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Overview Article

The role of fire on Earth

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Abstract

Fire is a defining feature of our biosphere, having appeared when the first plants colonized the land, and it continues to occur across the planet at different frequencies and intensities. Fire has been and remains as an evolutionary force in many plant and animal lineages and contributes to explaining the variability of our biodiversity. Fire has also shaped the structure of many ecosystems and the distribution of biomes, and it is an important contributor to the global biogeochemical cycles. In addition, fire has been a key factor in human evolution, and, in turn, humans have modified fire regimes with important consequences for the biosphere. Consequently, fire is an intrinsic factor on our planet. Our challenge now is to understand and predict the role of fire in a densely populated, highly technological world that imposes significant changes on the Earth.

Keywords: disturbance ecology, human ecology, terrestrial ecosystem, fire ecology, evolution

Fire occurs on our planet because the Earth has a biosphere with flammable components (plant biomass), an atmosphere rich in oxygen (but not too rich to be a threat), processes that generate sparks (e.g., lightning), and climates with seasons that alternate between growing seasons producing green biomass and seasons that convert this biomass into available fuels. Natural fires occur when and where these components (fuel, oxygen, ignitions, seasonal drought) co-occur simultaneously (Bradstock 2010, Pausas and Keeley 2021). Fossil charcoal suggests that this has happened throughout the entire history of terrestrial ecosystems (Glasspool et al. 2004, Glasspool and Gastaldo 2024), with periods of relatively low activity and others of very high activity (Scott 2018). That is, whereas fire was once considered merely an artifact of human environmental degradation, we now know that plants have been burning since they first colonized land and have continued to burn under varying regimes throughout all geological and human history (Pausas and Keeley 2009). In this article, we review how fire has influenced major aspects of the Earth system (figure 1), including its evolutionary role (Glikson 2013, He et al. 2016, Keeley and Pausas 2022), its influence on biome distribution (Bond 2019), its impact on the organic matter cycle (Pausas and Bond 2020a), and its role in shaping the anthroposphere (Gowlett 2016), among other processes. We present recent insights in which fire plays a key role, under the thesis that fire and the Earth system have been mutually dependent for millions of years, across multiple spatial scales and levels of biological organization. That is, we argue our planet is unimaginable without fire; it has shaped the past and will continue to shape our future. Viewing fire solely as a perturbation to be avoided is a misconception that fosters a counterproductive relationship with it. The fast anthropogenic changes we are imposing on our planet are perturbing natural and sustainable fire regimes, and some of the novel fire regimes may be detrimental to current biodiversity and human societies. We need a thorough understanding of fire's role on our planet (Bowman et al. 2009, Scott et al. 2014, Archibald et al. 2018) if we are to manage fire regimes so as to minimize destructive impacts on human society while sustaining processes dependent on fire.

Fire and the global biogeochemical cycles

Fire exerts significant modifications on the atmosphere, lithosphere, and hydrosphere, playing a major role in global biogeochemical cycles.

Atmosphere: The air we breathe

Life on Earth began in an oxygen-free atmosphere (Kasting 1993). Since the evolution of photosynthesis and the subsequent increase in the complexity of land vegetation, oxygen has been continuously released into the atmosphere. The burial of organic matter, mainly in oceanic sediments, without consumption by heterotrophs, produced a net increase in oxygen. However, during the last 370 million years, oxygen concentration has remained within relatively narrow limits (approximately 17%–30%). This calls for a stabilizing feedback mechanism, and fire is the candidate (Watson et al. 1978, Lenton and Watson 2000). This is because fire is extremely responsive to the level of oxygen, and there is fossil charcoal evidence of fire from the first communities that colonized the land in the Silurian, over 400 million years ago (Glasspool et al. 2004, Scott 2018, Glasspool and Gastaldo 2024). Indeed, atmospheric oxygen fluctuations have driven shifts between a high- and low-fire world throughout Earth's history (Glasspool and Scott 2010, Belcher et al. 2013). It is suggested that the periods of high atmospheric oxygen concentration enhanced fire activity so that fire, by reducing plant biomass (e.g., forest replaced by herbaceous vegetation), limits the weathering rate by plant roots and the total amount of organic carbon that is buried and locked away in oceanic sediments (table 1). This may be due to less phosphorus being transported from the terrestrial

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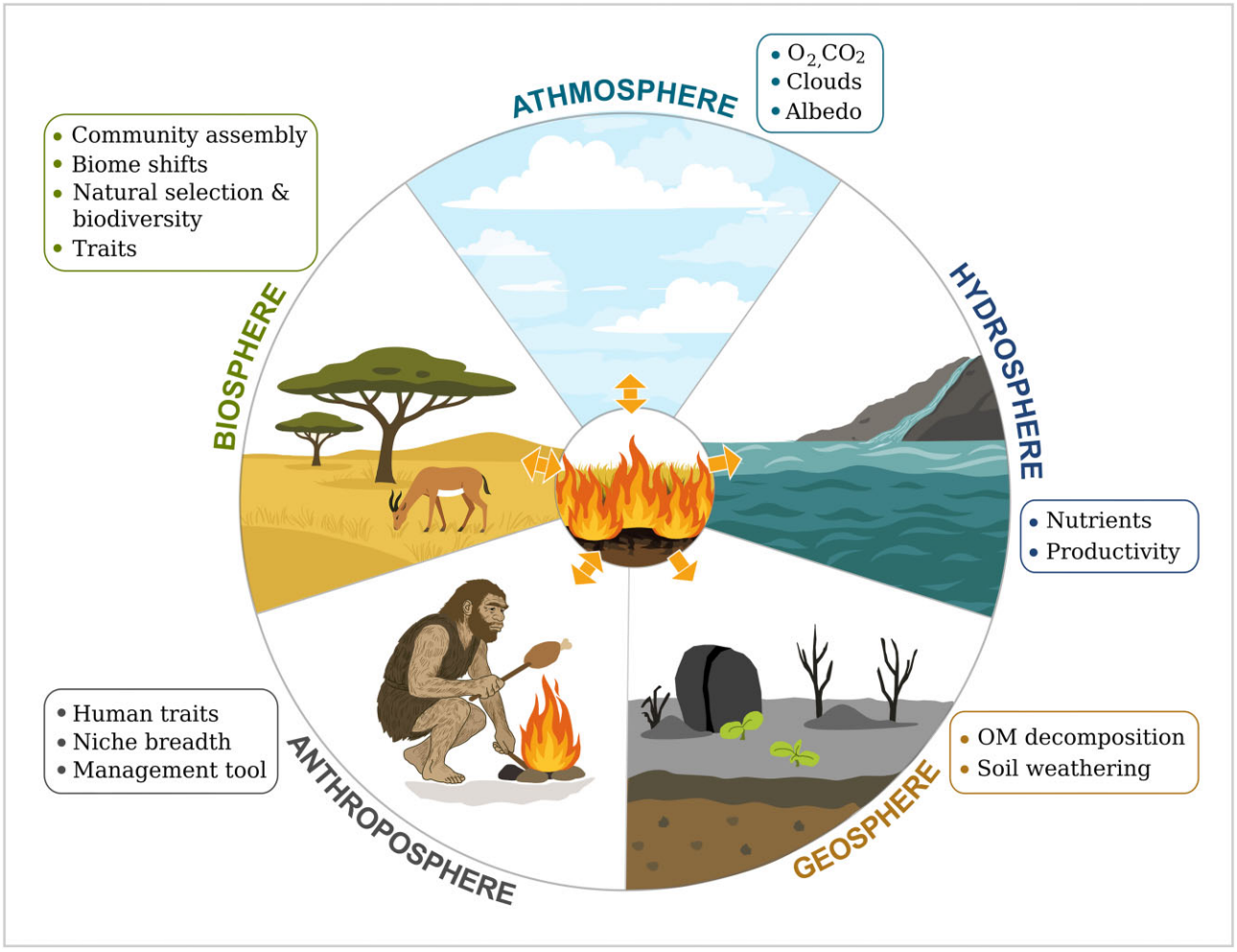

