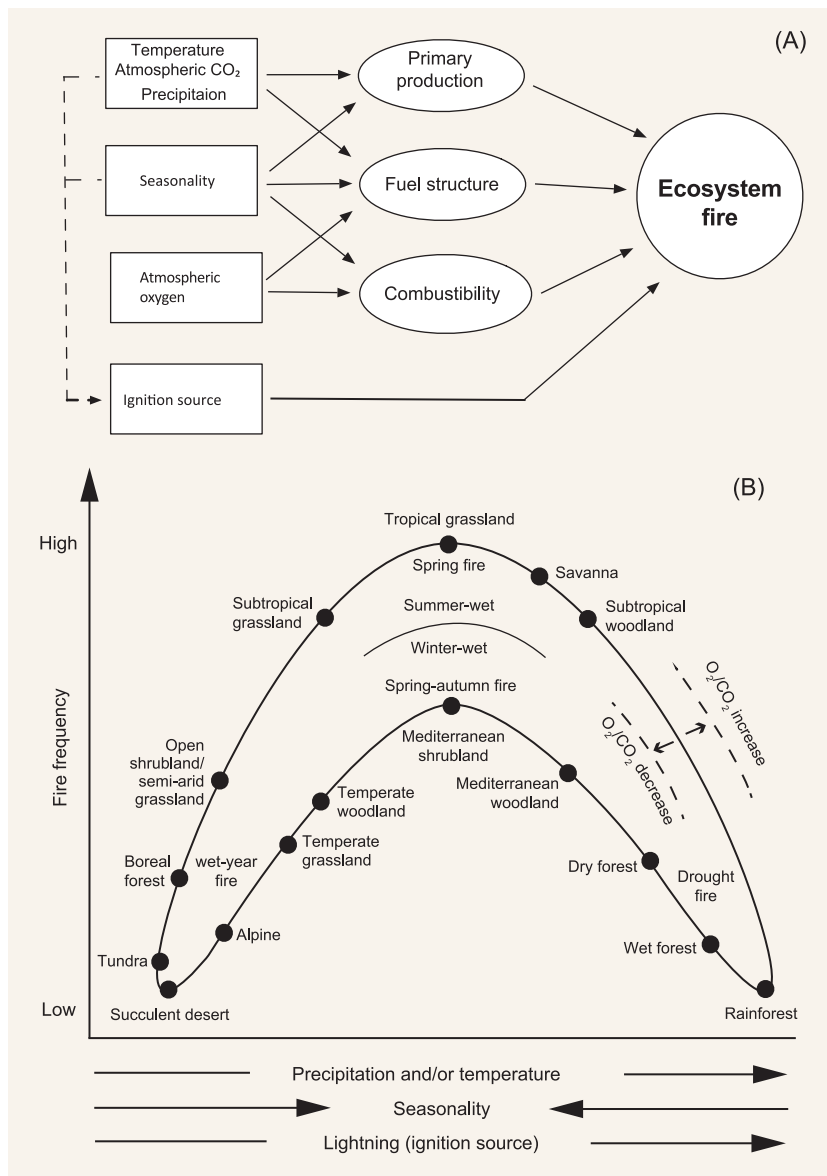


Figure 1. (A) Scheme of factors controlling fire as an ecosystem process. Sufficient primary production (a function of climate, nutrients and CO₂ level) as fuel is required to sustain a fire, but seasonally dry climates, in annual to decadal cycles, are required to remove moisture in green vegetation and convert it into combustible fuel. O₂ is essential for combustion; the level of O₂ in the atmosphere also influences the level of combustible fuel. Lightning, as the usual ignition source (prior to human activity), is also essential. The temporal and spatial structure of fuel determines the specific fire regime that shapes the evolution of plants. (B) Major vegetation types, characterized by differences in fire frequency and seasonality, are produced by the interaction of gradients in (a) precipitation and (b) temperature (they often are positively correlated except it is negative with change in altitude), (c) seasonality and timing (winter or summer wet) and (d) lightning occurrences. Historically, gradients of O₂ and CO₂ have also impacted on the position of the current boundaries of the fire regime ‘boomerang’ illustrated by the broken lines.

have risen to values not much less than 20% by 540 Ma [29]. While this level is sufficiently high to sustain fire on the Earth until the Late Silurian, 420 Ma. It was not until 60 My later in the early Carboniferous, when formation of early forests provided sufficient fuel for fossil charcoal to be identified in geological strata, that the first recorded link between the presence of fire and fire-

tolerant vegetation was provided. O₂ levels at the time were approaching 16%.

Despite wide disagreement on the actual concentration of paleo-atmospheric O₂, as it lacks proxies in reconstruction, the general trend of paleo-atmospheric O₂ fluctuation is consistent across the major models [30,31]. Fluctuations in O₂ levels have dramatically affected past fire regimes, and the

