Evolutionary Ecology of Fire

Jon E. Keeley[1,2] and Juli G. Pausas[3]

[1]United States Geological Survey, Western Ecological Research Center, Sequoia–Kings Canyon Field Station, Three Rivers, California, USA; email: jon_keeley@usgs.gov

[2]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

[3]Centro de Investigaciones sobre Desertificación, Consejo Superior de Investigaciones Cientificas (CIDE-CSIC), Montcada, Spain; email: juli.g.pausas@csic.es

Keywords

Abstract

Fire has been an ecosystem process since plants colonized land over 400 million years ago. Many diverse traits provide a fitness benefit following fires, and these adaptive traits vary with the fire regime. Some of these traits enhance fire survival, while others promote recruitment in the postfire environment. Demonstrating that these traits are fire adaptations is challenging, since many arose early in the paleontological record, although increasingly better fossil records and phylogenetic analysis make timing of these trait origins to fire more certain. Resprouting from the base of stems is the most widely distributed fire-adaptive trait, and it is likely to have evolved under a diversity of disturbance types. The origins of other traits like serotiny, thick bark, fire-stimulated germination, and postfire flowering are more tightly linked to fire. Fire-adaptive traits occur in many environments: boreal and temperate forests, Mediterranean-type climate (MTC) shrublands, savannas, and other grasslands. MTC ecosystems are distinct in that many taxa in different regions have lost the resprouting ability and depend solely on postfire recruitment for postfire recovery. This obligate seeding mode is perhaps the most vulnerable fire-adaptive syndrome in the face of current global change, particularly in light of increasing anthropogenic fire frequency.

INTRODUCTION

Fire is an ecosystem process that is dependent on plant-community flammability and sufficient biomass continuity for fire spread. In response, species evolve along different trajectories. Fundamental to understanding fire adaptations is the fire-regime concept, which involves the

conditions sufficient to explain the ecological patterns of fire activity and includes four parameters: primary productivity, seasonality, ignitions, and fuel structure (**Figure 1**). Fires require sufficient biomass continuity to spread, and this requires a seasonal climate with a wet season for biomass production, alternating with a dry season sufficient to convert these potential fuels to available fuels. In the absence of humans, an ignition source such as lightning is necessary. Patterns of burning play an important role in determining adaptive solutions that allow plants to persist in fire-prone environments, and fuel structure, including horizontal continuity of fuels and vertical vegetation structure, is critical in terms of adaptations to particular fire regimes. These regimes are not permanent features of an ecosystem but rather parameters such as frequency and intensity that can vary over time as fires, as well as other factors, reshape the environment.
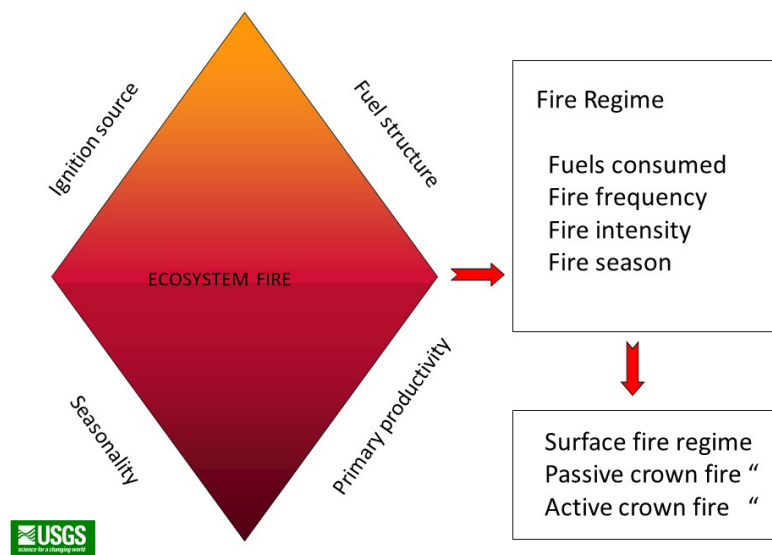

Figure 1. Factors necessary and sufficient for predicting the distribution of fire as an ecosystem process. A certain level of primary productivity is needed in order to spread fire, and climatic seasonality, with annual to decadal cycles of drying, is required to convert these potential fuels to available fuels that can combust. Fire regimes are controlled strongly by the types of fuels consumed (surface versus canopy), fire frequency, fire intensity, and fire season.

Fires vary in characteristics. Some spread in the canopies of shrubs or trees, generating high-intensity fires that affect most of the aboveground biomass (crown fires). Others (surface or understory fires) are confined to surface fuels and are of overall lower intensity, such as in many grasslands and savannas and certain forests in which fire consumes dead foliage on the surface, but taller trees are unaffected. Other fires spread underground in dense peat fields and can persist for months, often killing plants at the roots (ground fires).

Fires occur in many ecosystems on all continents save Antarctica. Mediterranean-type

climate (MTC) shrublands are particularly fire prone because they are characterized by a predictable annual drought of 3–4 months or longer in ecosystems with sufficient biomass to carry fire. Subtropical savannas are also fire prone on an annual basis due to the high fuel volume generated by C_4 grasses. Other climatic patterns generate fire regimes at different temporal scales. For example, droughts one or more times a decade lead to widespread fires in conifer forests in the Rocky Mountains and in boreal forests at high latitudes in North America. Regions with a decadal frequency of fires driven by El Niño events include areas on all three continents in the Southern Hemisphere (Chen et al. 2017).

FIRES THROUGH GEOLOGICAL TIME

The history of paleobotany has largely focused on the role of climate and soils in plant evolution and has paid little attention to the role of fire. However, there is ever-increasing evidence for a long paleontological, and globally widespread, fire history (Belcher 2013, Scott 2018), setting the stage for the evolution of fire-adaptive traits. The earliest fossil evidence of fire dates to the Silurian, over 400 million years ago (Mya), which coincides with the origin of land plants (Pausas & Keeley 2009). In the later Paleozoic, there is evidence not just of fire but of different fire regimes, including low-intensity surface fires, high-intensity crown fires, and smoldering ground fires. Devonian fires included surface fires in progymnosperm forests suggestive of a fire regime consisting of frequent understory fires that burned ferns and shrubs made flammable by dry season desiccation (Cressler 2001). Later Triassic fires are implicated in surface-fire regimes that left fire scars and were tied to antecedent droughts (Byers et al. 2020). In contrast, Carboniferous Lepidodendron forests on moister sites apparently dried out at less frequent intervals, allowing for greater fuel accumulation, which resulted in high-intensity crown fires, as evidenced by fossilized charred apices and other evidence (Falcon-Lang 2000). It is assumed that fires were largely ignited by lightning, and apparently droughts conducive to fires occurred at intervals ranging from 1 year to decades or longer.

Throughout this long history, fire regimes have varied both spatially and temporally. As climates have changed, so too have ecosystems, and regions, such as Antarctica, which today lack fire, have under prior climates been home to fire-prone forests (Kumar et al. 2011). Over time, the importance of fire has waxed and waned. Fossils reveal fires were common in the Carboniferous and Permian (Falcon-Lang 2000; Uhl & Kerp 2003), and these periods of high fire activity may be linked to high atmospheric oxygen, which stimulates fire activity (Scott & Glasspool 2006). As oxygen reached a quasi-equilibrium close to contemporary levels, the Cenozoic recorded fire activity that was controlled by climate and vegetation (Bond 2015). High fire activity is associated with the spread of angiosperms in the Cretaceous, and it appears fire was a causal factor in the diversification of flowering plants (Bond & Scott 2010). However, equally likely is the possibility that as angiosperms developed traits allowing them to invade more arid environments, this provided a fuel source on landscapes previously devoid of sufficient biomass to carry fire; thus, higher diversification may have contributed to a more

globally widespread presence of fire.

These broad paleontological divisions of fire activity probably do not capture the real picture, which likely varied spatially, as with fire today, and over finer time scales. The Eocene has been characterized as an equable climate (i.e., having a low annual range of temperature) that lacked an annual drought period, and some contend that fire would be relatively unimportant in such an aseasonal climate. However, aseasonal climates lacking an annual drought do experience recurrent droughts over longer time scales, from decades to centuries, that make them fire prone. In addition, modeling studies suggest substantial annual seasonality effects in continental interior landscapes during the Eocene (Sloan & Barron 1990). For example, during this epoch, seasonal aridity was evident in central Australia (Greenwood 1994), the southwestern USA (Peterson & Abbott 1979), and coastal southern California (Frederiksen 1991). Evidence of fire has been reported from some of these regions at this time. These fire-prone areas could have spread fire to more mesic forests during longer dry periods, leading to the expansion of fire-prone vegetation, as is occurring today in tropical forests (Cochrane 2003).

The most extensive Cenozoic evidence of fire is found in Oligocene and Miocene coal beds in southeastern Australia, which are interpreted as evidence of widespread fires in arid adapted sclerophyllous shrublands (Martin 1996). Also, Miocene deposits in Europe suggest a frequent fire regime in similar dry shrublands (Figueiral et al. 2002), and these later Neogene deposits reveal an increasing importance of fire (Herring 1985).

Understanding how vegetation responded to changing conditions has been captured in the geoflora concept popularized by Axelrod (1958). The geoflora concept, defined as an assemblage of plants that have been maintained with minor changes over epochs or periods of earth history, is reminiscent of Clementsian organismic communities. Some paleobotanists such as Mason (1947) and Wolfe (1964) rejected the concept, as they were more Gleasonian and did not see evidence that species in a community followed the same historical pattern. Distinguishing between the geoflora concept and individual species' histories is important for understanding the evolutionary ecology of fire because species in communities may have followed different adaptive trajectories in response to fire. Today, the geoflora concept may have some heuristic value, but it should be replaced by a more nuanced view of historical biogeography derived from the phylogeography of clades and other evidence.

