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Evolutionary fire ecology: An historical account and future directions

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Abstract

The idea that fire acts as an evolutionary force contributing to shaping species traits started a century ago, but had not been widely recognized until very recently. Among the first to realize this force were Edward B. Poulton, R. Dale Guthrie, and Edwin V. Komarek in animals and Willis L. Jepson, Walter W. Hough, Tom M. Harris, Philip V. Wells, and Robert W. Mutch in plants. They were all ahead of their time in their evolutionary thinking. Since then, evolutionary fire ecology has percolated very slowly into the mainstream ecology and evolutionary biology; in fact, this topic is still seldom mentioned in textbooks of ecology or evolution. Currently, there is plenty of evidence suggesting that we cannot understand the biodiversity of our planet without considering the key evolutionary role of fire. But there is still research to be done in order to fully understand fire's contribution to species evolution and to predicting species responses to rapid global changes.

Keywords: fire ecology, evolution, history, evolutionary ecology, adaptative traits

Nothing in fire science makes sense except in the light of evolution. (paraphrased from Dobzhansky 1973).

Our understanding of evolution by natural selection is largely a legacy of Charles Darwin. As a great naturalist, he observed a myriad of evidence of natural selection when traveling around the world. However, there is no evidence that he ever thought of fire as a natural phenomenon acting as a selective pressure, despite exploring fire-prone ecosystems in South America and Australia (Nicholas and Nicholas 2008). Here are some notes in the HMS *Beagle* diary (Keynes 2001) that show his contact with fire-prone ecosystems:

"*We have seen during the day the smoke from several large fires within the country: It is not easy to guess how they arise. It is too far North for the Indians and the country is uninhabited by the Spaniards*" (Keynes 2001: 95; 24 August 1832, Buenos Aires province, Argentina).

"*After having crossed the monotonous Savannahs of grass, the gardens and Orchards around the town are very pleasing*" (Keynes 2001: 316; 28 March 1835, Mendoza, Argentina).

"*In the whole country I scarcely saw a place without the marks of a fire; whether these had been more or less recent—whether the stumps were more or less black, was the greatest change which varied the uniformity so wearisome of the traveler's eye*" (Keynes 2001: 402; 19 January 1836, New South Wales, Australia).

"*We passed through large tracts of country in flames; volumes of smoke sweeping across the road and that I scarcely saw a place, without the marks of fires*" (Keynes 2001: 405; 23 January 1836, New South Wales, Australia).

Alexander von Humboldt, another great naturalist, also visited fire-prone ecosystems of South America (savannas) a few years earlier than Darwin and considered savannas as deforested environments (Pausas and Bond 2019). An evolutionary role for fire never occurred to these early explorers and naturalists because they carried a cultural bias of looking at the world through the view of Central European foresters, who considered fire as a human factor (Pausas and Bond 2019).

We have learned a lot since the early naturalists, and currently, there is overwhelming evidence that fires are very old in the geological history of the planet (Scott 2018) and that many plants and animals have adapted to the particular fire regimes they have been subject to through their history (Keeley et al. 2011, 2012, He et al. 2012, Simon and Pennington 2012, Charles-Dominique et al. 2015, Pausas 2015a,b, Pausas and Parr 2018, Lamont et al. 2019, 2020, Keeley and Pausas 2022). In the present article, we aim to make a tribute to early scientists (primarily earlier than 1970) who were ahead of their time by understanding the evolutionary force of fire, in an era when most were unconvinced or anathema to recognizing fire as a selective factor in trait evolution. These early scientists are a key part of the history of biology. Below, we ask who were those earliest researchers suggesting that fire could act as an evolutionary force generating adaptations. By doing so, we provide the first historical approach on the evolutionary adaptations to fire. Then we briefly mention why this is so important, and we end by outlining possible future directions.

In searching for old references, we focused on those published in English, because it is the language with the most information on the topic (and in science in general), although we have reviewed some papers in Romance languages (e.g., Pausas 1997). However, the possibility exists that we have missed some old references on evolutionary fire ecology from non-English researchers; if so, the authors would appreciate feedback on such omissions. And as you will see below, all early researchers with an evolutionary perspective of fire we are mentioning are male. The invisibility

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of women scientists is a long-standing problem; we would also appreciate very much feedback on any female scientists we may have omitted.

Early evolutionary fire ecology: Fauna

Edward B. Poulton (1856–1943) was an evolutionary biologist who was a strong supporter of Darwin; he was probably among the first to think that fire could generate an evolutionary pressure. And this idea came to him when investigating fire beetles (Buprestids, Coleoptera)—that is, wood-boring beetles that evolved infrared sensors to locate recently burned areas (as mating sites and an ideal environment for reproductive success).