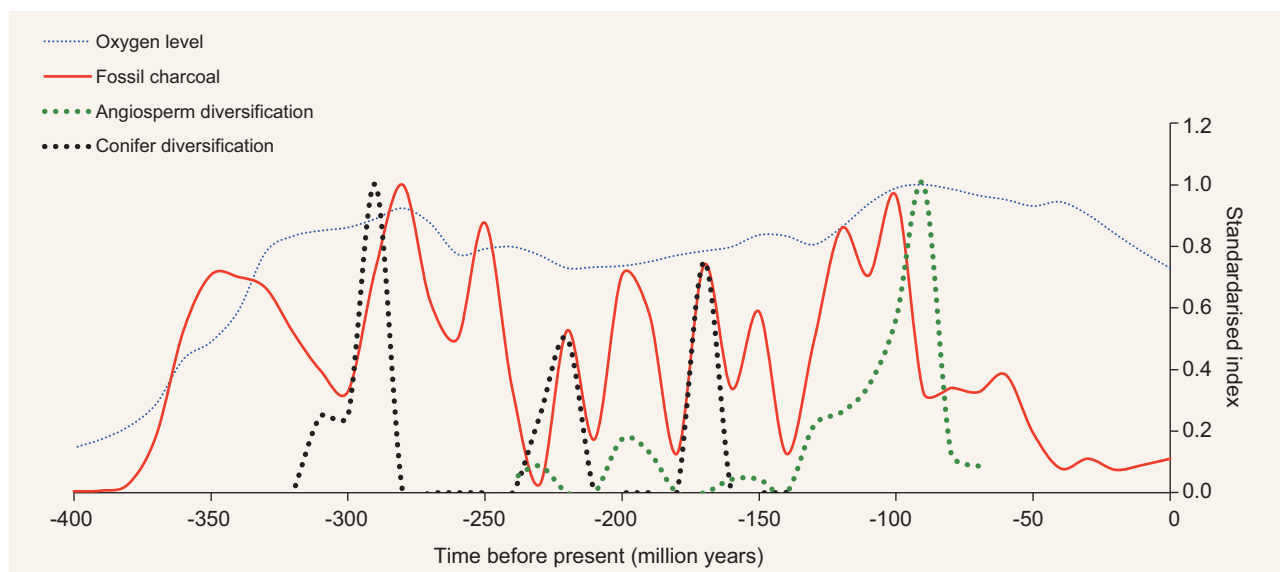


Figure 2. History of fluctuations in atmospheric O_2 and fossil charcoal over the last 400 million years and diversification of the major plant groups (conifers and angiosperms). Data sources: O_2 from [30]; fossil charcoal from [32]; diversification of conifers (origin of new families, both extant and extinct taxa) from [79]; diversification of angiosperms (origin of new plant orders) from [105]. Data were standardized to values between 0 and 1 to facilitate comparison using the formula $(\text{value} - \text{minimum})/(\text{maximum} - \text{minimum})$.

amounts of fossil charcoal varied closely with the estimated atmospheric O_2 levels (Fig. 2). During periods when atmospheric O_2 was elevated, for example in the Permo-Carboniferous when atmospheric O_2 is believed to have been high (likely reached $>30\%$) [30], fires were not only widespread and frequent [32], but also intense, in the form of crown fires [27]. Climate, via effects on precipitation, temperature and seasonality that control the extent to which potential fuel is converted into combustible fuel, has only had a more significant control than O_2 on the occurrence of fire during periods of low atmospheric O_2 . Throughout much of the Triassic and Jurassic periods, atmospheric O_2 levels were lower [30,31] (Fig. 2). In contrast, the Cretaceous, essentially from 120 to 80 Ma, was again highly flammable as a consequence of warmer temperatures and elevated O_2 levels (Fig. 2). The steady decline in O_2 from the end of the Eocene meant climate increasingly took over control of the fire regime in the Cenozoic.

Carbon dioxide, precipitation and seasonality as controllers of fuel properties

Atmospheric carbon dioxide (CO_2) remained at higher-than-present levels (c. 400 ppm) throughout the Phanerozoic, with CO_2 levels as high as >1000 ppm in the Middle Cretaceous [33]. Elevated CO_2 has been shown to promote aboveground biomass production [34] through increased photo-

synthetic rates and greater water-use efficiency [35]. Elevated atmospheric CO_2 may also promote tree branching [36] that increases the surface-volume ratio of fuel and facilitates fire spread [37].

The fire regime has a strong relationship with precipitation patterns, as high rainfall coupled with strong seasonality promotes biomass production, rapid ignition and intense fire [38]. In modern ecosystems, precipitation variability, in annual to decadal cycles, influences fire occurrences more strongly than does total annual precipitation [39]. For example, a long dry season every year creates fires at one- to five-year intervals in high rainfall areas of northern Australia that is dominated by the monsoon, which delivers ~ 1400 mm in four months followed by hot, dry weather for the rest of the year [40]. Precipitation has been variably seasonal away from the Equator since the Carboniferous, possibly as a result of fluctuations in atmospheric CO_2 and continental drift affecting distances of land from the oceans [41]. Falcon-Lang considered that Carboniferous fires in progymnosperm communities were associated with a monsoonal climate [27]. Francis [42] suggested that the mild surface fires among Jurassic gymnosperm forests were associated with moderate winter rain and summer drought, similar to current Mediterranean-type climates. The Early Cretaceous Period may have had reduced seasonality due to strong jet-stream transport of moist air during that time [41], but fire occurrences were maintained by the elevated O_2 levels and frequent lightning then.

PRESENCE OF FIRE THROUGHOUT THE EARTH'S HISTORY

Evidence for paleofires is preserved in the form of charcoal deposited in sediments. Fossil charcoal not only provides direct evidence of paleofire events, but it also gives significant insights into the evolution of terrestrial ecosystems and the atmosphere [32]. Charcoal has been recorded from all geological strata of sedimentary origin in all continents since the Silurian Period (Fig. 2), indicating the persistent presence of fire on a global scale [32,43,44]. Apart from the modifying influence of climatic variations, atmospheric O₂ levels have been a strong determinant of paleofire activities since the Devonian, 400 Ma [22]. As atmospheric O₂ levels have fluctuated over the last 400 My, so fire activities have waxed and waned throughout that time. By 25 Ma, seasonality took over from O₂ levels as the major determinant of the incidence of fire.

A Silurian origin for fire

Charcoal was identified from Silurian sediments soon after plants colonized land, 420 Ma [17]. Fire activities gradually increased in the Devonian, characterized by mild surface fires [21] that may have been the outcome of rising O₂ levels and positive feedback, in terms of available fuel, from fires themselves [22]. Evidence for intense fires has not been found in the Devonian fossil record [21,32], despite the existence of woody shrubs and small trees [45] and lowland forests dominated by progymnosperm trees [46] by the Middle to Upper Devonian. The occurrence of fires of low intensity in the Devonian, despite high fuel loads, may have been the result of non-seasonal humid climates [47], which discouraged ignition, and low ambient O₂ that limited fire intensity and spread.

Highly flammable Permo-Carboniferous period

Extensive charcoal in the Early Mississippian indicates well-established fire-prone systems [21,32]. With the appearance of the first woody shrub and tree forests in the Middle to Upper Devonian, the steady rise in atmospheric O₂ through the Late Devonian and Early Mississippian to a level comparable with extant levels (21%) allowed widespread burning for the first time [15,32]. The rise in O₂ was likely the result of elevated photosynthesis by the now largely vegetated land surface and positive feedback on productivity from fire itself. A surge in fossil charcoal from the Middle Carboniferous through to the Late Permian [32] indicates that fires were

widespread and frequent during this time. For 90 My, extending from the Mississippian to Late Permian, the fuel and climatic conditions were conducive to combustion—high temperatures, moderate rainfall and strong seasonality [15,17]. More importantly, with high atmospheric O₂ levels (28% in the Middle Permian, Fig. 2), there was sharply increased global fire activity [21] that had profound effects on the evolution of terrestrial plants—a legacy that remains in modern ecosystems.