FIRE ADAPTATIONS

Adaptive traits are characteristics that provide a fitness benefit, and those traits vary depending on the fire regime. An important evolutionary question about fire-adaptive traits is whether they represent true fire adaptations, i.e., traits whose origin can be traced to a direct response to fire. Fire-adaptive traits that originated in response to another environmental factor (e.g., drought, herbivory) and only subsequently became associated with a fire-prone ecosystem are considered exaptations (Gould & Vrba 1982). Distinguishing between adaptations and exaptations is problematic (Lauder et al. 1993, Keeley et al. 2011), and in many cases it is questionable

whether one can clearly distinguish between the two, let alone eliminate the many other potential explanations (Pigliucci & Kaplan 2000).

To understand the evolution of fire adaptations, we need to recognize those traits that are adaptive under different fire regimes and discover the timing of their origin. Plant megafossils are an important source of information; however, there is a potential bias in this record. Other than volcanic ash deposits, the majority of megafossils were laid down in riparian areas where leaf material was readily preserved. Since fire prone sites are typically arid uplands, the fossil record has an inherent bias against fire-adapted species (Keeley et al. 2012).

An alternative approach is to use dated phylogenies (e.g., Crisp & Cook 2013), which are increasingly available for many lineages. For a given lineage, it is possible to map the presence of fire traits in extant species and perform an ancestral reconstruction of the trait. The phylogenetic approach provides an estimation of the origin of the trait for a given lineage (Figure 2), that is, the time at which fires were frequent and predictable enough for selecting fire adaptations; however, it is a conservative estimate for the origin of the evolutionary role of fire, as it can be best applied to extant species and lineages.
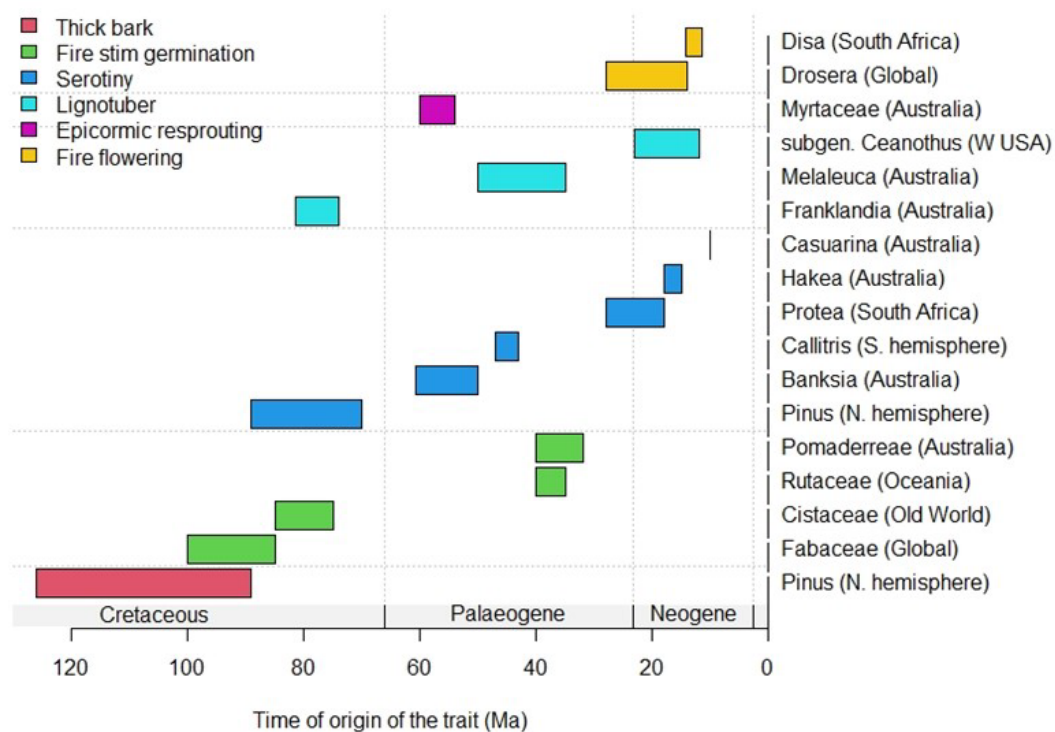

Figure 2. Time of origin (x-axis) of five different fire traits (different colors) for different lineages (y-axis) estimated from dated phylogenies. Bars expand the uncertainty of the time of origin (e.g., stem versus crown age). Figure based on data from Bytebier et al. (2011), Crisp et al. (2011), He et al. (2011, 2012), Heckenhauer et al. (2017), Lamont & He (2017), Lamont et al. (2017), Li et al. (2015), Pausas et al. (2018).

Traits that are adapted to fire fall into two categories: those that enhance survival and those that promote postfire regeneration. Understanding patterns of trait distribution requires consideration of the fire regime, as traits adaptive under a crown-fire regime differ considerably from traits selected for under a surface-fire regime; this is true for traits involved in both postfire survival and postfire regeneration.

Adaptations Promoting Postfire Survival

Resprouting from surviving vegetative structures is the primary means of persistence after fire (Figure 3). This commonly occurs from preformed buds at the base of stems (in the root crown) or in belowground organs (basal resprouting) that ensure survival of the genet. Belowground organs with a resprouting bud bank in woody species include roots, lignotubers, and woody rhizomes (Pausas et al. 2018). Herbaceous perennial species resprout from bulbs, corms, tubers, or rhizomes.

Figure 3. Examples of fire-adaptive traits. (*a*) Resprouting from lignotuber in *Adenostoma fasciculatum* (chaparral, southern California). (*b*) Epicormic resprouting in *Pinus canariensis* (Tenerife, Canary Islands). (*c*) Epicormic resprouting in *Eucalyptus* sp. (southeast Australia). (*d*) Fire-resistant thick corky bark of *Myrica bella* (savanna, central Brazil). (*e*) Enhanced flammability due to retention of fine dead biomass in *Ulex parviflorus* (matorral, Mediterranean Basin). (*f*) Enhanced flammability due to retention of dead branches by *Pinus banksiana* (boreal forest, Alberta, Canada). (*g*) Postfire seedling recruitment by serotinous *Protea* sp. (Cape Region, South Africa). (*h*) Prefire serotinous cones in *Pinus brutia* (forests, southern Turkey). (*i*) Postfire serotinous cones of *Cupressus sempervirens* (matorral, Mediterranean Basin). (*j*) Postfire pyro-endemic annuals (chaparral, southern California). (*k*) Postfire flowering of the geophyte *Tillandsia* sp. (fynbos, Cape Region, South Africa). Images in panels *a,c,f,g,j,k* provided by J.E. Keeley. Images in panels *b,d,e,h,i* provided by J.G. Pausas.

In woody dicotyledonous angiosperms, resprouting is a nearly ubiquitous trait (Wells 1969), with notable exceptions discussed below (section 'Mediterranean-Type Climate Ecosystems: Trade-offs Between Resprouters and Seeders'). Often, after repeated fires or other disturbances, a wide diversity of shrubs and trees form an enlarged woody burl, or root crown, sometimes referred to as a coppice. A specialized form of resprouting common in MTC ecosystems involves the lignotuber. It is not a developmental response to disturbance but rather an ontogenetic trait that forms a basal swelling during the early development of saplings; this lignotuber contributes to successful resprouting by storing carbohydrates and especially dormant buds (Figure 3*a*).

A distinctly different type of regeneration is epicormic resprouting (i.e., resprouting from canopy stems), which results in the survival of individual ramets. This is common in Australian *Eucalyptus* (Figure 3*c*) and Northern Hemisphere *Quercus*, as well as many other woody angiosperms. However, in gymnosperms, it is relatively rare, but *Sequoia sempervirens*, *Pseudotsuga macrocapa*, and *Pinus canariensis* are notable exceptions that resprout epicormically (Pausas & Keeley 2017).

Capacity for resprouting is a species-specific trait; however, a few taxa have both resprouting and nonresprouting subspecific taxa (Ojeda et al. 2005, Keeley et al. 2016). Resprouting also varies with age; e.g., many trees resprout from the base when saplings but not when mature (Del Tredici 2001). However, age effects are variable; for example, California chaparral shrubs have a higher probability of resprouting when older, but the opposite is true of subligneous California sage scrub species, which resprout when young but not when mature. It is hypothesized that in lineages where woody growth forms originated from herbaceous perennial ancestors, buds are buried by woody tissues, making resprouting less likely in older plants (Keeley 2006).

Evolution of the resprouting trait is difficult to ascribe to a response to fire, in large part because it is a nearly ubiquitous trait in woody angiosperms. However, it is characteristic of many extant taxa that date back to the Mesozoic (e.g., *Sequoia sempervirens*, *Wollemia nobilis*, *Ephedra* spp., and *Ginkgo biloba*), which was an era with abundant evidence of fire (Harris 1958). The obstacle in pointing to fire as a driver of resprouting is that this trait is also of

adaptive value following disturbances other than fire, such as extreme winds, severe frosts, drought, and animal browsing. However, some specific resprouting structures, like lignotubers and woody rhizomes, occur only in fire-prone ecosystems and likely evolved in response to fire (Pausas et al. 2018). In herbaceous perennials, resprouting is unlikely to have originated as an adaptation to fire, since these taxa normally die back during the dry season and resprout when growing conditions improve.