Figure 1. Fire affects all five major components of the Earth system; in some cases (atmosphere, biosphere, and anthroposphere), they may feed back and modify fire regimes. Illustration: DharmaBeren Studio (https://dharmaberen.com).

to the marine domain and limiting productivity (Kump 1988, 2010). Therefore, enhanced fire activity led to a net decrease in atmospheric oxygen levels that stabilizes the air we breathe. The exact mechanism and the strength of this feedback has been debated (Lenton 2013, Belcher et al. 2021, Vitali et al. 2022), but all evidence points to an important role of fire in the stabilization process. Life has adapted to these defined limits of oxygen, which also fall within the concentration range for sustaining fire activity without reaching the level that is destructive to components (plants) required to maintain a fire regime. That is, life and fire share the optimal window of oxygen concentration.

The smoke of fires, which includes gases, particles, ash, and soil dust, can produce ice-nucleating particles in the atmosphere and enhance the formation of cirrus clouds, sometimes far away from the fire, such as across continents (Engelmann et al. 2021, Mamouri et al. 2023). These clouds can have complex effects on the precipitation pattern (Twohy et al. 2021, Zhang et al. 2022). Under extreme fire weather conditions and high fuel amounts, fire can generate a dense, towering, vertical cloud (a pyrocumulonimbus; Pausas and Keeley 2021) that can inject a large amount of smoke into the stratosphere, which may circulate around the globe for months. This smoke reduces the radiative transfer of the atmosphere, and it therefore has a cooling effect (Kochanski et al. 2019, Blanchard-Wrigglesworth et al. 2025) similar to volcanic eruptions. Some smoke particles can be deposited on icy landscapes and therefore reduce the albedo contributing to the warmth of the Earth (Aubry-Wake et al. 2022). The effects of fire on albedo are complex and diverse. For instance, the dark postfire conditions may temporarily reduce albedo, but in snowy environments, the postfire reduction of trees may increase the exposure of snow and therefore increase the albedo. At a larger time scale, by reducing tree cover of dark evergreen conifers and promoting lighter open-canopy ecosystems, fire increases albedo and contributes to cooling (Randerson et al. 2006, Potter et al. 2020, Gayler and Skiles 2024). This cooling effect may be reduced by the northward colonization of the boreal forest tree following climate warming (Liu et al. 2005).

Lithosphere and hydrosphere: Nutrient cycling

Fire is a trophic competitor with herbivores (Bond and Keeley 2005) but differs from them in that its preferred diet is not limited by nutrients, but it plays an important role in nutrient cycling. By consuming aboveground plant biomass (green and dead), fire transforms organic matter into mineral elements available to plants, in a manner similar to soil decomposition (for dead biomass) and vertebrate herbivory (for green biomass; Pausas and Bond 2020a). Although the three decomposition drivers can be found in most ecosystems, soil decomposition dominates in moist environments; decomposition by herbivory is dominant in fertile environments, and decomposition by fire in dry and nutrient-poor

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Table 1. Examples of nonlinear dynamics and feedback loops involving fire at different scales.

	Interacting component	Process	Result	References
Climate-independent processes	Oxygen	More oxygen, more fire, less vegetation, less carbon burial, less net oxygen	Stable atmospheric oxygen concentration	Kump 1988, Lenton 2013, Belcher et al. 2021
	Vegetation	More vegetation (in seasonal climates), more fuel, more fires, lower biomass vegetation	Maintenance of fire-vegetation dynamics	
	Open ecosystems	Frequent fires, open vegetation, flammable vegetation, frequent fires	Maintenance of fire-driven savannas	Bond 2019
	Plants	Frequent fire, evolution of fire-released dormancy, evolution of flammability, frequent fire	Evolution of flammable seeder species	Bond and Midgley 1995, Pausas et al. 2017
	People	Frequent fires, fire suppression, fuel buildup, intense fires	Anthropogenic climate-independent fire regime changes	Covington and Moore 1994, Allen et al. 2002, Kreider et al. 2024
Climate-dependent processes (global warming)	Climate	Warming, more available fuel and for longer, higher intensity fires, more GHG emissions, more warming	Enhanced warming	Jones et al. 2024
	Tundra shrubs	Arctic warming, shrubification, more fires (and more intense), more shrubification	Tundra to fire-prone shrubland	Chen et al. 2024
	Permafrost	Arctic warming, permafrost thaw, fires in peatlands, GHG emission, more permafrost thaw	Enhanced warming	Gibson et al. 2018, Williams et al. 2020, Virkkala et al. 2025
	Albedo	Warming, more boreal forest fires, more grasslands, higher albedo	Cooling effect	Randerson et al. 2006