Less flammable Triassic and Jurassic

Fire activities were relatively low throughout the Triassic to Jurassic due to lower atmospheric O₂ levels [32] (Fig. 2). Thus, at 250–240 Ma, charcoal records reached an all-time low. Nevertheless, charcoal evidence indicates that fires were still present throughout this period on a global scale. For example, fossil charcoals are reported from the Late Jurassic (Kimmeridgian Stage) in Western and Central Europe [48], Late Triassic (Chinle Formation) in south-eastern Utah [49] and Middle Jurassic in China [50]. In environments with low ambient O₂ levels, climate might have had a stronger influence on fire regimes. Triassic and Jurassic climates have been described as strongly seasonal [26] so that burning activity was attributable to dry season ignition of denser fuels under relatively moist conditions, coupled with a shift in fuel from broad-leaved to narrow-leaved plant assemblages [51]. Most Jurassic fires would have been of the mild surface type [48].

The fiery Cretaceous

Fire activities were low at the beginning of the Cretaceous, following the trend in the Jurassic (Fig. 2). Low atmospheric O₂ levels together with weak seasonality [39] did not promote ignition and therefore retarded fire occurrences during the Late Jurassic to Early Cretaceous. With the rapid increase in O₂ levels from <21% to 28% during the Valanginian (140 Ma) to Turonian (94 Ma), fires become widespread, frequent and intense [19]. Brown *et al.* [43] collated literature on global Cretaceous charcoal records and showed that terrestrial sediments preserved abundant charcoal from the Valanginian throughout the Cretaceous. While these data are biased towards the northern hemisphere, recent reports from the southern hemisphere indicate abundant charcoal and wildfire in Cretaceous sediments here as well [52]. Atmospheric CO₂ concentrations and temperatures also were elevated during the Early to Middle Cretaceous [53]. Higher atmospheric

CO₂ levels would have led to an increase in primary production and therefore greater fuel loads. Combined with globally warm temperatures during this period [54] and high atmospheric O₂ levels, these conditions made the Cretaceous one of the most flammable periods in the Earth's history. Extensive wildfire activity in the Cretaceous coincided with major changes in the Earth's flora associated with the rise to dominance of the angiosperms, indicating a major role for fire in angiosperm diversification [55].

Fire-prone contrasts in modern ecosystems

Despite higher-than-ambient levels of atmospheric O₂, global fire activities gradually declined from the fiery Cretaceous to low levels since the Early Paleogene through to the present (Fig. 2), coinciding with the spread of modern fire-resistant tropical forests [56]. Bond and Midgley [57] suggested that fire-resistant broadleaf forests reduced fire because the closed canopies created deeply shaded and moist understories that reduced the accumulation of flammable surface fuels in tropical regions with uniform and high rainfall. On the other hand, the onset of Mediterranean-type climates in the Early to Middle Miocene [58] and monsoon climates in the late Middle Miocene initiated strongly fire-prone ecosystems in the temperate and subtropical latitudes [59]. Both mediterranean and monsoon climates are characterized by prolonged dry seasons with substantial rain occurring in the wet season, allowing accumulation of abundant combustible fuel. The global origin of savannas centred about 8 Ma has been hypothesized as the outcome of positive feedback from fire limiting tree recruitment in a low-CO₂ atmosphere and expansion of C₄ grasslands [60]. Conversion of fire-adapted traits from non-sprouting to resprouting and from seed storage to non-storage enabled surrounding clades to invade and diversify into these early savannas [61,62].

FIRE SHAPES THE STRUCTURE AND FUNCTION OF GLOBAL BIOMES

Fire is a key ecological process in major global biomes and has played a major role in the composition and physiognomy of many ecosystems [63,64]. Currently, fire-prone ecosystems cover ~40% of the land area [63] and fire regimes control the distribution, community structure and function of numerous biomes (savannas and tropical grasslands, mediterranean shrublands and woodlands, temperate sclerophyll forests, boreal coniferous forests). Increasing evidence indicates that fire has been an

important ecological and evolutionary process in these ecosystems (Table 1).

Fire-adapted mediterranean floras

Mediterranean-type climate (MTC) regions are characterized by strong seasonality with most of the precipitation in winter under mild temperatures and a pronounced dry season in the hot summer, resulting in abundant fuel (via primary production) accumulating in winter that is converted to highly flammable fuel in the hot dry summer. Coupled with high levels of wood, sclerophylly, leaf retention and tannins that reduce rates of decomposition, there is also a considerable buildup of highly combustible litter [72]. Fire is one of the most significant ecological processes in MTC regions, dominated by fire-prone ecosystems that comprise a diverse array of woody, herbaceous and graminoid vegetation types [73]. Plants in MTC regions have extraordinary adaptations to recurrent fire through predominantly crown fire regimes, though California also has substantial forests of tall conifers that are prone to surface fire regimes [73]. All MTC regions, except possibly Chile, exhibit a remarkable degree of evolutionary convergence in response to fire in the structure and function of their floras [73]. This is reflected in diverse functional traits allowing plants to persist in fire-prone environments, highlighting the intimate role that fire plays in directing the ecology and evolution of plant traits and community assembly in MTC ecosystems. It has been hypothesized that varying rainfall reliability accounts for differences in fire responses, such as levels of serotiny, in MTC ecosystems [58]. However, adaptations of plants to fire in MTC ecosystems and the presence of fire-related traits long predate the current climate regime, reflecting the antiquity of fire in these regions [67].

MTCs are widely assumed to have been in place in all five MTC regions only recently [73]. Hopper and Gioia believed that a Mediterranean climate was first present in south-western Australia no earlier than 20 Ma [74]. However, both molecular [12,71] and fossil evidence [11] indicate that fire-adapted floras dominated by Proteaceae shrublands have existed in the region at least since 76 Ma. While the onset of MTCs in western North America and the Cape region are believed to have occurred from the Early to Mid-Miocene, evidence suggests that fire-prone, Mediterranean-type shrublands predated the onset of MTCs by at least 50 My [66]. Thus, many woody sclerophylls that dominate vegetation in MTC regions are much older than the posited onset of MTCs in the Miocene-Pliocene.

Table 1. Antiquity of fire in some major ecosystems (based on fossils and/or trait-assignment techniques on dated phylogenies accepting that assignments refer to the supporting branch).