There are some taxa for which a reasonable case for resprouting as a fire adaptation can be made. *Pteridium aquilinum* is a fire-resilient fern that is distributed globally and resprouts vigorously after fire, as does *Gleichenia*, another resprouting fern that has a long association with fire in the Cretaceous and early Cenozoic (Collinson 2002). In addition, in some gymnosperm linages, the vast majority of species are nonresprouters after fire, but there are a few resprouting species in different lineages (Burrows 2021). *Pinus* (Pinaceae) is a noteworthy example. With over 100 species, resprouting is found in only a half-dozen taxa, and these are restricted to fire-prone habitats (Keeley & Zedler 1998). A similar pattern is evident in the Southern Hemisphere *Podocarpus* (Podocarpaceae) (Chalwell & Ladd 2005). The connection between resprouting in gymnosperms and fire is made even stronger by the combination of resprouting and production of serotinous cones that open only after fire, as in the Northern Hemisphere *Pinus canariensis* (Pausas & Keeley 2017), the shrubby Chinese pine *Pinus yunnanensis* (Pausas et al. 2021), and the Southern Hemisphere *Widdringtonia nodiflora* (Cupressaceae) (Keeley et al. 1999). In the Myrtaceae, epicormic resprouting occurs in distantly related genera from fire-prone ecosystems; molecular phylogenies suggest this trait arose early in the family, indicating fire has been important through much of the Cenozoic (Crisp et al. 2011).

Thick bark is another trait associated with survival, and it is common in woodland and savanna trees. Evidence that it was selected for by fire includes the observation that in arborescent *Quercus* and close relatives, thick bark is common under a surface-fire regime, but thin bark is found in *Quercus* shrub species subjected to crown-fire regimes (Zedler 1995). In tropical landscapes, there are congeneric species with thin and thick bark inhabiting adjacent nonflammable forests and fire-prone savannas, respectively (Dantas et al. 2013). In *Pinus*, thick bark originated approximately 125 Mya in the fiery environment of the Cretaceous (He et al. 2012).

In addition to traits that enhance postfire survival, some species persist in the face of severe fires by occupying refugia that escape destruction. These refugia provide seed sources for reestablishing in burned areas, persisting as a type of metapopulation (Downing et al. 2019). In a recent illustration of this principle, fire caused massive mortality of the Californian pine *Pinus sabiniana* restricting its range to mesic riparian refugia. As one moved away from the refugia, the age of postfire tree skeletons was found to decrease, consistent with invasion from the riparian refugia after the previous fire (Schwilk & Keeley 2006).

Adaptations Promoting Postfire Recruitment

Plant species differ in their dependence on postfire recruitment. In fire-prone ecosystems, many

species are obligate resprouters, with no seedling recruitment after fire (Keeley et al. 2012). Others may be obligate seeders, which are species that have no capacity for resprouting and are completely dependent on seedling recruitment after fire. There are also facultative seeders that both resprout and recruit seedlings after fire. Plants exhibit three modes of recruitment after fire: (*a*) endogenous reproduction from dormant seed banks stored in the soil, (*b*) endogenous reproduction from canopy-stored seeds in serotinous cones or fruits, and (*c*) seedling recruitment from postfire dispersal of seeds produced by surviving plants or unburned populations.

Recruitment from dormant soil-stored seed banks.

Many species in fire-prone environments produce seeds that are deeply dormant at dispersal and remain viable for decades to centuries. Typically, germination occurs in the first postfire growing season. Annual plants largely restricted to recruitment in the first postfire year are often referred to as pyroendemics or fire ephemerals. For many shrubs in MTC ecosystems, fire produces a pulse of recruitment, resulting in an even-aged cohort of seedlings.

Seed dormancy is broken by either physical or chemical stimuli (Keeley 1991, Pausas & Lamont 2022). Physical stimuli include abrasion and heat shock, both of which can occur in the absence of fire, but fire is the most predictable trigger; in addition, temperature thresholds for dormancy breaking are more compatible with fire than with summer temperatures. Dormancy is imposed by a water-impermeable seed coat; these hard-seeded species typically have a waxy cuticle covering a smooth seed coat, with densely packed palisade tissue beneath. Germination requires imbibition, and for hard-seeded species, this requires breaking the seed-coat barrier, usually by heat shock during a fire. Such heat-stimulated germination is known from a wide range of ecosystems (Probert 2000), but it is most prominent in fire-prone MTC regions (Pausas & Lamont 2022). Families include Anacardiaceae, Apiaceae, Cistaceae, Convolvulaceae, Fabaceae, Malvaceae, and Rhamnaceae.

In striking contrast, many species have seeds that imbibe water yet remain dormant, as they require an internal chemical stimulus. In MTC ecosystems, many species have deeply dormant seeds that require a chemical from biomass combustion, referred to as smoke-stimulated germination, although charred wood and other combustion products may also trigger germination (Keeley & Pausas 2018).

The California chaparral pyroendemic annual *Emmenanthe penduliflora* (Boraginaceae subfamily Hydrophylloideae) was the first species shown to be stimulated by charred wood (Wicklow 1977). Later it was demonstrated that the germination of the South African postfire fynbos shrub *Audouinia capitata* (Bruniaceae) was triggered by exposure to smoke (de Lange & Boucher 1990). The germination response has been shown to be the same following exposure to both combustion products, smoke and charred wood, and for a wide range of species from MTC vegetation, including those from California, South Africa, Australia, and the Mediterranean Basin (Brown 1993, Dixon et al. 1995, Keeley & Bond 1997, Moreira et al. 2010), as well as a few species from subtropical shrublands (King & Menges 2018) and savannas (Daibes et al. 2019, Pausas & Lamont 2022).

The mechanism behind smoke-stimulated germination is quite unlike that of hard-seeded species. Seeds lack a smooth water-impermeable seed coat but rather imbibe water while dormant; however, there does appear to be a subcuticle tissue that changes permeability upon exposure to smoke (Keeley & Fotheringham 1997). Both inorganic and organic compounds have been implicated as the active compound in smoke stimulation, and these appear to be species specific. The first report showed that NO_2, at levels found in smoke, stimulates 100% germination in the California chaparral annual *Emmenanthe penduliflora* following exposure to both smoke and smoke-treated water (Keeley & Fotheringham 1997).

In addition to NO_2, other nitrogenous compounds have been shown to have a role in smoke-stimulated germination in other postfire endemics (Flematti et al. 2011, Downes et al. 2014). Also, a class of organic molecules in smoke known as butanolides, in particular the chemical karrikin, can act as a trigger to stimulate germination for a wide range of plant species, including postfire ephemerals, as well as agricultural species, such as lettuce (*Lactuca sativa*) and tomatoes (*Solanum lycopersicum*), with no obvious relationship to fire (Flematti et al. 2004, van Staden et al. 2004). Karrikin is not a universal stimulant, as some smoke-stimulated fire ephemerals are known that fail to respond to this butanolide (Downes et al. 2010). Karrikin is widespread in nature and can trigger germination at extraordinarily low levels (10^{-7} M), raising questions about how it can stimulate germination immediately after fire and then disappear, a pattern required to explain the postfire pulse in fire ephemerals that is restricted to the immediate postfire years.

The phylogenetic tree of families with species that have demonstrated smoke-stimulated germination (Figure 4) illustrates that this trait is phylogenetically widespread across both Northern and Southern Hemisphere ecosystems (Keeley & Pausas 2018). Smoke-stimulated germination has arisen many times, in many lineages, from a diverse set of chemicals and provides a classic illustration of convergent evolution.