Note: We differentiate climate-independent processes (i.e., when climate is not a major factor for the process to occur although it can be a contributing factor) and climate-dependent factors that are directly driven by changes in climate (mostly global warming). *Abbreviation:* GHG, greenhouse gases.

ones (Orians and Milewski 2007). After a fire, some of the breakdown products remain at the site or nearby (ashes), including very recalcitrant forms that act as a soil carbon sink (pyrogenic carbon; Jones et al. 2019). Other forms move far from the site by air (via smoke) or across the land surface (via rain runoff) exported to other ecosystems, including aquatic ones such as rivers (Ball et al. 2021), lakes (Farruggia et al. 2024), and oceans (Riera and Pausas 2024). Ice core records also show the global effect of fire on carbon cycle (Riddell-Young et al. 2025). Consequently, wildfires can redistribute nutrients over very large spatial scales, making a great contribution to global biogeochemical cycles. For instance, African savanna fires can supply up to a half of the soluble phosphorus deposited annually in the Amazon basin (Barkley et al. 2019). That is, fire transforms organic matter into inorganic matter and spreads it out across the globe.

Fire also influences primary producers in marine ecosystems (Riera and Pausas 2024), resulting in changes in the phytoplankton composition (Kramer et al. 2020) and generating algal blooms and red tides (Tang et al. 2021, Ardyna et al. 2022, Seok et al. 2024). For instance, during the record-breaking Australian fires of 2019–2020, pyrogenic iron-rich aerosols initiated a protracted phytoplankton bloom in the Southern Pacific Ocean, lasting 4 months and surpassing previous records (Wang et al. 2022, Weis et al. 2022). This huge photosynthetic event is thought to have sequestered most of the carbon emissions from the fires (Wang et al. 2022), underscoring the critical but often underestimated role of marine ecosystems in mitigating fire emissions. There is growing evidence that wildfire emissions are important in explaining the dynamics of marine phytoplankton (Liu et al. 2022, Bergas-Masso et al. 2025), but further research would help to elucidate this dynamics (box 1).

Although fire can lower soil weathering by reducing vegetation, it also positively affects soil formation, because the heat from the fire may help break down rocks (Blackwelder 1927, Zimmerman et al. 1994; for a review, see Doerr and Shakesby 2013). Postfire sediment redistribution creates nutrient-enriched soils in depositional zones—including slope bases, riparian corridors, and floodplains—both within and downstream of burned areas (Santín and Doerr 2016). Ancient postfire erosion and deposition are prominent sedimentary process in fiery geological periods (e.g., carboniferous; Nichols and Jones 1992, Scott 2024) that contributed to shape our current landscapes.

Fire and trophic control of the distribution of ecosystems

Although climate may explain an important proportion of the variability in global vegetation types, estimates suggest that as much as a third of the vegetated land surface has a climate and soil suitable for forests but instead is covered by lower-biomass open-canopy ecosystems such as grasslands, shrublands, savannas, and open woodlands (Bond 2019). The absence of forests in those regions climatically suitable for forests is explained by the important role of plant consumers, especially vertebrate herbivores and fires (Vera 2000, Bond 2019). There is plenty of evidence suggesting that different fire regimes drive different vegetation types and different biomes (open versus closed-canopy biomes) even in similar climatic conditions (supplemental table S1); they can even cause physiological shifts such as the switch from C_3 to C_4 grasses in subtropical Miocene environments (Keeley and Rundel 2005). For instance, excluding fire (experimentally or

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Box 1. Ten challenges for better understanding fire on Earth

- Improve the understanding of the role of fire in carbon and nutrient cycling at a global scale, both in contemporary times and throughout geological history. This includes integrating terrestrial and aquatic systems (freshwater and oceans), and understanding how fires catalyze the transfer of nutrients from terrestrial to the aquatic domain.
- Improve the delimitation of fire-driven ecosystems, including alternative fire-driven vegetation states, to ensure their conservation; currently, they are often misunderstood and mismanaged. This also includes distinguishing between ecologically sustainable and unsustainable fire regimes across different ecosystems.
- Improve the understanding of evolutionary fire regimes shifts—that is, the fire regimes that shaped lineages and generated adaptations throughout geological history, as well as under contemporary novel fire regimes.
- Monitor the long-term ecological and evolutionary consequences of anthropogenic fire regimes (including prescribed and cultural burns) across the different biomes.
- Improve the understanding of the complex (non-lineal) interactions between fire and climate change. This includes understanding climate-driven fire regimes and the consequences of fires in a warmer, drier world (e.g., interactions among stressors).
- Emphasize causal understanding of fire mechanisms that avoids simply correlating changes with climate, at both ecological and evolutionary scales.
- Improve society's understanding of the role of fire—and disturbances in general—as there is currently a negative bias that is often counter to scientific evidence.
- Improve the understanding of the consequences of the different landscape-scale management techniques in different environmental and societal contexts.
- Incorporate fire thinking in urban planning and when designing nature-based solutions to global change challenges.
- Improve the understanding of the synergy between invasive plants and animals and changes in fire regimes, which can have cascading consequences for ecosystems function and services.