Fire-prone ecosystem	Fire present (Ma)	Dated fossils (+ charcoal) and lineages (+ fire-adapted traits) used as evidence	References
Coniferous forests in northern hemisphere	134, 126, 89	<i>Pinus</i>	[53,65]
Sclerophyll shrublands/woodlands in central and south-western Australia	101, 88, 76, 37	Anarthriaceae-Restionaceae, Proteaceae, other sclerophylls	[11,12]
Sclerophyll shrublands and associated geophytes in South Africa	81, 70, 50, 28	Restionaceae, Haemodoraceae, Xanthorrhoeaceae, Orchidaceae, <i>Protea</i>	[62,66,67]
Eucalypt woodland/forest in Australia	62	<i>Eucalyptus</i>	[68]
Savanna in South America	17, 5, 2	<i>Mimosa</i> , Melastomataceae	[61]
Savanna in South Africa	15, 5, 2	<i>Protea</i> , <i>Disa</i> , diverse geoxylic taxa	[62,69,70]
Savanna in northern Australia	9	<i>Banksia dentata</i>	[71]

For example, many genera in the family Proteaceae and Myrtaceae that dominate current Southwest Western Australia fire-prone ecosystems have a Paleogene origin [68,75].

A traditional view is that mediterranean floras are not actually adapted to the fire component of these regions, but to summer drought, as fire is considered too recent a phenomenon [8]. However, current research indicates that it is not MTCs *per se* that control the function and structure of vegetation in mediterranean regions, but fire [67]. The interaction between fire activities and climate is complex and climate is not a simple determinant of the fire regime [2]. Initially, the development of fire-prone systems was not controlled by a drying climate, but rather by changing levels of atmospheric O₂ [76], as high O₂ allows even sodden vegetation to burn [77]. Consequently, the relationship between fire activities and climate is to some extent decoupled [78]. Reconstructing the origin of fire-related traits in mediterranean regions shows that many fire-adapted traits have a Cretaceous or Early Cenozoic origin [12,68,71,79], highlighting the antiquity of fire in MTC regions. Fire-adapted biomes under MTCs, at least in south-western Australia [11,12] and the Cape [66], are much older than the MTC itself.

Fire-prone savanna and grassland biomes

Almost 30% of the Earth's land surface is dominated by grasses that use the C₄ photosynthetic pathway [80], and these biomes are among the most fire-

prone ecosystems in the world [2,5]. Many of these grassy ecosystems exist in regions where the climate and soils would support closed forests in the absence of fire [4,39]. Early ecologists believed that the forests in South Africa had been cleared by Iron Age farmers causing their replacement by the earlier successional grasslands that were maintained through human-lit fires [4]. Similarly, in Madagascar, the grasslands that cover much of the island were long thought to be the consequence of deforestation following human settlement a few thousand years ago [81]. Only recently has it become clear that fire-dependent (sub)tropical-grass systems predate human deforestation by millions of years and that fire shaped the regional vegetation long before human use of fire [63].

C₄ grasslands began to replace the C₃ grasslands in Africa 16–14 Ma, with a marked expansion at 9–4 Ma [82], as a response to the onset of summer rain, declining CO₂ concentrations, increasing drought associated with falling temperatures, more frequent fire and intensified herbivory [83,84]. By maintaining growth in a low atmospheric CO₂ coupled with strong seasonality, C₄ grasses provided sufficient fuel to promote frequent fire [85]. Fire frequencies increased to such an extent that previously dominant woody species adapted to infrequent fire now had insufficient time to complete their life cycles and only herbs and grasses could survive [84]. This feedback mechanism led to rapid spread of C₄ grasslands in the late Miocene/Pliocene [60,86,87].

The ancestral range of the woody shrub, *Protea* (Proteaceae), arising 28 Ma, was the Cape fynbos [88] with sufficiently frequent fire and

seasonality to promote serotiny, fire death of adults and post-fire recovery via seedlings [62]. Proteas did not invade the grasslands until 13 Ma and further net speciation was delayed until 7 Ma. The reasons for this delay may have been due to limited availability of C₄ grasslands at that time but more particularly the adaptive inertia associated with the need for both non-serotiny and resprouting to evolve for survival in frequently burnt grasslands. Once this barrier was overcome, speciation in the increasingly widespread grasslands was rapid, especially in the Pliocene [62]. Many other fire-resprouting (geoxylous) lineages evolved at this time, converting the grasslands to subshrub savannas [70]. This scenario has parallels with the origin of the South American Cerrado [61] that developed about the same time, except that the geoxyles there arose from non-sprouting rainforest ancestors, whereas the South African geoxyles arose from fire-prone ancestors that were far less frequently burnt.

Fire in coniferous forests

Boreal forests are highly flammable, high-latitude coniferous forests that burn during dry summers. Although glaciers covered most of the area occupied by today's boreal forests until 12 000 years ago, fires have played an essential role in the origin of coniferous species [79], and shaped the evolution of key functional traits that enable conifers to persist in fire-prone environments [53,89]. Falcon-Lang *et al.* [65] recently reported the earliest, fire-preserved *Pinus* fossil dated to 140–130 Ma, providing direct evidence that fire in the Early Cretaceous has driven the evolution of functional traits in the Pinaceae, as hypothesized by He *et al.* [53]. High-intensity crown fires are prevalent in boreal forests of North America, whereas lower-intensity surface fires are dominant in Eurasia. Rogers *et al.* [90] have suggested that the key driver of these distinctive fire regimes was the different composition of dominant species in each area. *Picea mariana*, dominating North American boreal forests, has a suite of functional traits allowing persistence under a crown fire regime, such as retaining old branches and storing its seeds on the tree then releasing them in response to fire [53]. In Eurasia, boreal forests are dominated by coniferous species with thick bark and sparse lower branches that can suppress crown fires. Given the antiquity of coniferous forests and their fire-adapted traits, and the newly formed landscapes of 12 000 years ago, species-level functional traits control the fire regime in current boreal forests, highlighting the positive feedback of floras on fire activities in fire-prone ecosystems.