Species exhibit marked variation with respect to seed germination cues that is dependent on their environment (Keeley et al. 2012). For example, in California chaparral, there are a number of hard-seeded Fabaceae annuals with dormant seed banks that germinate only after heat shock from fire. However, in adjacent grasslands, these same species regularly establish in the spring; apparently, summer radiation on these open sites is sufficient to trigger germination. Another example is the chaparral pyroendemic *Emmenanthe penduliflora*, which is dependent on smoke for germination; desert populations not subjected to fire can also germinate without exposure to combustion products (J.E. Keeley, unpublished data).
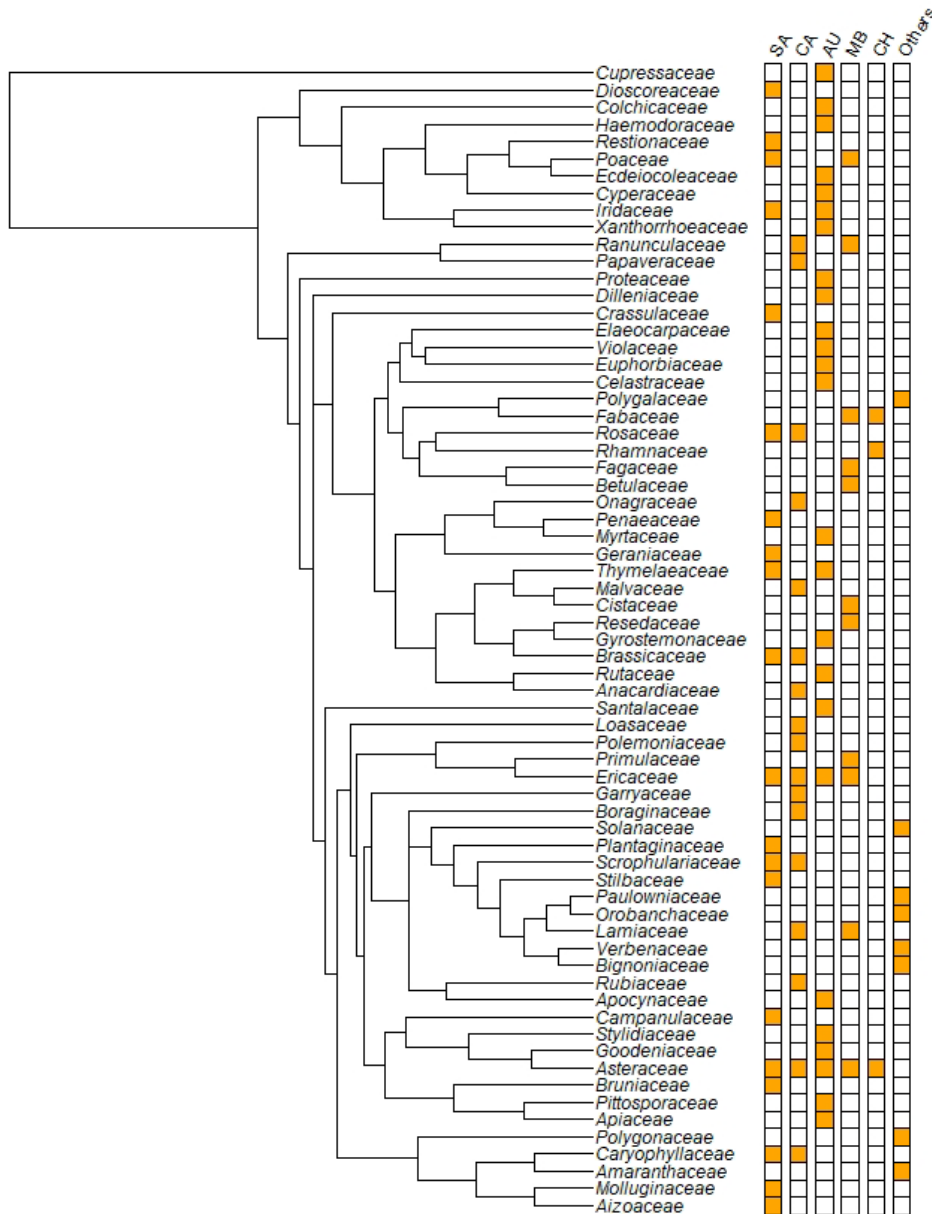
Figure 4. Phylogenetic tree of plant families with evidence of smoke-stimulated germination and their distribution in the five Mediterranean-type climate ecosystems and other regions. Figure based on data from Keeley & Pausas (2018) and Pausas & Lamont (2022). Abbreviations: AU, southern and southwestern Australia; CA, California; CH, central Chile; MB, Mediterranean Basin; SA, South African Cape Region.

Recruitment from dormant canopy-stored seed banks.

In addition to postfire seedling recruitment from soil seed banks, recruitment may also occur from serotiny (seeds released from closed cones or fruits) in which opening is normally delayed

until after fires (Lamont et al. 2020). Dormancy is the result of being enclosed in fruiting structures, and seeds germinate readily following postfire dispersal. Serotiny is a fire-adapted trait found primarily in crown-fire ecosystems, including shrublands and forests. Cones or fruits open en masse and disperse seeds within days of fire, producing a pulse of seedling recruitment that leads to even-aged cohorts, and further recruitment is limited until the next fire. One limitation to serotiny is that when fire intervals are very long and plants die before the next fire, seeds are released but seldom recruit successfully in the unburned vegetation (Lamont et al. 2020). Thus, canopy seed banks are less resilient to long fire intervals than are soil seed banks, which can remain viable for many decades after the plant dies.

In the Northern Hemisphere, serotiny is restricted to conifers, specifically in *Cupressus* and *Hesperocyparis* (Cupressaceae) and *Pinus* (Pinaceae), and these trees are always in crown-fire regimes with little tree survival following fires (Zedler 1977, Keeley et al. 1999, Ne'eman & Arianoutsou 2021). One widespread serotinous pine in the USA is *Pinus contorta*, and although it is distributed from California to Wyoming, the species is serotinous only in northern Rocky Mountain populations, where productivity is low and fuels are conducive to crown fires. The degree of serotiny varies in populations, with increasing frequency of serotinous cones being correlated with increasing fire frequency (Perry & Lotan 1979). This relationship between frequent crown fires and serotiny has been shown in pines from the Mediterranean, California, and Boreal regions (Hernández-Serrano et al. 2013).

Since *Pinus contorta* is an obligate seeder, it is at risk of extirpation if fire intervals are too short and there is insufficient cone production (Keeley & Pausas 2019, Turner et al. 2019). *Pinus attenuata* is a closed cone pine endemic to the MTC of California and Oregon that has also been shown to be at risk of extirpation if fire intervals are too short (Keeley et al. 1999). Zedler (1995) framed this situation in terms of immaturity risk if intervals are too short versus senescence risk if intervals are too long. When *P. attenuata* is evaluated across a broad region, it is apparent that both types of risk have been exacerbated by humans, as we have suppressed fires on some landscapes and increased fires on others (Reilly et al. 2019).

In the Southern Hemisphere, primarily in the MTC South African Cape fynbos and Western and South Australia heathlands, serotiny occurs in a dozen conifers in three genera of Cupressaceae (Ladd et al. 2013). However, unlike in the Northern Hemisphere, Serotiny is also widespread among angiosperms, including Asteraceae, Bruniaceae, Casuarinaceae, Ericaceae, Rosaceae, Myrtaceae, and Proteaceae (Lamont et al. 2020). Indeed, there is an order of magnitude more serotinous species in these two Southern Hemisphere MTC shrublands than in Northern Hemisphere MTC shrublands. The highly weathered fynbos and heaths of the Southern Hemisphere are also nutrient poor relative to Northern Hemisphere shrublands (Hopper 2009). Serotiny in low-nutrient soils may have played an important selective role by protecting nutrient-rich seeds from ground-dwelling predators (Keeley et al. 2012). In poor soils, nutrient-rich seeds are particularly attractive to predators, and therefore, retention within the fruiting structure may provide some level of protection. Of course, this provides an opportunity to canopy predators (e.g., squirrels and birds), thus serotinous cones also evolved defenses against such predators

(Mequida & Benkman 2005).

Serotiny has been dated in several plant lineages (Figure 2). In the Northern Hemisphere *Pinus*, macrofossils indicate a mid-Cretaceous origin (Mays et al. 2017), which is consistent with phylogenetic estimations (He et al. 2012). In Australia, serotiny in *Banksia* (He et al. 2011) originated approximately 60 Mya, concurrent with the acquisition of epicormic resprouting in eucalypts (Crisp et al. 2011) (Figure 2); this corresponds with the origin of seasonally hot and dry climates on the continent.

Recruitment from postfire dispersal.

Some species recruit into recently burned sites by dispersal. Many forest types with moderate to high productivity have trees that survive fire by outgrowing surface fuels and dropping dead branches to produce a gap between surface fires and their canopies. However, they lack a dormant seed bank and are not serotinous. Postfire regeneration occurs in subsequent years from seeds produced by surviving trees that take advantage of the postfire open spaces in the understory. Examples include the western North American *Pinus ponderosa* and the Mediterranean Basin *Pinus nigra*. This mode of regeneration is typical of many trees found in surface-fire regimes, such as temperate mixed conifer forests and subtropical savannas. This mode of recruitment, however, is greatly affected by the size of gaps in the canopy. In recent years, with increasing fuel levels due to fire suppression, as well as other global changes, gap size has increased, and this can slow the rate of recruitment.

Other species can recruit into burned areas from populations outside the fire perimeter, and these typically have light, wind-dispersed seeds; examples include *Baccharis sarothroides*, which invades California chaparral, and the common fireweed, *Chamaenerion angustifolium*, which colonizes many western North American burned forests. The success of this strategy is greatly influenced by fire size, as this increases the dispersal distance required for establishment into burned landscapes.

Adaptations Illustrated by Other Fire-Related Traits

A trait that it is conspicuous in many fire-prone ecosystems is fire-stimulated flowering (Lamont & Downes 2011); that is, profuse flowering after fire, with limited flowering between fires. It occurs in a large diversity of MTC monocot and dicot geophytes (e.g., Orchidaceae, Liliaceae, Iridaceae, Droseraceae) (Le Maitre & Brown 1992, Groom & Lamont 2015) and in the Australian *Xanthorrhoea* or grasstrees (Lamont & Downes 2011) and is common in some subtropical savanna species (Zirondi et al. 2021). In general, it is thought that postfire flowering occurs in response to higher light levels, temperatures, and nutrient levels. However, there are examples of species with flowering strictly tied to fire. The South African *Cyrtanthus ventricosus* produces floral buds in bulbs that remain dormant for years; they are stimulated to develop only by smoke and often sprout and flower within days of a fire, regardless of the season (Keeley 1993). Phylogenetic studies suggest that postfire flowering is an old characteristic; for example, the origin of postfire flowering in *Disa* (orchids) in South Africa was traced back to the

mid-Miocene, just after the rise of the drought and fynbos vegetation in the region (Bytebier et al. 2011), and it is possibly older in other lineages, e.g., Haemodoraceae, Asphodelaceae (Lamont et al. 2019).

Flammability is another trait that varies with fire regime, due to characteristics of plant structure, including retention of dead branches and chemical composition. Mutch (1970) proposed that species in fire-prone communities have evolved greater flammability as a means of outcompeting less fire-tolerant species. This has been criticized on the grounds it is group selectionist (Snyder 1984, Troumbis & Trabaud 1989). However, Bond & Midgley (1995) provided an individualistic argument for the evolution of flammability. Their simulation models supported the conclusion that flammability may enhance inclusive fitness if the resulting fires kill neighboring, less-flammable individuals, which increases the recruitment possibilities for the fire-adapted flammable individual. In fact, flammability may have evolved as a form of niche construction (Schwilk 2003, Schwilk & Kerr 2003).