by fire suppression policies) in many open-canopy ecosystems dominated by shade-intolerant plants drives the systems to closed-canopy states, typically forests dominated by shade-tolerant plants. Vegetation models that simulate plant growth and ecosystem structure from daily climate input (dynamic vegetation models) predict more forested landscapes than the observed ones where fires are naturally occurring (Bond and Keeley 2005). Forestry plantations and the trees that invade open-canopy systems from them (Richardson et al. 1994, Simberloff et al. 2010) support the idea of the presence of plant consumers limiting biomass. Historical and palaeoecological data provide evidence of past shifts between savanna and forest (Gillson 2015, Aleman et al. 2018). Therefore, there are large parts of the planet (uncertain ecosystems *sensu* Bond 2019) where the vegetation is open or closed, depending on the feedback loops generated by fires (Pausas and Bond 2020b, 2022). Because the fire regime can vary in different parts of the landscape, there are mosaics of forest and nonforest ecosystems in environments suitable for forests. At a specific point on the landscape, the dominant biome may change if the fire regime changes (interannual wetter periods increase fire intervals and enhance forests; interannual dry periods reduce fire intervals and favor nonforests). Open and closed ecosystems sharing the same climate have markedly different species composition (Power et al. 2017, Aleman et al. 2020, Schwartz et al. 2025), each with a different suite of traits. For instance, fire-resistant, fire-recruiting, and fire-promoting traits are common in open ecosystems but are rare or lacking in closed ecosystems dominated by shade-tolerant fire-sensitive species (Hoffmann et al. 2003, Dantas et al. 2013, Charles-Dominique et al. 2015, 2017, 2018). Given that the two biomes are maintained by nonlinear feedback processes, intermediate cases are unstable. These alternative biome states (Pausas and Bond 2020b), which are based on the more general theory of alternative stable states (May 1977, Scheffer et al. 2015), have been demonstrated by remote sensing (bimodality; Staver et al. 2011, Hirota et al. 2011), as well as by field data (Dantas et al. 2016). Tropical forest–savanna mosaics are the best-studied case of fire-driven alternative biome states, but there is now a growing body of evidence suggesting that this occurs in many other environments beyond the tropics (table S1; Pausas and Bond 2020b), from Mediterranean (e.g., Coetsee et al. 2015, Lu et al. 2022) to cold environments (Ramírez et al. 2025). Further research would allow us to better map the relative role of alternative stable states at the global scale (box 1).

Fire is a key driver of the open, nonforested state of many mosaic ecosystems at the global scale. This role likely increased with the extinction of the megafauna as herbivory can reduce fuels sufficiently to stop fires from spreading (Johnson 2009, Karp et al. 2024). Indeed, it has been proposed that the arrival of humans in North America concurrent with disappearance of megaherbivores resulted in changes in fire regimes that had transformative impacts on postglacial vegetation (Pinter et al. 2011, O'Keefe et al. 2023). New Zealand provides another case of fire-driven vegetation shift: Following human arrival and the subsequent extinction of endemic avifauna (particularly large browsers), low-flammability vegetation was replaced by a high-flammability vegetation state with different composition, structure, and function (Perry et al. 2014).

Fire as an evolutionary force: Biodiversity

The most defining feature of Earth is life (Lovelock and Margulis 1974), and a key characteristic of life is evolution. One of the most striking functions of fire on Earth is its evolutionary role. Fire not only generates vegetation gaps and landscape heterogeneity, giving opportunities to low-competitive and shade-intolerant species, but it also selects for traits that increase fitness in fire-prone ecosystems. This was long a controversial view but has become more widely accepted in ecology and evolutionary biology (Pausas and Keeley 2023). The importance of fire in the deep past became apparent with the recognition of fossil charcoal, and with it, the role of fire in selecting growth forms in ancient landscapes (Scott 2018, 2024). From ancient fern savannas to the

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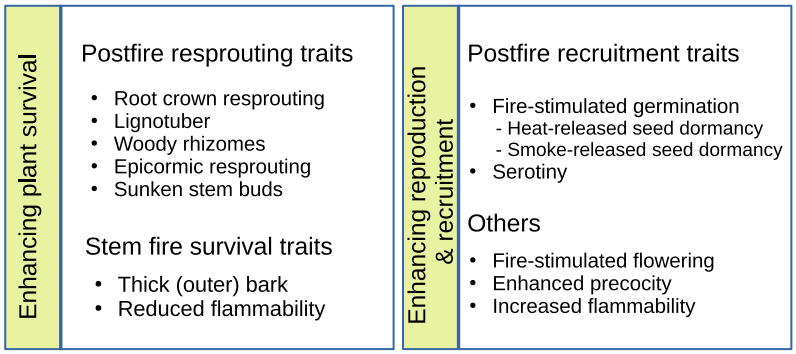

Figure 2. Main plant traits that enhance survival (left) and that enhance reproduction and recruitment (right) in fire-prone ecosystems.

Table 2. General fuel and fire regime characteristics of different ecosystem types, including the current trend (twenty-first century changes) in increasing (+) or decreasing (–) the frequency and intensity of fires, and the main driver of these changes.

		Historical fire regime		Twenty-first century changes	
Ecosystem type	**Vegetation fuels**	**Frequency**	**Intensity**	**Trend**	**Driver**
Rainforests	Low flammability woody fuels generating shady environments	Low	Low	+ frequency, + intensity	Deforestation (drought)
Grasslands, savannas	Grassy highly flammable fuels and low flammability woody species	High	Low	– frequency, + intensity	Invasive species, fire exclusion
North American boreal forests	High flammability woody fuels (conifers)	Low	High	+ frequency	Climate warming
Coniferous woodlands	Gap between surface and crown fuels	High	Low	+ intensity	Fire and herbivore exclusion
Mediterranean shrublands	Flammable woody fuels	Interm.	High	+ frequency	Ignitions, herbivores lost
Temperate deciduous forests	Litter, herbaceous plants	Low	Low	+ intensity	Fire exclusion, herbivores lost, invasive species
Arid ecosystems	High flammability fuels	Low	Low	+ frequency, + intensity	Invasive grasses

Note: Climate warming may influence flammability in most cases (Twenty-first century changes / Driver) but may not be the primary driver. The frequency of fires is classified in relation to the most common fire interval: high (less than a decade), intermediate (several decades), and low (centuries). Intensity is classified by the spread pattern of fires: high (crown fires, fueled by woody plants) and low (surface fires, fueled by grassy fuels). Mixed fire regimes are also possible.

mid-Cretaceous spread of angiosperm shrubs to the late Miocene rise of C_4 andropogonoid grasses in the tropics, major changes in terrestrial vegetation have been associated with novel fire regimes (Bond and Scott 2010, Belcher et al. 2013). Fossil evidence is reinforced by phylogenies that showed the ancient origin of many fire-related traits in plants (He et al. 2012, 2019, Lamont et al. 2019, Keeley and Pausas 2022). That is, many of those fire-related traits are plant adaptations selected through geological times as they increased survival and reproduction under recurrent fires (figure 2). And fire not only acts through natural selection, it may also generate genetic variability by enhancing mutations (He and Lamont 2018, He et al. 2019), hybridization (Ortego et al. 2017), and perhaps even polyploidy (Glennon et al. 2024). In addition, by modifying the population dynamics, fires alter the genetic diversity and structure of populations, with ecological and microevolutionary consequences (Segarra-Moragues and Ojeda 2010, Banks et al. 2013, Leonard et al. 2018, Gutiérrez-Larruscain et al. 2025).