Fire in tropical broad-leaved forests

Modern broad-leaved, closed forests are generally fire-resistant, i.e. they do not ignite readily [39]. However, rare prolonged dry seasons may render rainforests vulnerable to fire. Fire-resistant rainforests are usually composed of fire-intolerant trees though basal-resprouting and root suckering may be common [91]. Fire-adapted traits such as fire-stimulated seed storage or release, lignotubers, accessory buds, dead biomass retention and fire-stimulated flowering are unknown [61,62,71]. Absence of these traits may be a secondary development where fire-prone lineages returned to fire-protected forests or other non-fire-prone habitats [68,71]. Despite the occurrence of mosaics of broad-leaved forests with grasslands, savannas or shrublands, fires rarely penetrate more than a few meters beyond the forest edge [57]. This is to be contrasted with highly flammable, broad-leaved, temperate, sclerophyll forests dominated by eucalypts in Australia and arising 60–50 Ma whose fitness was enhanced by the combination of thick bark and sunken epicormic buds [68,91,92]. Bond and Midgley [57] observed that the evolution of broad-leaved angiosperms, whose litter decomposes readily under perpetually warm, dark, moist conditions and is constantly wet, reduces the presence of flammable surface fuels in closed forests and suppresses fire. Flammable ecosystems and fire-resistant broad-leaved forests have been proposed as alternative ecosystem states [39,57], reflecting the differential effects of plants on the ecology of fire. The coexistence of communities with such alternative ecosystem states (fire-promoting vs. fire-excluding) under the same broad climate [but different (self-induced) microclimates] supports the central argument that fire plays a major role in driving ecosystem distribution and community structure.

ANTIQUITY OF FIRE-STIMULATED EVOLUTION AMONG SEED PLANTS

Both molecular phylogenetic evidence [79,93] and the fossil record [94] show that conifers originated during the Middle Carboniferous, 340–310 Ma, and rapid diversification followed during the Carboniferous through to the Permian. The number of new coniferous families, both extant and extinct, peaked at 300–280 Ma (Fig. 2). Large deposits of fossil charcoal in Pennsylvanian and Permian strata suggest that fires at this time were large, frequent and intense. In response, many modern coniferous species exhibit diverse fire-adapted morphologies, such as on-plant, seed-storing (serotinous) cones or thick bark and shedding of dead

branches [53,79,89]. Robinson [95] suggested that ‘the apparent propensity to fire tolerance that runs through gymnosperm [conifer] taxa may be a carry-over from the role of fire in natural selection during the period in which gymnosperms originated’. Available fossil evidence points to a fire-prone biome in the Carboniferous that possessed a wide suite of fire-adapted traits similar to that present in modern-day fire-prone ecosystems [95]. Using a dated molecular phylogeny and Bayesian ancestral state reconstruction, He *et al.* [79] showed that the common ancestor of modern conifers was serotinous—a functional trait that is exclusively expressed in fire-prone environments in modern ecosystems [96]. The existence of serotinous structures is also supported by fossil records in the Carboniferous [97]. The *Lepidodendron* and progymnosperm forests in the Carboniferous showed charred apices indicating crown fires [27] that is consistent with the association of serotiny with crown fires in modern ecosystems [79].

Similarly, orderly branch abscission and healing has been reported in Carboniferous Voltzialean conifers [98,99] and a sparse crown as a consequence of shedding old lower branches is considered a fire adaptation, as it prevents fire climbing to the canopy [89,100]. Thick bark that protects meristematic tissues from fire was also recorded in the pro-conifer, *Protopytis buchiana*, in Early Mississippian strata [101]. Permo-carboniferous fires have shaped the evolution of fire-adapted morphologies in numerous unrelated clades of fossil plants, such as the lepidodendrids, *Calamites*, *Psaronius*, lyginopteridaleans, medullosans and Cordaites [102]. The ability to resprout in response to fire allows plants with low fecundity to persist in fire-prone environments [103]. He *et al.* [79] showed that resprouting is common among modern conifers, with at least 94 coniferous species in 41 genera among all six extant families that have a resprouting capability after disturbance, which implies that it must have had an early origin in the conifer phylogeny. The widespread and ancient origins of fire-adapted morphologies, together with overlap in time of the origin and initial diversification of conifers with the time when fire was widespread during the Carboniferous through to the Permian, point to the significant role of fire in the origin and evolution of conifers. Fire activities have waxed and waned since the Early Triassic through to the Jurassic, predominantly as a consequence of fluctuations in atmospheric O₂ [32] but coniferous families owe their origin and early diversification to the earlier strongly fire-prone periods (Fig. 2).

Molecular evidence suggests that angiosperms may have originated 180 Ma in the Jurassic or

even earlier in the Triassic [104,105], predating the oldest known angiosperm fossils from the Cretaceous [106]. However, it was not until the Aptian–Cenomanian, 110–90 Ma, that rapid diversification of angiosperms occurred [107]. Indeed, 42 angiosperm orders, out of the 71 recognized, originated at that time (Fig. 2). Several hypotheses have been proposed to explain the rise of angiosperms to environmental dominance at this time [108]. Augusto *et al.* [109] suggested that flowering plants responded to a new regime of climatic and environmental disturbance, and biotic interactions may have played a role in the later stages of angiosperm expansion within temperate regions. The origin and early radiation of angiosperms may have been stimulated by feedbacks between recurrent fire and the evolution of fire-adapted traits at a time when climatic conditions were conducive to frequent fires [55,57].

Recent simulation on the effect of fire behaviour on early angiosperm expansion under the influence of superambient atmospheric O₂ levels showed that early angiosperms provided an easily ignitable fuel that enhanced both the seasonal intensity and frequency of surface fires [110,111]. The addition of shrubby understory angiosperm fuels promoted more intense surface fires, resulting in greater mortality and reduced post-fire recruitment of gymnosperms. The higher productivity and reproductive output of angiosperms relative to gymnosperms likely allowed angiosperms to recover quickly post fire, accumulating biomass more rapidly and promoting more frequent and intense fires in turn. He *et al.* [53] demonstrated the transition of fire regimes from surface fire at 130 Ma to crown fire at 90 Ma. Therefore, current evidence supports the hypothesis that the early spread of angiosperms was promoted by the novel fire regimes that angiosperms themselves created under conducive climatic and atmospheric conditions.