Flammability is a complex trait that consists of different strategies to increase fitness in different contexts (Pausas et al. 2017). In crown-fire ecosystems, some plants have increased reproductive success by increasing their flammability, i.e., their ignitability and fire intensity (hot-flammable strategy); this occurs in plants that undergo fire-stimulated germination (postfire seeder species) when fires open vegetation gaps that are safe sites for seedling recruitment (Bond & Midgley 1995). Examples include MTC shrubs with high levels of standing dead biomass, thin twigs and leaves, twigs and leaves with high levels of volatile compounds, or low live-fuel moisture during the fire season (Pausas et al. 2012, 2016; Pivovaroff et al. 2019). In surface-fire regimes, other plants have increased survival by reducing their flammability (nonflammable strategy). Examples are shrubs and trees in South American savannas that have very sparse branches with thick bark and leaves that contribute to the survival of surface fires (Pausas et al. 2017) and pines that grow quickly and self-prune their lower branches to avoid fire reaching the crowns (see the section titled Evolutionarily Stable Fire Strategies). A third strategy is seen in plants that have a highly flammable part (typically leaves) to ensure a quick burning (fast-flammable) strategy, while protecting the other key parts of the plant where meristematic tissues are located (Gagnon et al. 2010). Examples of this survival strategy include the Australian grasstrees (*Xanthorrhoea*).

These strategies represent alternative ways to persist in the face of recurrent fires (Pausas et al. 2017). Even within the same community, species composition reflects different flammability strategies. Adaptive evolution is expected to result in functional traits that are appropriate for a particular community, and there is some evidence that flammability traits have evolved consistent with niche conservatism (Cui et al. 2020). Also important are ecological sorting processes in which functional traits are influenced by trait combinations in other taxa in the community (Ackerly 2003). This is particularly relevant in fire-prone communities, as the flammability characteristics of neighbors affect trait selection. For example, species dependent on postfire seedling recruitment are typically highly flammable, and based on community composition, they often cooccur with obligate resprouting species, which have leaf

characteristics that dampen fire impacts (Bond & Midgley 1995).

Keeley & Bond (1999) hypothesized that enhanced flammability was a selective factor behind the semelparous flowering cycles of some bamboos, where all individuals of a species flower in synchrony and subsequently die. These dense bamboo stands are often overtopped by forest trees; masting events, which occur at 30–100 year intervals, result in a sudden and massive accumulation of fuels that leads to crown fires, thus reducing tree canopy competition and improving conditions for bamboo seedling recruitment.

EVOLUTIONARILY STABLE FIRE STRATEGIES

Plants living in fire-prone ecosystems tend to show evolutionarily stable strategies as a response to the selective pressure exerted by recurrent fires. These strategies are often similar within the same fire regime but illustrate how regime changes result in trait changes.

Radiation Into Different Fire Regimes

Different fire regimes have selected for very different fire strategies. This is well illustrated by the genus *Pinus*, which originated in the mid-Mesozoic Era and radiated during the Cretaceous across the northern continent of Laurasia (He et al. 2012, Keeley 2012). *Pinus* has two lineages that have radiated into contrasting fire regimes. Subgenus *Strobus* has many species adapted to less competitive, low-productivity landscapes driven by low-nutrient soils and extremes in hot and cold or in high-productivity mesic forests, none of which have a highly predictable fire regime. In contrast, the subgenus *Pinus* has radiated into fire-prone ecosystems with moderate to high productivity and exhibits different fire syndromes in response to different fire regimes. These two lineages have acquired different traits to live in their non-fire-prone and fire-prone landscapes, respectively (Schwilk & Ackerly 2001).

Different combinations of fire traits such as serotiny, resprouting, thick bark, and self-pruning segregate into four clear-cut syndromes that have been specifically defined for pines (Keeley & Zedler 1998, Schwilk & Ackerly 2001, Keeley 2012): (*a*) fire-tolerator pines survive frequent understory fires thanks to their thick bark and self-pruning of the lower branches, which creates a gap between surface fuels and the canopy, and surviving trees provide a seed source for recruitment; (*b*) fire-embracer pines occur in crown-fire regimes, often as the result of slow growth rates that leave the canopy unable to outgrow surface fuels and a hot-flammable strategy that selects for the retention of dead branches and serotiny, sometimes coupled with resprouting; (*c*) fire-avoider pines occupy landscapes with limited fires, often in desert and alpine environments; and (*d*) fire-refugia pine species live in fire-prone ecosystems but survive in parts of the landscape with limited fuel loads (e.g., outcrops, riparian zones, grasslands). Most pine species can be assigned to one of these syndromes, although, in some species, the variability among populations subject to different fire regimes may reflect different syndromes (Tapias et al. 2004). These syndromes result in different population dynamics. For example, fire embracers

complete their life cycle within a single fire cycle, and populations persist on the same sites, whereas fire-refugia species have very dynamic population fluctuations, during which their range is constricted by fire then expands in subsequent years. These different population dynamics may have consequences for the genetic and evolutionary potential of the population (Castellanos et al. 2015). These syndromes were defined for pines, as they include a high level of variability of fire traits and illustrate how closely related species have evolved responses to a diversity of fire regimes. However, similar syndromes are found in a diversity of different taxonomic groups.

Mediterranean-Type Climate Ecosystems: Trade-Offs Between Resprouters and Seeders

MTC ecosystems have a highly predictable annual fire regime, essentially ensuring a fire within the life span of woody species and thus increasing the selective value of fires (Keeley et al. 2012). Evaluating trait distribution and origins in these five ecosystems (California, Mediterranean Basin, central Chile, Cape of South Africa, and Western and South Australia) highlights some of the most prominent fire-selected traits (Rundel et al. 2018). Due to winter rains with mild temperatures alternating with hot, dry summers, these regions are dominated by closed-canopy shrublands with evergreen sclerophyllous-leaved species (Mooney & Dunn 1970). This climate is conducive to high fire potential on an annual basis. All are dominated by resprouting shrubs, a globally widespread trait in woody fire-prone ecosystems, but these MTC ecosystems have lineages of woody species that have lost the resprouting capacity in favor of obligate seeding recruitment after fire (Keeley et al. 2012). In other words, reproduction is fire dependent. This is a risky life history, as there are potential costs to delaying reproduction (Gadgil & Bossert 1970), as opposed to spreading the risk out over climatically different years. Therefore, an important question is, What selective factors have led these species to invest all reproduction in a single cohort after fire? We contend the answer is that dense, closed canopy shrublands present limited opportunities for seedling recruitment, in contrast to postfire conditions. However, why do some species depend solely on resprouting (obligate resprouters) while others have given up resprouting and depend solely on postfire seedling recruitment (obligate seeders)?

In some lineages, resprouting is basal, and obligate seeding is a derived trait (Wells 1969), although that may not be universally true (e.g., Lamont & Wiens 2003). Wells (1969) hypothesized that the obligate seeding mode had been selected to produce 100% turnover of individuals, which increased the genetic variability of offspring and, in effect, sped up the rate of evolution, allowing for close tracking of environmental changes.

Ecological models have considered selective factors that affect (*a*) seedling recruitment, (*b*) adult competition, or (*c*) disturbance impacts; however, these need not be mutually exclusive. The gap-dependent recruitment model (Keeley et al. 2016) focuses on factors affecting the success of postfire seedling recruitment. This model proposes that postfire recruitment is selected against on sites where high resource availability favors a high density of resprouts but is favored on open sites with large postfire gaps favoring seedling recruitment. There is evidence that in the California *Arctostaphylos* and *Ceanothus* species there has been selection for obligate seeding

subspecies in areas of larger postfire gaps (Keeley et al. 2016; J.E. Keeley, unpublished data). Although niche conservatism of the obligate seeding mode is considered to have played an important role in the rapid diversification of these two genera, adaptive radiation (Ackerly 2009) has played, and perhaps continues to play, an evolutionary role in some taxa.

Another ecological model that illustrates the evolutionary trade-offs between seeding and resprouting can be equated to published models of the trade-offs between annuals and perennials (given a time scale of fire cycles rather than years) (Keeley et al. 2012, Pausas & Keeley 2014). Specifically, Charnov & Shaffer (1973) found that the evolutionary trade-offs between annuals and perennials (which we equate to seeding versus resprouting), could be explained by life history evolution tied to differences in adult versus seedling survivorship. Resprouting would be expected when the average postfire clutch size of an obligate seeder is increased in individuals for which survivorship is greater in juveniles than adults. Thus, when resprout success is high and seedling recruitment is low, resprouting should be of greater selective value than seedling recruitment. The seeding strategy has high selective value when resprouting success is low and seedling success is high. This is consistent with distribution of resprouters and seeders in MTC climate shrublands; typically, resprouters are most successful on mesic sites that lead to rapid dominance of resprouts that preempt space for successful seedling establishment. In contrast, seeders tend to dominate on arid, open sites that are less favorable for resprouting but have abundant gaps for seedling recruitment.

Fire frequency has been proposed to be a widespread factor controlling the selective value of resprouting versus seeding (Bellingham & Sparrow 2000). The Bellingham and Sparrow model attempts to provide a global explanation for all ecosystems but fails to appreciate the different impacts of fire regimes on plant traits. For example, adaptive traits in forests with surface-fire regimes are very different from those in crown-fire shrublands. Conclusions about trait evolution must recognize that trait evolution follows different trajectories in different fire regimes.