But the relation between fire and plants is not one way; plants also modify fire regimes through their flammability, and, in fact, there is a complex ecoevolutionary dynamic among plants, community flammability, and fire (figure 2, table 1) that define global pyromes (Archibald et al. 2013). At the community scale, different ecosystems have different fuel properties that determine their fire regimes, and these fire regimes maintain the stability of communities (table 2). From the evolutionary point of view, some plants have acquired traits that increase their flammability, because burning hotter increases the probability of breaking seed dormancy of their own seed bank and decreases survival of less tolerant competitors (figure 2; Bond and Midgley 1995, Pausas et al. 2017). Other woody plants reduced their flammability to resist fire and survive in flammable fuel beds such as grassy savannas (figure 2; Pausas et al. 2017).

Fire also acts as an evolutionary pressure in animals (Pausas and Parr 2018). There is evidence of morphological adaptations in animals such as fire detectors in certain beetles (e.g., *Melanophila*; Evans 1964, 1966) or the cases of melanism for avoiding predation postfire in a variety of animals (Lillywhite et al. 1977, Forsman et al. 2011, de Alcantara Viana et al. 2024). However, many adaptations in animals are behavioral and difficult to depict (Pausas and Parr 2018, Jones et al. 2023), but they are becoming increasingly

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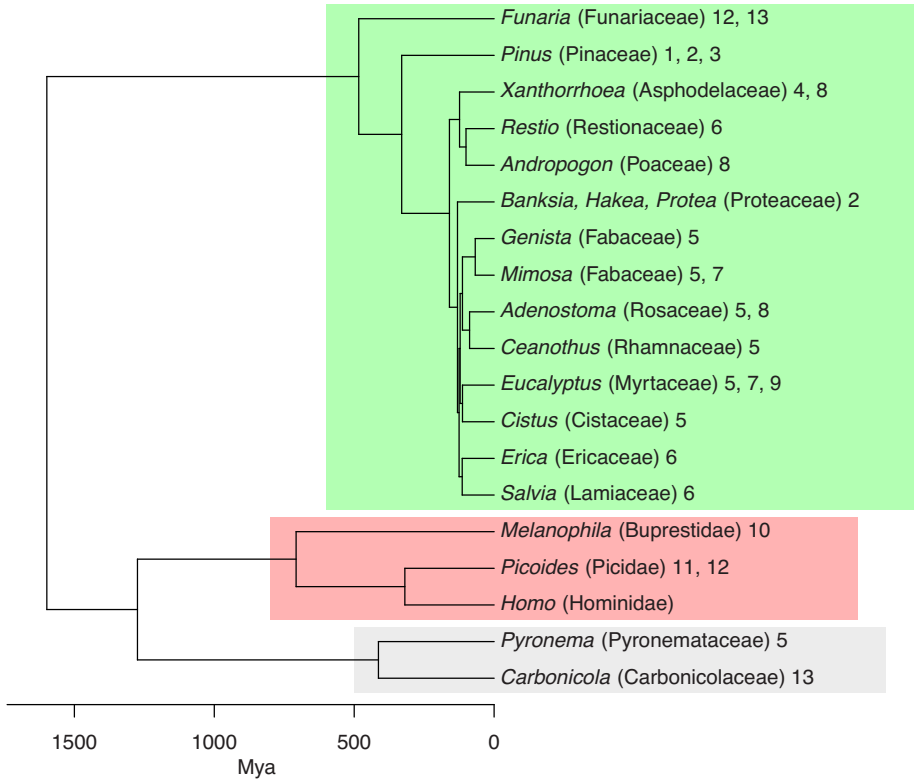

Figure 3. Iconic examples of fire-dependent (pyrophylous) taxa in the plant (top clade), animal (middle clade), and fungi (bottom clade) kingdom, and their phylogenetic relationship (eukaryote phylogeny, in millions of years). Tips of the phylogeny are genus, with family in brackets. The number indicates the fire-adaptive trait as follows (for more details and references, see table S2): 1, thick bark; 2, serotiny; 3, self-pruning (low flammability); 4, fire-stimulated flowering; 5, heat-stimulated germination; 6, smoke-stimulated germination; 7, underground woody organs (lignotuber, xylopodium); 8, high flammability; 9, epicormic resprouting; 10, infrared fire detectors; 11, dark cryptic colors; 12, postfire specialist; 13, charcoal specialist. ***Homo*** refers to ***Homo sapiens***, whose fire traits are detailed in the text. The phylogeny was elaborated with the help of TimeTree5 (Kumar et al. 2022).

apparent thanks to experimental evidence. For instance, in Australian arboreal mammals, smoke and ash presumably act as cues for torpor induction because they signal an impending lack of food after fire (Nowack et al. 2018). And mediterranean lizards from fire-prone ecosystems are more sensitive to recognizing fire smoke as a threat than lizards from populations of the same species living in non-fire-prone ecosystems (Álvarez-Ruiz et al. 2021). In addition, most animals have no specific adaptations to resist fire as they can move to safe microsites during the fire but show adaptations to fire-prone habitats (open environments maintained by fire). That is, some animals are fire dependent, despite lacking direct adaptations to fire (fire dependent versus fire adapted; Pausas and Parr 2018). And as we'll see below, humans also have traits likely selected by fire.

There are also apparent fire adaptations in fungi; for example, some species require fires for completing vital components of their life cycle (Seaver 1909, Fox et al. 2022). Typical examples are some Pezizales (e.g., Pyronemataceae; figure 3) that quickly grow and fruit almost exclusively in recently burnt areas, because not only do they have heat-resistant spores (Hughes et al. 2020), but the germination is also heat dependent (El-Abyad and Webster 1968). There are some pyrophilous Basidiomycota too (Raudabaugh et al. 2020, Hughes et al. 2020) and even lichens (e.g., *Carbonicola anthracophila*) and mosses (e.g., *Funaria hygrometrica*; Hoffman 1966) specialized on charcoal. Fire adapted plant–fungal mutualisms has also been described (Baynes et al. 2012). Some bacteria (*Arthrobacter* and *Blastococcus*) are also much more abundant in burned than in unburned soils (Fernández-González et al. 2017, Whitman et al. 2019), suggesting some fitness benefits. In addition, the smoke of fires contributes to the dispersal of bacteria and other microbes (Kobziar et al. 2018, 2022, Bonfantine et al. 2024).