ANTIQUITY OF FIRE-RELATED FUNCTIONAL TRAITS

Fossil evidence is necessary to confirm the occurrence of ancient fire but it is not sufficient to infer fire-driven evolution, as plants do not adapt to fire *per se*, but rather to particular fire regimes [112]. *Fire-related traits* are plant features that are typically associated with fire-prone environments but whether they are the outcome of selection by fire is unknown or unstated [67,113]. *Fire-adapted traits* are only expressed as a consequence of selection by fire or one of its components or byproducts (e.g. heat, smoke, charates). Thus, such traits confer superior fitness in the presence of a particular fire

regime and become genetically fixed through time. Despite long awareness by ecologists of the benefit particular traits confer in fire-prone environments [114,115], fire-related traits have often been viewed as adaptations to drought but exaptations to fire on the (mis)understanding that drought preceded fire historically [8,75]. Current evidence, however, shows that fire either preceded or coincided with drought historically in many cases [67]. High levels of O₂ during the Paleozoic-Mesozoic (coupled with high temperatures and primary productivity) meant that the vegetation was fire-prone independently of, but often exacerbated by, strong seasonality. Fire has directed the evolution of an array of plant traits, including whole-plant fire responses, serotiny (canopy seed bank), and fire-stimulated seed germination and flowering [112]. These traits are adaptive in fire-prone environments and are the key to superior species fitness under specific fire regimes. Where these traits are confined to fire-prone habitats and increase fitness in the presence of fire, tracing their origin can indicate when fire became sufficiently extensive and recurrent to select for such fire-related traits, confirming their fire-adapted status [68,71]. The burgeoning molecular evidence points to the antiquity of fire-adapted traits and, increasingly, their purported dates of origin are supported by fossil evidence [11,65].

Evolution of fire-stimulated seed release

Serotiny is the persistence of mature cones/fruits in the plant crown until an environmental cue triggers seed release, usually fire heat that causes death of the supporting stem [96]. Serotiny of cones/fruits is closely tied to fire in most plant groups, and fire-cued seed release from serotinous cones/fruits (pyriscence) ensures seed germination under post-fire conditions that are optimal for seedling recruitment [96,116]. Serotiny is common among plants in ecosystems prone to crown fires, including those dominated by both gymnosperms and angiosperms [96,117]. It is best represented in the mediterranean regions of south-western Australia and to a lesser extent the Cape region of South Africa, California and the Mediterranean Basin. It is also present in temperate, maritime and boreal regions that experience occasional drought, even if not seasonal, that makes them prone to crown fires. Cupressaceae is the oldest known modern family possessing serotiny, stretching from the Mid-Cretaceous (*Callitris* clade of Australia 106 Ma) to the close of the Cretaceous (*Widdringtonia* of South Africa 65 Ma) [118]. He *et al.* [79] reconstructed the evolutionary history of serotiny in conifers and showed that this trait

was diagnostic for early conifers from 332 Ma (Late Carboniferous). Related research showed that the origin of serotiny in modern-day Pinaceae was delayed until 89 Ma when fire became more frequent and of greater intensity, switching from surface to crown fires in the Middle Cretaceous [53]. Among angiosperms, serotiny evolved at least 74 Ma in the Proteoid clade of Proteaceae [12], while it arose 62 Ma among ancestral banksias in the Grevilleoid clade [71].

Serotinous cones/fruits in different plant groups show remarkable similarity in physiological mechanisms that account for serotiny. The mechanism among conifers and certain angiosperms involves a high melting point resin (various polymers of isoprene units, terpenes) that seals the valves of follicles or scales. Early studies [119] indicated that the composition of resin might determine the melting point, bond strength and stability of the resin, which in turn determines the level of serotiny. Serotiny is a highly heritable trait among pines [120]. Recent evidence suggests that a polygenic quantitative control is responsible for this trait [121]. The composition of resin is determined by the molecular structure and composition of terpenes in the resin. In plants, the family of terpene synthases (TPSs) is responsible for the synthesis of the various terpene molecules. TPS genes encode enzymes (TPS gene family) that use similar substrates and yield similar products but have diverged in different species [122]. It is likely that the resin in any one species contains a mixture of terpene polymers that define the melting point, stability and bond strength of that resin, which may be related to the level of serotiny. The evolution of TPS genes and changes in their expression level ultimately determines the composition of the resin mixture and therefore the degree of serotiny. Interestingly, the capacity to produce and store terpenes is also considered a flammability-enhancing trait and could have an independent adaptive value in fire-prone ecosystems [123]. The TPS gene family has a common origin in gymnosperms and angiosperms with different gene subfamilies expanding in different lineages by gene duplication and divergence [122], pointing to a common origin for the mechanism responsible for sustaining serotiny in both gymnosperms and angiosperms.

Evolution of fire-stimulated germination and the KAI-gene signalling system

Fire promotes the germination of soil-stored seeds. The mechanisms vary greatly from (a) heat cracking the thick cuticle or outer tissues or dislodging the strophiole to allow imbibition to occur;

(b) chemicals in smoke, charate or ash that stimulate germination by breaking physiological dormancy; to (c) wider diurnal temperature fluctuations that increase permeability to water [124,125]. This ensures that germination is cued to post-fire conditions when light, water and nutrient resources are optimal for seedling recruitment [112]. While almost 100 families in fire-prone regions possess fire-stimulated germination [126], details about this trait in an evolutionary context are only known for Proteaceae, Restionaceae, Ecdeiocoleaceae, Anarthriaceae, Centrolepidaceae, Haemodoraceae, Cistaceae and Fabaceae. Fire-stimulated germination originated in the Proteaceae, subfamily Proteoideae, 81 Ma, 15 My after the family became fire-prone. Similarly, the entire family Haemodoraceae has been fire-prone since its inception 89 Ma but soil-stored seeds appeared 8.5 My later in the subfamily, Conostyloideae [66]. Germination in this group is essentially smoke-stimulated [127], with the chemical inducer, glyconitrile, becoming effective at least 42 Ma and, nested within that, the karrikin, KAR₁, 18 Ma. The graminoid order, Poales, is among the oldest group of flowering plants that shows fire-related traits. The fire-prone Anarthriaceae-Restionaceae clade separated from its non-fire-prone sister 101 Ma and, by the time the two families parted 91 Ma, soil-stored seeds with fire-stimulated germination were firmly established [2,66]. Smoke-stimulated germination is the ancestral condition for at least the South African restios and probably the Australasian clade as well [128].