Despite considerable evidence for convergent evolution across the five MTC ecosystems (Rundel et al. 2018), there are marked differences that reflect different pathways in the evolution of obligate seeding shrubs. While MTC regions have similar climates, soils are markedly different; the younger and more fertile soils of California, the Mediterranean Basin, and central Chile stand in stark contrast to the much older, low-fertility, eroded landscapes of the MTC regions of South Africa and Australia (Hopper 2009). The paleontological history of fire in the more fertile MTCs has been largely controlled by climate, in contrast to the prominent role of soil infertility in producing highly flammable vegetation in South Africa and Australia.

In California, the Mediterranean Basin, and Chile, the majority of shrub genera are obligate resprouters. California has an extensive macrofossil record indicating that chaparral taxa such as *Frangula*, *Quercus*, *Rhamnus*, *Garrya*, *Prunus*, *Cercocarpus*, *Rhus*, and *Malosma* have been present in western North America in more or less their current form since the Eocene, suggesting postfire resprouting is a rather ancient trait. In contrast, three genera, *Adenostoma*, *Arctostaphylos*, and *Ceanothus*, have seeds that are triggered to germinate after fire, and in the latter two genera, the majority of species are obligate seeders; this appears to have a more recent

origin in the mid-Miocene, coincident with the rise of the MTC (Keeley et al. 2012, Rundel et al. 2018). In the Mediterranean Basin there are also many obligate resprouter taxa, e.g., *Quercus*, *Rhamnus*, *Pistacia*, *Arbutus*, *Myrtus*, *Daphne*, and *Viburnum*, which occurred early in the fossil record, but genera such as *Cistus* and some legumes that are obligate seeders appear to be of more recent origin (Herrera 1992, Guzmán & Vargas 2009).

In contrast, in infertile ecosystems, including South African fynbos and southern Australian heathlands, obligate resprouters are less common, and postfire seeding (by both obligate and facultative seeders) is widespread in many genera (Keeley et al. 2012). The phylogenetic evidence for these postfire seeders supports an origin in the early Cenozoic (Crisp & Cook 2013). This early origin of seeding is hypothesized to have been a response to a predictable fire regime, initially driven not by the MTC but rather the arid-type vegetation induced by infertile soils (Keeley et al. 2012, Rundel et al. 2018).

Savanna Strategies

Temperate and tropical savannas are some of most extensive fire-prone ecosystems, but unlike MTC ecosystems, they are characterized by a lower intensity surface-fire regime, which has selected for a different suite of trait syndromes, mostly based on survival rather than postfire recruitment. Two dominant and coexisting life forms are flammable grasses, which resprout readily after fire, and less flammable trees. These grasses are typically C_4 grasses with rapid growth rates capable of carrying annual fires (Keeley & Rundel 2005). Trees survive high fire frequency by growing quickly, which helps to positioning their crowns above the flame height (Bond et al. 2012), and producing thick bark, which protects the cambium and the stem buds that produce epicormic resprouts (Charles-Dominique et al. 2015). If we break this system into component parts, we recognize that grasses exist in a crown-fire regime, whereas the trees exist in a surface-fire regime; not surprisingly, these two components have traits that resemble crown-fire and surface-fire trait syndromes. Within the crown-fire component are geoxyles, woody plants with an extensive underground woody base, and like their associated grasses, they are vigorous resprouters (Simon et al. 2009, Pausas et al. 2018).

These savannas are quite unlike MTC ecosystems, as seedling recruitment is limited, and obligate seeders unknown, a strategy not expected to be successful under a frequent-fire regime. Seed germination is not generally restricted to postfire conditions, but some species show enhanced germination after heat shock and smoke (Daibes et al. 2019).

Boreal Forests

Boreal forest types comprise the world's largest terrestrial biome and are highly fire prone. These forests are dominant at high latitudes in North America, Europe, and Asia and are subject to 6–8 months of freezing temperatures. Considering the extensive range of the boreal forest biome, it contains different community associations with a variety of fire adaptations and, not surprisingly, trait syndromes adapted to very different fire regimes.

These differences have been highlighted as evidence for distinctly different fire regimes

between North American and Eurasian boreal forests despite similar climates (Rogers et al. 2015), although soils were not considered. Many North American boreal landscapes are dominated by slow-growing pines and spruces that accumulate dead branches and are conducive to high-intensity crown fires, and many of these have serotinous cones (Johnson 1992). In contrast, a common dominant plant in European boreal forests is *Pinus sylvestris*, a faster-growing, taller species that prunes dead branches and thus is often associated with surface-fire regimes (Conard & Ivanova 1997).

Rogers et al. (2015) contend that differences in species composition and their associated traits cause these differences in fire regimes. This example illustrates a need to distinguish proximate causes from ultimate causation. Proximate causes are the mechanisms directly underlying the behavior, whereas the ultimate causes are the selective processes that have shaped these traits. The proximate causes of differences in boreal fire regimes are certainly tied to species composition and associated traits; however, this does not address the ultimate causation. One model that addresses ultimate causation (figure 1 in Keeley & Zedler 1998) contends that fire regimes are a function of site productivity and fire return interval. As discussed in earlier sections (section 'Radiation Into Different Fire Regimes'), forests with moderately high productivity result in trees that grow rapidly, outgrow the surface fuels, and are thus conducive to surface-fire regimes; when fire frequency is high, this is associated with selection for traits that enhance tree survival such as thick bark and self-pruning of dead branches. Less productive environments produce slower growth rates, making trees vulnerable to crown fires, which has selected for traits such as retention of dead branches that enhance flammability and serotinous cones. There is some evidence of differences in site productivity between North American and Eurasian boreal forests (Gower et al. 2001) consistent with this hypothesis. A rigorous test of this is complicated by the fact that even within boreal regions there is substantial spatial and temporal variation in fire regimes (e.g., Sannikov & Goldammer 1996, Hanes et al. 2019).

CONCLUSIONS

An understanding of fire regimes is critically important given the rapid global changes we see unfolding. Fire-adaptive traits that have evolved over eons are now faced with more rapid changes due to direct and indirect human impacts. Some traits such as resprouting occur in a wide range of fire regimes, whereas others are restricted to a small subset of regimes. Perhaps most vulnerable are those taxa that have the obligate seeding postfire response, as they have invested their future in a single burst of postfire reproduction (Pausas & Keeley 2014). This is risky because this strategy is highly dependent on fire intervals long enough to allow for sufficient seed banks to develop (but not so long as to incur senescence risk). Obligate-seeding species are sensitive to changes in fire regime, in particular increased fire frequency (Enright et al. 2015). Human perturbations are having major impacts on fire regimes (Keeley & Pausas 2019). For example, in many MTC ecosystems, humans are the primary ignition source for wildfires, and as populations grow, so too do the chances of shorter fire return intervals. In

California chaparral it is widely accepted that the natural fire regime is a fire interval of 30–130 years; however, in recent decades we have been seeing much shorter intervals. Many studies have shown that short intervals can extirpate species (Zedler 1995, Pausas & Keeley 2014, Enright et al. 2015, Turner et al. 2019), and research now shows that the current fire frequency with 10–15 year intervals is lethal to species in the two most diverse shrub genera in California, *Arctostaphylos* and *Ceanothus*, leading in some cases to marked declines in biodiversity (J.E. Keeley, Brennan, Syphard, unpublished data).

Global warming is an additional threat, as it is expected to change fire regimes. However, climate-related factors fail to explain all of the complexity of global fire-regime changes, as many direct anthropogenic impacts play major roles (Pausas & Keeley 2021). As an example, although models show that one obligate-seeding shrub is projected to be threatened by global warming, more immediate threats from population growth resulting in habitat destruction may extirpate this species long before climate change is involved (Lawson et al. 2010). That study illustrates the need for broader concern about all global changes occurring now and predicted to continue into the future.

Overall, evolutionary fire ecology not only provides an understanding of the origin and history of our biota, it also sets the basis for the management of our ecosystems in a world undergoing fire-regime changes.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

LITERATURE CITED

Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.* 164:165–84

Ackerly DD. 2009. Evolution, origin and age of lineages in the Californian and Mediterranean floras. *J. Biogeogr.* 36:1221–33

Axelrod DI. 1958. Evolution of the Madro-Tertiary geoflora. *Bot. Rev.* 24:433–509

Belcher CM. 2013. *Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science*. Chichester, UK: Wiley-Blackwell

Bellingham PJ, Sparrow AD. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89:409–16

Bond WJ. 2015. Fires in the Cenozoic: a late flowering of flammable ecosystems. *Front. Plant Sci.* 5:749

Bond WJ, Cook GD, Williams RJ. 2012. Which trees dominate in savannas? The escape hypothesis and eucalypts in northern Australia. *Austral Ecol.* 37:678–85

Bond WJ, Midgley JJ. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 73:79–85

Bond WJ, Scott AC. 2010. Fire and the spread of flowering plants in the Cretaceous. *New Phytol.* 188:1137–50

Brown NAC. 1993. Seed germination in the fynbos fire ephemeral, *Syncarpha vestita* (L) B-Nord is promoted by smoke, aqueous extracts of smoke and charred wood derived from burning the ericoid-leaved shrub, *Passerina vulgaris* Thoday. *Int. J. Wildland Fire.* 3:203–6

Burrows GE. 2021. Gymnosperm resprouting—a review. *Plants* 10:2551

Byers BA, DeSoto L, Chaney D, Ash SR, Byers AB, et al. 2020. Fire-scarred fossil tree from the Late Triassic shows a pre-fire drought signal. *Sci Rep.* 10:20104