In summary, there is evidence of fire adaptive traits across the entire Tree of Life (figure 3). As a consequence, many fire-prone ecosystems are biodiversity hotspots (Myers et al. 2000). In fact, there is a tendency for increasing diversity with increasing fire activity across different regions of the globe, for both plants (Pausas and Ribeiro 2017) and some animals (Moritz et al. 2023). Further research should improve our understanding of the evolutionary consequences of past and novel fire regime shifts providing more specific ideas on the role of fire as a causal agent in biodiversity (box 1; Kelly et al. 2025).

The importance of fire in creating opportunities for low-competitive and shade-intolerant species has led to the use of prescribed burns to enhance biodiversity in many ecosystems. Examples of prescribed burns for enhancing biodiversity include surface fire regimes in coniferous forests (Granström 2001, Mitchell et al. 2006), tropical savannas (Andersen et al. 2012), and grasslands (Twidwell et al. 2013). These burns are sometimes targeted to provide habitat for a very specific plant or animal species (e.g., Alexander et al. 2020). Such practices may also preserve the evolutionary potential of fire, although little research has been conducted to test this process (box 1). However, prescribed burns have also been used for an aggressive fuel reduction by increasing the frequency of fires beyond their historical range, with negative consequences for biodiversity (Pastro et al. 2011, Keeley and Pausas 2019). This highlights the importance of the fire regime concept;

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that is, species are not adapted to fire per se but to specific fire regimes. Given that different species may require different optimal fire regime characteristics, landscape-scale variation in fire regimes (pyrodiversity) often enhances biodiversity (Martin and Sapsis 1992, Ponisio et al. 2016, He et al. 2019). Further research to distinguish between ecologically sustainable and unsustainable fire regimes across different ecosystems would inform restoring fire regimes and habitats for biodiversity conservation (box 1).

Fire-shaped humans: The fire–human feedback

Fire shaped the evolution of many species, including our own iconic *Homo sapiens*, which is the only extant species known to create and control fire (Gowlett 2016). Many primates understand wildfires and predict their behavior (e.g., chimpanzees; Pruetz and LaDuke 2010) and make use of fire for their benefit (Jaffe and Isbell 2009, Herzog et al. 2014, 2022), suggesting that the conceptualization of fire may be an ancient trait in primates. The steps by which humans evolved a pyrotechnic capacity may have resulted from adapting to an increasingly fire-prone savanna environment 2–3 million years ago (Parker et al. 2016). As was discussed above, fire played a role in the expansion of savannas and other open ecosystems, which would have been a prerequisite for the evolution of endurance running, a critical human trait for acquiring the high-protein diet necessary for brain development (Bramble and Lieberman 2004). Hunting through endurance running is believed to have emerged with *Homo erectus* (Lieberman et al. 2007), and the emergence of this species from its more primitive ancestors was significantly influenced by the ability to cook with fire (Wrangham 2009). Cooking provides higher caloric intake and detoxified food, thereby expanding the variety of edible resources and offering a fitness advantage. In addition, the act of cooking and smoking meat for preservation implies a delayed food consumption, fostering the development of social skills for cooperative tasks such as gathering, cooking, and protecting food, as well as stealing it. Fire–human interaction played a role in the evolution of larger brains, smaller teeth, shorter guts, modern body proportions, and other human traits, including complex social behaviors (Wrangham 2009). For instance, by making food softer, fire may have preserved dental health and extended lifespans, which could have allowed the grandmother effect, which links extended childcare to social evolution (Hawkes 2004). Fire also facilitated human migration into colder regions, aiding human dispersal and ultimately contributing to the global distribution of *Homo sapiens* (Jiang et al. 2025). Campfires, in addition to providing protection from predators, extended the length of waking hours for social exchange of information (Pyne 1991), contributing to the important role of small talk (i.e., gossip) in generating social minds and influencing the upper thresholds of social group size (Škorić et al. 2019). Language and fire are two things that humans have brought with them wherever they have traveled throughout the world. It is tempting to speculate that watching the hypnotizing dance of the flames in a bonfire played an important role in the origin of myths, legends, and spirituality. That is, the habitual use of fire was a turning point in human evolution and in the origin of culture.

During the Paleolithic and Mesolithic, fire was widely used in practices known as *fire-stick farming* (Bird et al. 2008). This technique, which is still used today by indigenous cultures, involved the deliberate use of fire for multiple purposes, including clearing land for habitation, facilitating movement, eliminating pests, hunting, and rejuvenating plant food sources for humans and other animals. Fire was also used for tribal warfare. The Neolithic agricultural revolution saw fire employed to transform perennial vegetation into landscapes dominated by annual plants. It is suggested that people favored living in fire-prone areas because burning offered significant benefits for hunting, foraging, agriculture, and herding livestock (Pyne 1995). Fire was being used to modify rock properties for toolmaking, a precursor to metallurgy, by 130,000 years ago (Brown et al. 2009). Clearly, humans used fire to construct their niche (Kendal et al. 2011).

As human societies developed, they became less dependent on fire (and on nature in general) and more dependent on combustion. That is, humans moved from using extant fuels (wood) to high-carbon fossil fuels with higher energy density (industrialization; Glikson 2013, Pyne 2016, 2021). However, the long interaction with fire during the Paleolithic (99% of human history) left some imprints in current behaviors and a disconnect between evolutionary adaptations and cultural changes (Lieberman 2013). In contrast, the long exposure to domestic fires may have allowed humans to tolerate pollution, and this preadapted them (us) to smoke cigarettes and to live in car-dominated cities and industrial centers. It has been hypothesized that the lower sensitivity to lung cancer in human populations from cold climates was due to their higher ancestral use of fire for heating (in caves) and therefore higher historical exposure to smoke (Platek et al. 2002). The absence of placenta consumption by humans has also been linked to this heavy use of fire because the placenta accumulates toxic components from smoke; maternal placentophagy may have had deleterious consequences for the fitness of mother or offspring (Young et al. 2012).