"*Poulton said that the instinct of the beetle, like the wonderful fire-resisting powers of many Australian trees, had probably been developed in ancient times as a response to bush fires*" (Poulton 1915: iv).

It is interesting that he compared these observations of fire beetles with Australian trees, so he perhaps also thought that fire-resisting traits in plants were fire adaptations. In 1926, after his visit to Africa, he suggested another fire adaptation in animals—specifically, the adaptation of some insects to the postfire environment (fire mimicry):

"*Another difference often observable follows from the fact that a grass-fire sweeps rapidly through the dry growth and leaves the stronger stalks scorched and charred but standing. Many species are adapted to this environment not by developing a melanic form, but one in which the black and darkened straw colour are combined*" (Poulton 1926).

Increased postfire melanism was also proposed as an adaptive response to postfire environments (camouflage) in ground squirrels by R. Dale Guthrie (born 1936; Guthrie 1967). In a review of the role of fire on animal behavior, Edwin V. Komarek Jr. (1905–1995) concluded that

"*it is evident that many animals are adapted to a fire environment and that natural selection has been a major factor in such adaptation*" (Komarek 1969).

Despite those early observations (and others a few years later, e.g., Lillywhite et al. 1977), little has been done to demonstrate the role of fire as generating adaptations in the animal kingdom (Pausas and Parr 2018). Certainly, there are many examples of animals that are more abundant after a fire or in fire-prone ecosystems, suggesting that they are likely adapted to fire environments (e.g., Hutto 2008; for a review, see Pausas and Parr 2018), but few studies on animals have used an evolutionary approach in relation to fire. The mobility of animals suggests many of the adaptations to be behavioral rather than morphological (as in plants) and, therefore, more difficult to tie to fire (Pausas and Parr 2018). Apparently, early biologists were not aware of those potential behavioral adaptations; only recently, there has been an increase in behavioral studies testing the sensitivity of animals to fire cues (e.g., smoke, fire sound; Stromberg 1997, Stawski et al. 2015, Nowack et al. 2018, Álvarez-Ruiz et al. 2021, Nimmo et al. 2021). Among recent papers that have been focused on fire melanism, a key example is the study of natural selection to postfire conditions in grasshoppers (Forsman et al. 2011); apparently, no such studies have been done in vertebrates.

Early evolutionary fire ecology: Flora

The oldest published mention of a fire adaptation in plants that we are aware of is by Willis L. Jepson (1867–1946) in discussing the role of fire in the life cycle of the California chaparral shrub *Arctostaphylos sensitiva* (Jepson 1922). This is a postfire obligate seeder species—that is, a species that does not resprout but, rather, recruits profusely only after fire. As Jepson stated,

"*After fires, it reappears promptly on 'burns,' and fruits at the age of 5 or 6 years. It thus adapts itself to short fire intervals and is a true fire-type shrub*" (Jepson 1922).

Jepson also noted the large burls at the base of some *Arctostaphylos* species and the important role they played in postfire resprouting (figure 1). This is a significant observation as other early botanists who studied such structures were perplexed with their functional significance and did not draw this conclusion. For example, Kerr (1925) wrote an extensive paper on these structures that develop in seedlings of many *Eucalyptus* species and named them *lignotubers*, a structure today widely viewed as a fire adaptive trait (Keeley and Pausas 2022). He noted that, after fire, resprouts emerged from these lignotubers, but he attached no great significance to the role of fire in the evolution of this trait.

A few years later, in 1926, Walter W. Hough (1859–1935) implicitly suggested fire adaptations in trees subjected to recurrent fires (thick bark), although he did not mention the term *adaptation*:

"*If, as appears probable, forests have been swept by fire at intervals throughout their history, it is likely that there has been established in some tree species a resistance to the effect of heat. There may be seen in the thickening of the bark near the ground perhaps a protective device*" (Hough 1926: 8).

In 1958, Tom M. Harris (1903–1983) published a paper on Mesozoic (Jurassic) fires, perhaps the first paper providing evidence (fossil charcoal) of fires in deep time. This evidence of ancient fires was largely ignored until quite recently. He also mentioned the possibility of species (animals and plants) from open ecosystems having evolved because of gaps opened by fire:

"*The objection usually urged against accepting fusian as charcoal produced by fire is that there is too much of it and in too many layers.… If occurring at intervals of a few centuries they wildfires might not change the forest climax, but they would destroy patches of young or mature forests and provide a home for the animals and plants of open ground or younger stages in the forest succession.… It would help us to understand the origin of the vast number of species which today seem to depend on fire; they may have already evolved in strength and have been ready to seize the increase opportunities offered by man*" (Harris 1958: 449, 453).