Bytebier B, Antonelli A, Bellstedt DU, Linder HP. 2011. Estimating the age of fire in the Cape flora of South Africa from an orchid phylogeny. *Proc. R. Soc. B.* 278:188–95

Castellanos MC, González-Martínez SC, Pausas JG. 2015. Field heritability of a plant adaptation to fire in heterogeneous landscapes. *Mol. Ecol.* 24:5633–42

Chalwell STS, Ladd PG. 2005. Stem demography and post fire recruitment of *Podocarpus drouynianaus*: a resprouting non-serotinous conifer. *Bot. J. Linn. Soc.* 149:433–49

Charles-Dominique T, Beckett H, Midgley GF, Bond WJ. 2015. Bud protection: a key trait for species sorting in a forest-savanna mosaic. *New Phytol.* 207:1052–60

Charnov EL, Schaffer WM. 1973. Life-history consequences of natural selection: Cole's result revisited. *Am. Nat.* 107:791–93

Chen Y, Morton DC, Andela N, van der Werf GR, Giglio L, Randerson JT. 2017. A pan-tropical cascade of fire driven by El Niño/Southern Oscillation. *Nat. Ecol. Evol.* 7:906–11

Cochrane MA. 2003. Fire science for rainforests. *Nature* 421:913–19

Collinson ME. 2002. The ecology of Cainozoic ferns. *Rev. Palaeobot. Palynol.* 119:51–68

Conard SG, Ivanova GA. 1997. Wildfire in Russian boreal forests—potential impacts of fire regime characteristics on emissions and global carbon balance estimates. *Environ. Pollut.* 98:305–13

Cressler WL. 2001. Evidence of earliest known wildfires. *Papaios* 16:171–74

Crisp MD, Burrows GE, Cook LG, Thornhill AH, Bowman DMJS. 2011. Flammable biomes dominated by eucalypts originated at the Cretaceous–Palaeogene boundary. *Nat. Commun.* 2:193

Crisp MD, Cook LG. 2013. How was the Australian flora assembled over the last 65 million years? A molecular phylogenetic perspective. *Annu. Rev. Ecol. Evol. Syst.* 44:303–24

Cui X, Paterson AM, Wyse SV, Alam MA, Maurin KJL, et al. 2020. Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nat. Plants.* 6:355–59

Daibes LF, Pausas JG, Bonani N, Nunes J, Silveira FAO, Fidelis A. 2019. Fire and legume germination in a tropical savanna: ecological and historical factors. *Ann. Bot.* 123:1219–29

Dantas VL, Batalha MA, Pausas JG. 2013. Fire drives functional thresholds on the savanna–forest transition. *Ecology* 94:2454–63

de Lange JH, Boucher C. 1990. Autecological studies on *Audouinia capitata* (Bruniaceae). I: Plant-derived smoke as a seed germination cue. *S. Afr. J. Bot.* 56:700–3

Del Tredici P. 2001. Sprouting in temperate trees: a morphological and ecological review. *Bot. Rev.* 67:121–40

Dixon KW, Roche S, Pate JS. 1995. The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* 101:185–92

Downes KS, Lamont BB, Light ME, van Staden J. 2010. The fire ephemeral *Tersonia cyathiflora* (Gyrostemonaceae) germinates in response to smoke but not the butenolide 3-methyl-2*H*-furol[2,3-*c*]pyran-2-one. *Ann. Bot.* 106:381–84

Downes KS, Light ME, Pošta M, Kohout L, van Staden J. 2014. Do fire-related cues, including smoke-water, karrikinolide, glyceronitrile and nitrate, stimulate the germination of 17 *Anigozanthos* taxa and *Blancoa canescens* (Haemodoraceae)? *Aust. J. Bot.* 62:347–58

Downing WM, Krawchuk MA, Meigs GW, Haire SL, Coop JD, et al. 2019. Influence of fire refugia spatial pattern on post-fire forest recovery in Oregon's Blue Mountains. *Landscape Ecol.* 34:771–92

Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ. 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Front. Ecol. Environ.* 13:265–72

Falcon-Lang HJ. 2000. Fire ecology in the Carboniferous tropical zone. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 164:355–71

Figueiral I, Mosbrugger V, Rowe NP, Utescher T, Jones TP, et al. 2002. Role of charcoal analysis for interpreting vegetation change and paleoclimate in the Miocene Rhine Embayment (Germany). *Palaios* 17:347–65

Flematti GR, Ghisalberti EL, Dixon KW, Trengove RD. 2004. A compound from smoke that promotes seed germination. *Science* 305:977

Flematti GR, Merritt DJ, Piggott MJ, Trengove RD, Smith SM, et al. 2011. Burning vegetation produces cyanohydrins that liberate cyanide and stimulate seed germination. *Nat. Commun.* 2:360

Frederiksen NO. 1991. Pulses of middle Eocene to earliest Oligocene climatic deterioration in southern California and the Gulf Coast. *Palaios* 6:564–71

Gadgil M, Bossert WH. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1–

24

Gagnon PR, Passmore HA, Platt WJ, Myers JA, Paine CET, Harms KE. 2010. Does pyrogenicity protect burning plants? *Ecology* 91:3481–86

Gould SJ, Vrba ES. 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15

Gower ST, Krankina O, Olson RJ, Apps M, Linder S, Wang C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* 11:1395–411

Greenwood D. 1994. Palaeobotanical evidence for Tertiary climates. In *History of the Australian Vegetation: Cretaceous to Recent*, ed. RS Hill, pp. 44–59. Cambridge, UK: Cambridge Univ. Press

Groom PK, Lamont BB. 2015. *Plant Life of Southwestern Australia: Adaptations for Survival*. Berlin: De Gruyter Open Ltd.

Guzmán B, Vargas P. 2009. Historical biogeography and character evolution of Cistaceae (Malvales) based on analysis of plastid rbcL and trnL-trnF sequences. *Organ. Div. Evol.* 9:83–99

Hanes CC, Wang X, Jain P, Parisien M-A, Little JM, Flannigan MD. 2019. Fire-regime changes in Canada over the last half century. *Can. J. For. Res.* 49:256–69

Harris TM. 1958. Forest fire in the Mesozoic. *J. Ecol.* 46:447–53

He T, Lamont BB, Downes KS. 2011. Banksia born to burn. *New Phyto.* 191:184–96

He T, Pausas JG, Belcher CM, Schwilk DW, Lamont BB. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytol.* 194:751–59

Heckenhauer J, Samuel R, Ashton PS, Turner B, Barfuss MHJ, et al. 2017. Phylogenetic analyses of plastid DNA suggest a different interpretation of morphological evolution than those used as the basis for previous classifications of Dipterocarpaceae (Malvales). *Bot. J. Linn. Soc.* 185:1–26

Hernández-Serrano A, Verdú M, González-Martínez SC, Pausas JG. 2013. Fire structures pine serotiny at different scales. *Am. J. Bot.* 100:2349–56

Herrera CM. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* 140:421–446

Herring JR. 1985. Charcoal fluxes into sediments of the North Pacific Ocean: the Cenozoic of burning. In *The Carbon Cycle and Atmospheric CO2: Natural Variations Archean to Present,* eds TT Sundquist, WS Broecker, pp. 419–42. Washington, DC: Am. Geophys. Union

Hopper SD. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322:49–86

Johnson EA. 1992. *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*. Cambridge, UK: Cambridge Univ. Press.

Keeley JE. l991. Seed germination and life history syndromes in the California chaparral. *Bot. Rev.* 57:81116

Keeley JE. 1993. Smoke-induced flowering in the fire-lily *Cyrtanthus ventricosus*. *S. Afr. J. Bot.* 59:638

Keeley JE. 2006. Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. *Madroño* 53:373–79

Keeley JE. 2012. Ecology and evolution of pine life histories. *Ann. For. Sci.* 69:445–53

Keeley JE, Bond WJ. 1997. Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecol.* 133:153–67

Keeley JE, Bond WJ. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *Am. Nat.* 154:383–91

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16:406–11

Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012. *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge, UK: Cambridge Univ. Press

Keeley JE, Fotheringham CJ. 1997. Trace gas emissions and smoke-induced seed germination. *Science* 276:1248–50

Keeley JE, Keeley MB, Bond WJ. 1999a. Stem demography and post-fire recruitment of a resprouting serotinous conifer. *J. Veget. Sci.* 10:69–76

Keeley JE, Ne'eman G, Fotheringham CJ. 1999b. Immaturity risk in a fire-dependent pine. *J. Medit. Ecol.* 1:41–48

Keeley JE, Parker TV, Vasey MC. 2016. Resprouting and seeding hypotheses: a test of the gap-dependent model using resprouting and obligate seeding subspecies of *Arctostaphylos*. *Plant Ecol.* 217:743–50

Keeley JE, Pausas JG. 2018. Evolution of "smoke" induced seed germination in pyroendemic plants. *S. Afr. J. Bot.* 115:251–55

Keeley JE, Pausas JG. 2019. Distinguishing disturbance from perturbations in fire-prone ecosystems. *Int. J. Wildland Fire* 28:282–87

Keeley JE, Rundel PW. 2005. Fire and the Miocene expansion of C_4 grasslands. *Ecol. Lett.* 8:683–90

Keeley JE, Zedler PH. 1998. Evolution of life histories in *Pinus*. In *Ecology and Biogeography of* Pinus, ed. DM Richardson, pp. 219–50. Cambridge, UK: Cambridge Univ. Press

King RA, Menges ES. 2018. Effects of heat and smoke on the germination of six Florida scrub species. *South Afr. J. Bot.* 115:223–30