The best-studied and most widespread mechanism for fire-stimulated germination is the presence of butenolide-related compounds, karrikins (KARs), in smoke that couple with specific proteins in the seed to form hydrolases that catalyse reactions that allow germination to commence [129]. These KARs form during intense burning of plant matter from the combustion of polymeric primary cell wall material [130] to form simple pyranbutenolides. KARs, along with other germination-stimulating compounds such as glyconitrile, ethylene and nitrous oxide, are carried in smoke and charred residues from where they are adsorbed by soil particles and soil-stored seeds. KARs diffuse, or are washed via soil leaching, into seed embryos where KAR₁ in particular attaches to a protein, encoded by the KAI2 gene [129]. In evolutionary terms, butenolide-sensitivity and the KAI2 gene complex can be traced back to bacteria and they have an unbroken history through to the most advanced of flowering plants [131,132] (Table 2). The earliest butenolides had a biotic origin, acting as signalling compounds within the organisms of synthesis (endogenous source), but also diffusing

out of those organisms to affect the metabolism of other (related) organisms (exogenous source). KAR has a strictly abiotic (combustion) origin, although some flowering plants may produce much more complex (fatty acid-carotene-sterol-related) butenolides. In addition, many seed-bearing plants synthesize and secrete strigolactones that stimulate growth of mycorrhizal fungi in their rhizosphere and also germination of the soil-stored seeds of many root parasites [133]. However, it is only KAR (from smoke) that stimulates germination of seeds in general.

With the advent of recurrent fire, an environmental cue (transducer) associated with fire (e.g. heat, smoke, ash, increased diurnal temperatures) was required to trigger germination. Simple butenolides were present in smoke and a butenolide-transducer system that promoted growth already existed among seed plants, so the most parsimonious adaptive solution was to take advantage of KAR to stimulate post-fire germination. The early origins of KAR-sensitivity among gymnosperms were fitful and restricted: the Cycadales, Pinales and Podocarpaceae show little post-dispersal seed dormancy, reflecting a limited seasonal and fire-prone past and rendering KAR-sensitivity of restricted adaptive value. Conifers in particular have a long history of on-plant seed storage (serotiny) and fire-stimulated seed release (pyriscence) associated with seasonality [79] as an alternative adaptation to fire. Since flowering plants more clearly arose in a fire-prone environment (as described in previous sections), this means that the presence of KAR-sensitivity among flowering plants can be traced back to their fire-prone origins, so that independent multiple innovation events were not required. Adaptation would have been rapid, as developing seasonality and intensifying fire (a) promoted population turnover, (b) increasingly restricted recruitment to the wet season following fire and (c) reliably produced KAR to select for orthologous modification of the KAI2 gene system inherited from their ancestors [129]. Lack of KAR(smoke)-sensitivity came later as plants developed alternative traits (e.g. heat cue for hard seeds) or migrated into non-fire-prone environments.

There are many instances in the literature where the experimental application of smoke to seeds induced germination of species considered not native to fire-prone habitats. These records can be explained as either (a) fire-mimicking selection where the chemical promoter may also have non-fire origins, (b) incidental (neutral) mutations retained, as they do not reduce fitness and previously lacked the fire cue for their expression (pre-adaptation), (c) the species actually has a fire-prone ancestry or (d)

Table 2. Hierarchical listing of prokaryotes (bottom) through to the most advanced photosynthetic eukaryotes (top) in relation to their ability to produce and respond to karrikins (KAR1) and other butenolides, presence of the KAI2 gene system, their habitat type, presence of soil-stored seeds and whether they are fire-prone or not.¹ KAR1 stimulates germination.² Smoke-stimulated germination.

Taxonomic group	Example taxon	Butenolide present and bioactive			Habitat type		Soil-stored diaspores	Fire-prone	Reference
		Endogenous origin	Exogenous origin	KAI2 protein present	Moisture	Climate			
Fire-prone									
Flowering plants	<i>Conostylis</i> (Haemodoraceae)	?	KAR1 ¹	Expected	Moderate	Mediterranean	Yes	Yes	[127]
	<i>Arabidopsis</i> (Brassicaceae)	?	KAR1 ¹	Yes	Moderate	Mediterranean	Yes	Usually	[134]
	<i>Peucedanum</i> (Apiaceae)	?	KAR1 ²	Expected	Moderate	Mediterranean	Yes	Usually	[135]
Gymnosperms	<i>Callitris</i> (Cupressaceae)	?	KAR1 ²	Expected	Moderate	Mediterranean	No (serotinous)	Yes	[136]
	<i>Picea</i> (Pinaceae)		?	Expected	Moderate	Subalpine	No	Yes	[137]
Non-fire-prone									
Lycopods, mosses, liverworts	<i>Selaginella</i> (Lycophyta)	?	KAI1 ineffective	Yes	Waterlogged	Aseasonal	Rarely	No	[132]
	<i>Marchantia</i> (Bryophyta)	Strigolactone	Synthetic strigolactones stimulate growth	Yes	Waterlogged	Aseasonal	No	No	[131]
Algae, fungi, bacteria	<i>Nitella</i> (Charophyta)	Strigolactone	Synthetic strigolactones stimulate growth	Yes	Aquatic	Not apply	No	No	[131]
	<i>Enterobacter</i> (Bacteria)	Agglomerins	Agglomerins (bactericide)	?	Aquatic	Not apply	No	No	[138]

incorrect assignment to non-fire-prone environments. Far from being exceptions to the rule, further analysis shows that explanation (c) is the most likely [67]. Thus, fire remains central to understanding smoke-sensitivity even in (apparently) non-fire-prone environments where the fire-response mechanism may remain heritable but dormant. Research on the biochemistry of germination is pointing to the presence of a karrikin-coupling protein (KAI2) among seed plants generally [132] that also implicates fire in directing the evolution of KAR-sensitivity. The evolution of seed plants was initiated in a fire-prone environment with smoke/KAR-sensitivity an ancestral trait (Table 2) rather than it needing to arise numerous, independent times through their evolution. If anything, the reverse is true: some lineages have lost KAR-sensitivity and adapted to their non-fire-prone environment or evolved other traits for responding positively to fire, such as heat-induced testa-cracking among the hard seeds of legumes.