Therefore, there is much evidence that fire shaped the biological and cultural evolution of humans. To emphasize the significant role of humans and fire throughout history, we often use the term *Pyrocene* (Pyne 2021), which can be divided into three phases (Glikson 2013): the Early Pyrocene (fire and human evolution during the Stone Age), the Middle Pyrocene (widespread use of fire as a tool beginning in the Neolithic), and the Late Pyrocene (the use of industrial combustion in more recent times; the Petrocene *sensu* Vaillant 2023, see Pausas 2025). Humans also shaped fire regimes, with increasing influence from the Neolithic to the present. The impact of humans on fire regimes is sometimes direct—that is, through burning (deliberately or accidentally) and extinguishing fires—or indirect—by changing the ecosystem and landscape structure (and therefore their flammability and fire proneness) and more recently (Late Pyrocene), by changing the climate. Many human activities contribute to these changes, some increasing fire activity (e.g., slash and burn, fire-stick farming, extinction of large herbivores) and many others reduced it (livestock husbandry, fragmentation, and fire prevention) depending on the environment and social conditions. For instances, fire use by Australian aborigines had likely shifted fire regimes from few large and relatively intense fire to many, small, low-intensity fires (Bird et al. 2024), as likely happened with other indigenous cultures (e.g., Swetnam et al. 2016). By doing so, humans changed the fire–climate relationships in many ecosystems (Bird et al. 2012, Syphard et al. 2017). The expansion of areas allocated to agriculture and livestock grazing in temperate zones reduced fuel connectivity and fire activity, and the later abandonment of those rural activities increased wildfires (Dubinin et al. 2011, Pausas and Fernández-Muñoz 2012). However, the overall tendency at the global scale is a reduction of the annual area burned due to agricultural expansion (Marlon et al. 2008, Jones et al. 2022), with some areas of recent intensifying fire activity (i.e., increasing size, frequency or severity; Westerling 2016, Scholten et al. 2021, Descals et al. 2022, Cunningham et al. 2024, Wang et al. 2025).

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The last frontier: Novel fire regimes

Atmospheric composition, climate, vegetation, and fire regimes have been relatively stable since the last Ice Age (i.e., during the Holocene), with some minor and regional variations (e.g., Medieval Warm Period, Little Ice Age). During this period, the biosphere has become relatively predictable in the distribution of climates, vegetation, and fire regimes, and many species have adapted to those conditions. The high density of humans in technologically sophisticated societies over the last few decades has disturbed this stability by significantly modifying the Earth's cover and atmospheric composition, leading to reduced biodiversity and global warming during the Late Pyrocene. Many ecosystems are experiencing a warmer, dryer, and longer flammable season, and when fire occurs, the warmer nights reduce the critical time window for slowing (or extinguishing) fires (Balch et al. 2022). As a consequence of land cover and climate changes, fire regimes are changing, often moving to the extremes of the historical variability in intensity, size, frequency, or spread rate (intensified fire regimes; e.g., Westerling 2016, Scholten et al. 2021, Descals et al. 2022, Cunningham et al. 2024, Abatzoglou et al. 2025). Fires are now occurring in ecosystems that were too wet, too cold, or too dry for fire to spread (as a response to, e.g., deforestation, climate warming, and plant invasion or afforestation, respectively; table 2). Many forests with historical fire regimes of low-intensity surface fires are now experiencing high-intensity crown fires often as a response to long-term fire exclusion (Covington and Moore 1994, Kreider et al. 2024, Parks et al. 2025). Ecosystems under historically infrequent crown fires (e.g., many boreal and mediterranean ecosystems) are now subjected to increased frequency, intensity and size, resulting in a vegetation shift (Enright et al. 2015, Turner et al. 2019), including vegetation-type conversion from native shrublands to nonnative herbaceous communities (Syphard et al. 2019) or from forest to shrublands (Coop et al. 2020). The spread of invasive plant species, especially grasses, is transforming many ecosystems by promoting frequent fires where there were few or none (D'Antonio and Vitousek 1992, Rahlao et al. 2009, Setterfield et al. 2010, Fusco et al. 2019).

Some fire regime changes may trigger adaptive responses (Guiote and Pausas 2023) but only to a limited extent because of the rapid pace of the change (Kelly et al. 2025). That is, negative consequences for the biodiversity and ecosystem functioning are expected (Enright et al. 2015, Turner et al. 2019, 2025, Coop et al. 2020, Grau-Andrés et al. 2024), with a reorganization of the assemblages and ecosystem processes. But the specific impacts on biodiversity and the extent of ecosystem resilience are still not fully understood. Intensified fire regimes—that is, with increased frequency or intensity—may have other effects on the Earth system (Bowman et al. 2020) by, for example, reducing air quality for humans and the biota (Grosvenor et al. 2024), enhancing emissions to the atmosphere (Jones et al. 2024), depleting the ozone layer (McNeill and Thornton 2023, Solomon et al. 2023), or contributing to positive temperature anomaly (Gomez et al. 2024, Zhong et al. 2024). For instance, fires are a source of greenhouse gases, notably carbon dioxide; the carbon emissions are typically balanced by postfire recovery. However, under more frequent or intense fires and postfire droughts, regeneration is limited, shifting the balance toward a carbon source that further enhances warming (box 1). In addition, wildfires are challenging massive afforestation projects aiming to sink carbon dioxide (Gómez-González et al. 2024, Stevens and Bond 2024). Another growing concern, especially with increasing global population and expansion into the wildland–urban interface and intermix, is the rising human exposure to wildfire smoke and its associated health impacts; these factors are poorly considered in wildfire impact assessments, which are typically focused more on injuries and infrastructure losses (Johnston et al. 2021, Grosvenor et al. 2024).

Implications for managing fire in the Late Pyrocene

Given the magnitude and speed of global changes, a major challenge is the management of landscapes in a way that reduces their susceptibility to novel high-intensity fires without exacerbating the negative effects on biodiversity already imposed by global warming (box 1). A range of landscape management tools can help build sustainable fire regimes; these often involve creating fuel discontinuities and landscape mosaics (e.g., vegetation clearing, prescribed burns, cultural burns, wildfire management, rewilding, traditional agriculture, and pastoralism). The appropriate tools for each landscape depend not only on the environmental and vegetation characteristics but also on the socioeconomic context (e.g., rewilding versus livestock; modern prescribed burns versus traditional cultural burning). In addition, the effectiveness of these approaches varies depending on factors such as whether the ecosystem has grassy or woody fuels and whether fires are fuel driven or wind driven (*sensu* Keeley and Syphard 2019). In some cases, the system has changed so drastically from the original ecosystem (e.g., due to heavy encroachment or invasion by alien species) that a complex combination of multiple tools may be required to redirect its dynamics.