Kumar M, Tewari R, Chatterjee S, Mehrotra NC. 2011. Charcoalified plant remains from the Lashly Formation of Allan Hills, Antarctica: evidence of forest fire during the Triassic Period. *Episodes* 34:109–18

Ladd PG, Midgley JJ, Nield AP. 2013. Serotiny in southern hemisphere conifers. *Aust. J. Bot.* 61:486–96

Lamont BB, Downes KS. 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecol.* 212:2111–25

Lamont BB, El-ahmir SM, Lim SL, Groom PK, He T. 2017. Contribution of transition and

stabilization processes to speciation is a function of the ancestral trait state and selective environment in *Hakea*. BioRxiv 20737. https://doi.org/10.1101/207373

Lamont BB, He T. 2017. Fire-proneness as prerequisite for the evolution of fire-adapted traits. *Trends Plant Sci*. 22:278–88

Lamont BB, He T, Yan Z. 2019. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biol. Rev.* 94:903–28

Lamont BB, Pausas JG, He T, Witkowski ETF, Hanley ME. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. *Crit. Rev. Plant Sci.* 39:140–72

Lamont BB, Wiens D. 2003. Are seed set and speciation rates always low among species that resprout after fire, and why? *Evol. Ecol.* 17:277–92

Lauder GV, Leroi AM, Rose MR. 1993. Adaptations and history. *Trends Ecol. Evol.* 8:294–97

Lawson DM, Regan HM, Zedler PH, Franklin J. 2010. Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Glob. Chang. Biol*. 16:2518–29

Le Maitre DC, Brown PJ. 1992. Life cycles and fire-stimulated flowering in geophytes. In *Fire in South African Mountain Fynbos*, ed. BW Van Wilgen, DM Richardson, FJ Kruger, HJ Van Hensberge, pp. 145–60. Berlin: Springer-Verlag

Li H-L, Wang W, Mortimer PE, Li R-Q, Li D-Z, et al. 2015. Large-scale phylogenetic analyses reveal multiple gains of actinorhizal nitrogen-fixing symbioses in angiosperms associated with climate change. *Sci. Rep.* 5:14023

Martin HA. 1996. Wildfires in past ages. *Proc. Linn. Soc. N.S.W.* 116:3–18

Mason HL. 1947. Evolution of certain floristic associations in western North America. *Ecol. Monogr.* 17:201–10

Mays C, Cantrill DJ, Bevitt JJ. 2017. Polar wildfires and conifer serotiny during the Cretaceous global hothouse. *Geology* 45:1119–22

Mezquida ET, Benkman CW. 2005. The geographic selection mosaic for squirrels, crossbills and Aleppo pine. *J. Evol. Biol.* 18:348–57

Mooney HA, Dunn EL. 1970. Convergent evolution of Mediterranean climate evergreen sclerophyll shrubs. *Evolution* 24:292–303

Moreira B, Tormo J, Estrelles E, Pausas JG. 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. *Ann. Bot.* 105:627–35

Mutch RW. 1970. Wildland fires and ecosystems—a hypothesis. *Ecology* 51:1046–51

Ne'eman G, Arianoutsou M. 2021. Mediterranean pines – adaptations to fire. In *Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin*, eds. G Ne'eman, Y Osem, pp. 457–80. Cham, Switz.: Springer Int. Publ.

Ojeda F, Brun FG, Vergara JJ. 2005. Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. *New Phytol.* 168:155–65

Pausas JG, Alessio GA, Moreira B, Corcobado G. 2012. Fires enhance flammability in *Ulex parviflorus*. *New Phytol*. 193:18–23

Pausas JG, Alessio GA, Moreira B, Segarra-Moragues JG. 2016. Secondary compounds enhance

flammability in a Mediterranean plant. *Oecologia* 180:103–10

Pausas JG, Keeley JE. 2009. A burning story: the role of fire in the history of life. *BioScience* 59:593–601

Pausas JG, Keeley JE. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol.* 204:55–65

Pausas JG, Keeley JE. 2017. Epicormic resprouting in fire-prone ecosystems. *Trends Plant Sci.* 22:1008–15

Pausas JG, Keeley JE. 2021. Wildfires and global change. *Front Ecol. Environ.* 19:387–95

Pausas JG, Keeley JE, Schwilk DW. 2017. Flammability as an ecological and evolutionary driver. *J. Ecol.* 105:289–97

Pausas JG, Lamont BB. 2022. Fire-released seed dormancy – a global synthesis. *Biol. Rev.* https://doi.org/10.1111/brv.12855

Pausas JG, Lamont BB, Paula S, Appezzato-da-Gloria B, Fidelis A. 2018. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytol.* 217:1435–48

Pausas JG, Su W-H, Luo C, Shen Z. 2021. A shrubby resprouting pine with serotinous cones endemic to Southwest China. *Ecology* 102:e03282

Perry DA, Lotan JE. 1979. A model of fire selection for serotiny in lodgepole pine. *Evolution* 33:958–68

Peterson GL, Abbott PL. 1979. Mid-Eocene climatic change, Southwestern California and Northwestern Baja California. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 26:73–87

Pigliucci M, Kaplan J. 2000. The fall and rise of Dr Pangloss: adaptationism and the *Spandrels* paper 20 years later. *Trends Ecol. Evol.* 15:66–70

Pivovaroff AL, Emery N, Sharifi MR, Witter M, Keeley JE, Rundel PW. 2019. The effect of ecophysiological traits on live fuel moisture content. *Fire* 2:28

Probert RJ. 2000. The role of temperature in the regulation of seed dormancy and gemination. In *The Ecology of Regeneration in Plant Communities*, ed. M Fenner, pp. 261–92. Wallingford, UK: CABI

Reilly MJ, Monleon VJ, Jules ES, Butz RJ. 2019. Range-wide population structure and dynamics of a serotinous conifer, knobcone pine (*Pinus attenuata* L.), under an anthropogenically-altered disturbance regime. *For. Ecol. Manag.* 441:182–91

Rogers BM, Soja AJ, Goulden ML, Randerson JT. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nat. Geosci.* 8:228–34

Rundel PW, Arroyo MTK, Cowling RM, Keeley JE, Lamont B, et al. 2018. Fire and plant diversification in Mediterranean-climate regions. *Front. Plant Sci.* 9:851

Sannikov SN, Goldammer JG. 1996. Fire ecology of pine forests of northern Eurasia. In *Fire in Ecosystems of Boreal Eurasia*, eds. JG Goldammer, VV Furyaev, pp. 151–67. Dordrecht, Neth.: Springer Netherlands

Schwilk DW. 2003. Flammability is a niche-construction trait: Canopy architecture affects fire intensity. *Am. Nat.* 162:725–33

Schwilk DW, Ackerly DD. 2001. Flammability and serotiny as strategies: correlated evolution in

pines. *Oikos* 94:326–36

Schwilk DW, Keeley JE. 2006. The role of fire refugia in the distribution of *Pinus sabiniana* (Pinaceae) in the southern Sierra Nevada. *Madroño* 53:364–72

Schwilk DW, Kerr B. 2003. Genetic niche-hiking: an alternative explanation for the evolution of flammability. Oikos 99:431–42

Scott AC. 2018. *Burning Planet: The Story of Fire through Time*. Oxford, UK: Oxford Univ. Press

Scott AC, Glasspool IJ. 2006. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. Proc. Natl. Acad. Sci. USA. 103:10861–65

Simon MF, Grether R, De Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009. Recent assembly of the Cerrado, a Neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *PNAS* 106:20359–64

Sloan LC, Barron EJ. 1990. "Equable" climates during Earth history? *Geology* 18:489–92

Snyder JR. 1984. The role of fire: Mutch ado about nothing? *Oikos* 43:404–5

Tapias R, Climent J, Pardos JA, Gil L. 2004. Life histories of Mediterranean pines. *Plant Ecol.* 171:53–68

Troumbis AY, Trabaud L. 1989. Some questions about flammability in fire ecology. *Acta Oecol.* 10:167–75

Turner MG, Braziunas KH, Hansen WD, Harvey BJ. 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *PNAS* 116:11319–28

Uhl D, Kerp H. 2003. Wildfires in the Late Palaeozoic of Central Europe – The Zechstein (Upper Permian) of NW-Hesse (Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 199(1):1–15

Van Staden J, Jäger AK, Light ME, Burger BV. 2004. Isolation of the major germination cue from plant-derived smoke. *S. Afr. J. Bot.* 70:654–59

Wells PV. 1969. The relation between mode of reproduction and extent of speciation in wood genera of the California chaparral. *Evolution* 23:264–67

Wicklow DT. 1977. Germination response in *Emmenanthe penduliflora* (Hydrophyllaceae). *Ecology* 58:201–5

Wolfe J. 1964. *Miocene Floras from Fingerrock Wash Southwestern Nevada.* Washington, DC: U.S Gov. Print. Off.

Zedler PH. 1977. Life history attributes of plants and the fire cycle: a case study in chaparral dominated by *Cupressus forbesii*. In *Proceedings of the Symposium on Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems*, ed. HA Mooney, CE Conrad, pp. 451–58. Gen. Tech. Rep. WO-3. Washington, DC: USDA Forest Service

Zedler PH. 1995. Fire frequency in southern California shrublands: biological effects and management options. In *Brushfires in California: Ecology and Management*, ed. JE Keeley, T Scott, pp. 101–12. Fairfield, WA: Int. Assoc. Wildland Fire

Zirondi HL, Ooi MKJ, Fidelis A. 2021. Fire-triggered flowering is the dominant post-fire strategy in a tropical savanna. *J. Veget. Sci.* 32:e12995