Inspired by Jepson's early observations, Philip V. Wells (1928–2004), also referring to postfire nonresprouting seeders of the genus *Arctostaphylos* and *Ceanothus* (California), concluded,

"*A quickening of the tempo of evolution in major sections of Arctostaphylos and Ceanothus in California would appear to stem from their unique abandonment of the conservative, crown-sprouting mode of reproduction in favor of a nonsprouting, obligately seeding response to recurrent fire that results in a greater frequency and intensity of selection*" (Wells 1969: 266)

And in 1970, Robert W. Mutch (born 1934) proposed his famous hypothesis on the evolution of flammability (see Pausas et al. 2017 for a current review on this topic):

"*Fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favored development of characteristics that make them more flammable*" (Mutch 1970).

During the 1970s, many other researchers began to accept the evolutionary role of fire, but it was not yet widely recognized. For instance, Axelrod wrote extensively on the origin of Californian flora (Axelrod 1973, Raven and Axelrod 1978, 1989) and assigned no role to fire in the evolution of this fire-adapted flora (Keeley et al. 2012).

Figure 1. Two of the manzanitas from Jepson (1916): *Arctostaphylos glandulosa* (left) and *Arctostaphylos nummularia* (right). The former is an obligate resprouter (note the basal burl) and the latter is an obligate seeder (note the even-aged cohort). Manzanitas were among the first plants that made scientists think about the role of fire in plant evolution (Jepson 1922).

It is interesting to note that, outside the English-speaking world, there were also some researchers aware of the evolutionary role of fire during the 1970s. This is the case of Leopoldo M. Coutinho (1934–2016, Sao Paulo, Brazil), who discussed fire adaptations in South American savannas during that time (e.g., Coutinho 1976, 1977); his view was quite advanced in understanding the evolutionary role of fire compared with the mainstream knowledge (Pausas 2017).

Since the 1970s, there have been a large number of studies showing the adaptive value of many plant traits to fire (table 1). Many of those studies focused on Mediterranean-type vegetation and pine or oak woodlands, following Jepson, Wells, and Mutch, and only more recently, evolutionary fire ecology has been applied to savannas (e.g., Simon and Pennington 2012, Maurin et al. 2014). At the same time, there was the recognition that fires were ancient at the geological scale (for a review, see Scott 2018), and, therefore, rescuing Harris's ideas. The availability of molecular phylogenies in the 2000s boosted the study of plant evolution; ancestral reconstructions along phylogenies showed that fire adaptive traits are very old and their origin are often linked to geological times when fire activity was especially high (Bytebier et al. 2011, Crisp et al. 2011, He et al. 2012, Crisp and Cook 2013, Lamont et al. 2019). Therefore, the existence of fire adaptations (traits shaped by fire), in addition to fire adaptive traits (traits that confer adaptive value under fires), is now unambiguous.

Fire enlightens evolutionary biology

Despite the fact that, in the 1970s, there was already evidence of fire acting as an evolutionary process, the idea is only slowly percolating into mainstream ecology and evolutionary biology. In fact, evolutionary fire ecology is still rarely considered in most ecology textbooks. Many studies on plant ecology and evolution have either ignored fire or treated it as an incidental process without adequately considering the ecological and evolutionary feedback loops among fire, vegetation, climate, and geology. Even less studied is the interaction of fire with other evolutionary forces (e.g., drought, species interactions) in the evolution of plant traits. There are examples in the scientific literature of failures to consider fire as a possible explanation when studying ecological and evolutionary processes in fire-prone ecosystems. For instance, some of the plant mortality attributed to climate warming may be better explained by fire history (Schwilk and Keeley 2012); seed dormancy has often been suggested to be an adaptation to seasonal climates, but a more proximal explanation may be that it is a response to the fires occurring in those climates (Pausas et al. 2022); and the diversity and distribution of many species cannot be explained without considering fire (Pausas and Lamont 2018). This fire blindness is likely to be a legacy of the cultural bias by early European naturalists (Pausas and Bond 2019). However, few ecological processes are so disrupting as wildfires; they can produce large-scale disturbances consuming massive amounts of plants and affecting all organisms in a biome. But fire-prone ecosystems are hotspots of diversity, not despite fires but, at least in part, because of them (Cowling 1987, He et al. 2019). Below, we list some key contributions that fire ecology has made to evolutionary biology.

First, fire has affected plant communities from the very origin of land plants, in the Silurian (Glasspool et al. 2004); since then, fire regimes have been fluctuating as a consequence of changes in vegetation, climate, herbivores, and atmospheric oxygen concentration (Scott 2018). Therefore, fire is among the earliest disturbance processes in plant communities and among the earliest potential evolutionary pressures in land plants.