FLAMMABILITY AS A COLLECTION OF FIRE-RELATED TRAITS

Flammability can be defined as the capacity for plant biomass to burn [139]. (High) flammability is an umbrella term for traits that vary from those under tight genetic control, such as persistent dead flowers and leaves whose ignition serves to ensure opening of serotinous fruits in response to fire [71] or the release of sufficient ethylene to promote pyrogenic flowering [140], through to ready combustibility of the vegetation and associated litter as a ‘niche-created’ property that gives the component species a fitness advantage over potential, less-fire-tolerant competitors [139]. Some traits, such as small, dry leaves and ‘twiggy’ foliage, may primarily be adaptations to drought, sun-derived heat or low nutrients, but also increase flammability (exaptations), though, without a time-based phylogeny and knowledge of the associated habitats, the reverse is also possible [67]. Such

multifunctionality may be adaptive in the context of fire if it can be shown that enhanced flammability also increases fitness. This requires demonstrating that flammability is coupled with other fire-related but non-flammable traits, such as fire dependence (e.g. smoke-stimulated germination), resistance (thick bark), avoidance (sunken epicormic buds) or tolerance (recovery from a lignotuber) [91, 139, 141]. However flammability is viewed, we show here that, as the essence of fire-proneness, flammable traits are ancient adaptive responses to the presence of fire, but so too are the associated non-flammable traits that enable plants to survive fire.

PLANT–ANIMAL INTERACTIONS IN RELATION TO FIRE

Some plants utilize animals to bury their seeds, which takes advantage of soil storage, positioning the seed in an ideal location to receive the heat pulse for germination. The best-researched examples are aril-bearing (elaiosome) diaspores that are buried by ants that have arisen in many fire-prone families up to 40 Ma so it is a late development among clades with soil storage [12, 142]. More recently, Midgley *et al.* [143] have shown a role for dung beetles in burying the ball-shaped fruits of the restiad, *Ceratocaryum argenteum*, in a fire-prone genus that arose 11 Ma [3, 66]. Inflorescences of some advanced species with pyrogenic flowering are dark red or black (*Disa atrorubens*, *Macropidia fuliginosa*, *Monadenia ophrydea*, *Pyrorchis nigricans*), suggestive of an anti-herbivore response, but experimental studies are unknown [66, 144, 145]. Many species with pyrogenic flowering take advantage of the improved opportunities for pollination and seed set and dispersal following fire and reduced abundance or satiation of herbivores, florivores and granivores [140]. Pyrogenic flowering can be traced to the Upper Cretaceous in some clades [67]. Seeds of many serotinous species are brown, black or mottled in general, some of which can be traced back to the early-mid-Cenozoic (*Banksia*, *Hakea*, *Leucadendron*, *Melaleuca*, *Pinus*, *Protea*, *Xylomelum*) that suggests an anti-granivore role via crypsis among charred litter, but fitness studies are rare or inconclusive [12]. The arrival of the strong-billed parrot clade, *Calyptrorhynchus*, into south-western Australia about 18 Ma, at a time when the genus, *Hakea*, with its highly nutritious seeds in serotinous fruits, was diversifying, led to the gradual evolution of large, woody, parrot-resistant fruits that ensured seeds remained intact by the time they were released in response to fire [146]. How animals are adapted to fire in terms of behaviour, such as survival of fire [147] or

post-fire opportunities for herbivory, pollination or granivory [148] or crypsis in the post-fire environment (many insects active after fire are brown, black or mottled), have received little study.

FURTHER BURNING ISSUES—FUTURE RESEARCH NEEDS

What are the priorities for future studies of fire-driven evolution? The importance of fire as a selective agent is gaining increased attention, although it remains poorly understood. Comparative experiments are required to demonstrate the superior fitness of a particular functional trait in the presence of fire compared with other possible determining factors such as drought or infertile soil. Future research requires modelling how changing climates (temperature, seasonality, rainfall) and atmospheric gas levels trigger changes in fire regimes, and how these in turn trigger adaptive responses of fire-related traits, and the resultant changes in vegetation structure and function. Research needs to focus on the mechanisms of the morphological, physiological and genetic transitions that enable the evolutionary switch between alternative states of fire-related traits (e.g. resprouting vs. fire-killed with seed storage) that can be scaled up to a switch between one type of fire regime to another [149]. It is clear that fire-dependent biomes, such as tropical grassland systems, originated million of years before human deforestation, but much later in the evolutionary history of terrestrial biomes. Various hypotheses have been proposed to explain such late origins of these highly flammable biomes [82, 49] and the actual causes of this late spread require further research [150]. In addition, the causes of fire resistance in rainforests arising since the Early Paleogene require further research. Lastly, the evidence we present supports the hypothesis that fire promoted the evolution and early spread of angiosperms, during which intrinsic responses of the plants themselves were critical [57]. Future research frontiers require new experiments and models of how trait innovations among angiosperms, as responses to changing climates and O₂ and CO₂ levels, led to greater species fitness and created novel vegetation and fire regimes [151]. Finally, while we have touched on plant–animal interactions in relation to fire, it seems likely that animals have also adapted to fire, but the entire topic has yet to be explored.

CONCLUDING REMARKS

We have shown that fire has been a pivotal ecological and evolutionary force shaping the structure

and function of major global biomes over the last 400 My. This finding indicates that there is a need to review policies on ecosystem management and biodiversity conservation. For example, the tropical savannas of Africa and the Cerrado of central Brazil harbour diverse species with high levels of endemism [61]. The misconception that these ecosystems were the consequence of human deforestation and human-lit fires led to long-term fire suppression, resulting in the elimination of long-lived forbs as a result of shading by the accumulation of dense undecomposed grass litter [4]. In mediterranean heathlands, frequent management fires can lead to the elimination of serotinous species that are slow to mature, while long fire intervals lead to the demise of those same species [152]: such research reveals the optimal fire regimes for species and community conservation, and this is often in disagreement with traditional management. Recently, the Atlantic coastal plain grasslands of North America have been recognized as a significant biodiversity hotspot [153] that acknowledges the fundamental role of fire in maintaining those flammable ecosystems.

Finally, the groundwork for ecology and evolutionary biology was undertaken by researchers who were rarely located in fire-prone environments, and thus fire has not featured in the development of much ecological and evolutionary theory [7]. Biologists in general need to overcome their cultural bias against viewing fire as a fundamental agent of natural selection on biota throughout the history of terrestrial life on the Earth, and to reassess ecological and evolutionary theories that underpin current understanding of how nature operates. The greatest challenge for fire ecologists is to communicate the science of fire ecology and fire-directed evolution to the general public, media and politicians. Informed fire management is required in the face of global climate change, population growth and ever-expanding encroachment into flammable landscapes [154]. Human activities are having an increasing influence on fire regimes. Allowing arsonists to dictate fire occurrences and attempting to put out fires immediately is not fire management. Projections of future fire activity and vegetation responses point to the need for greater human intervention to ensure effective management procedures for natural resource conservation in fire-prone regions [155].

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