In grasslands, long-term fire suppression and the disruption of cultural burning has led to woody plant encroachment, to the point where grasses are eliminated. In several regions, including cattle ranches in the United States and national parks in Africa, high-intensity fires have been used to reduce tree densities, open ecosystems, and promote grasses and sun-loving biota. This approach will likely become even more important in the future (Twidwell et al. 2013, Smit et al. 2016). However, in a world with high propagule pressure from alien species, fire may facilitate alien plant establishment (D'Antonio and Vitousek 1992), making fire management more challenging. Herbivores, whether wild or domestic, can be used to maintain these grasslands, whereas reintroducing cultural burning, where feasible, is another option that is gaining momentum (Long et al. 2021, Greenler et al. 2024). In many conifer forests such as those of western North America, nearly a century of fire suppression has altered the ecosystem, fuel structure, and fire regime. In North America, fuel management (particularly clearing of understory plants) has been widely practiced, and prescribed burning has been reintroduced either by the government agencies but more often by the community, rangers, and farmers. However, these management tools may not be appropriate in woody-dominated vegetation such as mediterranean shrublands, especially when fires are wind driven (Keeley and Syphard 2019).

Wind-driven fires spread through embers and firebrands, easily crossing major highways, rendering firebreaks ineffective as passive barriers to fire spread. These fires are among the most damaging in terms of property and human safety, particularly those driven by downslope hot and extremely dry winds (Abatzoglou et al. 2023), as often affect heavily urbanized coastal areas. An iconic example is the recent Los Angeles fire (January 2025), which will undoubtedly stimulate new research on fires in wildland–urban interface and intermix zones in the face of global changes in population growth and climate warming. Such catastrophes present challenges in adapting to this new fire scenario, particularly in the context of significant economic impacts

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that appear to lead to reduced environmental protections and more lenient building restrictions, likely driven by extreme real estate costs (Syphard and Keeley 2020). Similar wind-driven fires are common in many Mediterranean climate regions worldwide and have caused disproportionate damage to urban areas in western North America and other regions (Abatzoglou et al. 2023, Flores Quiroz et al. 2023, González et al. 2024). For such fires, the responsibility for controlling fire spread shifts from landscape management agencies to the building industry and homeowners, who must create fire-safe gardens and structures (Syphard and Keeley 2019, 2020). In addition, urban planning plays a critical role. The most severe damage from wildland fires often occurs in newly developed estates where houses are intermixed with vegetation. Even traditional European Mediterranean towns that are highly resilient to fires (stone-built houses and narrow streets) are now expanding in low-density patterns, making them more vulnerable to fire. Fire science integrated into urban planning would help guide the location of new developments and limit fire risk. However, fire researchers face persistent barriers in translating science through bureaucracy and socioeconomic pressures.

Under certain conditions, managing fires is becoming even more challenging. For example, boreal soils are the largest terrestrial carbon stock on Earth in one of the most rapidly warming parts of the globe (Bradshaw and Warkentin 2015). The combination of warming and fire accelerates permafrost thaw, increasing flammability, and enhancing the release of greenhouse gases (carbon dioxide and methane; table 1). These positive feedback loops are difficult to halt and are increasingly significant in Arctic ecosystems (Virkkala et al. 2025).

Considering fire when implementing nature-based solutions to global warming challenges is important (box 1). For instance, projects to plant trees, especially conifers and eucalypts, to sequester carbon generally ignore fire risk (Leverkus et al. 2022). But carbon losses from fire when plantation forests burn are much greater than from native forest or pristine grasslands that they replace and can cause major soil erosion losses (Gómez-González et al. 2024, Stevens and Bond 2024).

Conclusions

The idea that fire is born, breathes (i.e., consumes oxygen), grows, reproduces, and dies has led to the suggestion that it is a form of (nonbiological) life! Fire is not inherently alive, but like viruses, it depends on the living world to sustain itself. Fire requires a biosphere, and our biosphere cannot be fully understood without fire; the idea that "a world without fire is like a sphere without roundness; i.e., unimaginable" (Pausas and Keeley 2009) is becoming overwhelming. Fire and the biosphere are mutually dependent and deeply intertwined, sometimes in a complex manner (table 1). The profound role of fire in shaping Earth system components across geological timescales, including its impact on humans and societies, suggests that it is part of our natural heritage and should be preserved through sustainable management. Viewing fire solely as a threat to humans and ecosystems is akin to viewing rain, herbivory, or biodiversity as threats because of their potential negative impacts (such as floods, overgrazing, or toxic species) on human societies. Certainly, there are fire regimes, as well as rainfall patterns, grazing pressures, and species, that can be detrimental to humans. However, a broader, more holistic perspective on their roles at different scales and levels of organization is needed in order to understand the multifunctional role of fire on our planet (figure 1). The role of fire in shaping biodiversity, biome distribution, and the global nutrient cycling is now well documented, despite more research being needed (box 1). There is also no doubt that humans are children of fire. However, our disconnection from fire and nature is driving societies to make counterproductive decisions that have negative consequences. Therefore, current challenges are not only scientific but also the management of landscapes to coexist sustainably with fire for the benefit of both biodiversity and human populations (box 1). Humans drove most big, fierce animals extinct (Johnson 2009). Attempts to eliminate fire through fire suppression (e.g., in the United States, during the early twentieth century) seemed successful initially but merely delayed the inevitable so that heavy fuel loads now contribute to very severe fires. Land management would benefit from accepting fire as core to many ecosystems and replacing prevention and suppression policies with the management of sustainable fire regimes (e.g., Boisramé et al. 2017) and, given the complexity and changing conditions, would also benefit from being adaptive and embracing uncertainty. To do so, land and resource managers would benefit from better understanding and implementation of safety measures to reduce hazards to human settlements and of the many cascading consequences to nature of changing fire regimes. Many species may go extinct in the next few decades, but this is not the case for fire. Fire was here long before us and will be here long after we are gone.

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Author contributions

Juli G Pausas (Conceptualization, Data curation, Funding acquisition, Investigation, Visualization, Writing – original draft), Jon E Keeley (Writing – review & editing), William J Bond (Writing – review & editing).

Supplemental data

Supplemental data are available at *BIOSCI* online.

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