Second, fires were recurrent and predictable enough to select fire adaptive traits and contributed to the diversification of lineages, at least since the Cretaceous (Crisp et al. 2011, He et al. 2012) but probably earlier (Keeley and Pausas 2022). Therefore, fire has contributed to the evolution of many plant traits since early plant evolution.

Third, fire likely contributed to the spread and evolution of large lineages such as early angiosperms (Bond and Scott 2010) and C_4 grasses (Keeley and Rundel 2005, Scheiter et al. 2012), and it is therefore responsible for the rise of species-rich savannas (Simon et al. 2009, Maurin et al. 2014).

Fourth, fire ecology provides examples of how different regimes select for radically different adaptations across species. For instance, recurrent fires with low or with high intensity selects

Table 1. Summary of traits that are adaptive to fire-prone environments with some key references. Some of them are indicated as poorly known, but listed to stimulate further research.

Trait enhancement	Type of trait	Fire trait	Comment	References
Survival	Resprouting traits (plant survival)	Root crown	Widespread	Pausas et al. (2018)
		Lignotuber	Crown fires	Paula et al. (2016), Pausas et al. (2018)
		Woody rhizomes	Surface (and crown) fires	Maurin et al. (2014), Pausas et al. (2018)
		Epicormic resprouting	Surface fires (savannas), crown fires (e.g., eucalypts)	Charles-Dominique et al. (2015), Pausas and Keeley (2017)
		Sunken stem buds	Eucalypts, savanna trees	Burrows (2002), (2013), Charles-Dominique et al. (2015)
		Smoke-induced nutrient translocation	Poorly known	Rabideau-Childers et al. (2022)
	Stem survival	Thick (outer) bark	Surface fires	Jackson et al. (1999), Pausas (2015a)
		Reduced flammability	Surface fires, pines (self-pruning), savannas (corky strategy)	Keeley and Zedler (1998), Dantas and Pausas (2013), Pausas et al. (2017)
Reproduction and recruitment		Heat-released dormancy	Crown fires (e.g., many Fabaceae, Cistaceae)	Keeley (1991), Keeley and Fotheringham (2000), Pausas and Lamont (2022)
		Smoke-released dormancy	Crown fires (e.g., many Ericaceae and Labiatae)	Keeley (1991), Keeley and Fotheringham (2000), Pausas and Lamont (2022), Lamont and Pausas (2023)
		Seed traits enhancing seed survival	Poorly studied	Gómez-González et al. (2011), Liyanage and Ooi (2018), Tangney et al. (2019)
		Serotiny	Crown fires; large shrubs and trees	Lamont et al. (2020)
		Fire-stimulated flowering	Crown and surface fires; mainly in geophytes	Lamont and Downes (2011)
		Increased flammability (chemically or structurally)	Crown fires; associated to heat-released dormancy or serotiny	Bond and Midgley (1995), Pausas et al. (2017)
		Precocity (i.e., early reproduction)	In woody nonresprouters under short fire intervals	Guiote and Pausas (2023)
		Elaiosomes (ant dispersal)	Seed burial for insulation; Crown fires; poorly known	Berg (1975), Pausas and Lamont (2022)

contrasting traits in plants (e.g., thick bark versus serotinous cones in pines; Keeley and Zedler 1998, Pausas 2015b). Similarly, different fire frequencies also select quite different traits: high frequency (resprouting) and moderate fire frequency (postfire seeding and the loss of resprouting; Pausas and Keeley 2014). At the landscape scale, different fire regimes generate different evolutionary frameworks for a given environmental conditions (e.g., savannas versus forests; Pausas and Bond 2020).

Finally, fire ecology provides evidence that different selective regimes generate trait divergences among populations and therefore the evolution of fire related traits (Gómez-González et al. 2011, Pausas et al. 2012, Hernández-Serrano et al. 2013, Vandvik et al. 2014, Guiote and Pausas 2023, Keeley 2023). Fire, by opening vegetation gaps, provides opportunities for the evolution of many light-demanding shade-intolerant species (Bond 2019, Pausas and Lamont 2022).

That is, we cannot understand the biodiversity of our planet without considering the key evolutionary role of fire ("*a world without fires is like a sphere without roundness—i.e., we cannot imagine it*"; Pausas and Keeley 2009).

Future directions in evolutionary fire ecology

The thinking about the evolutionary role of fire started over a century ago and accelerated only recently. There is still much research to do before we fully understand the role of fire in the evolution of species. It is imperative to continue performing basic natural history observations (e.g., Keeley 2023), especially in Africa, South America, and Asia (e.g., Pausas et al. 2021), because there may be some fire strategies currently unknown. In fact, we still do not know the response of many species to fire, which makes predictions under fire regime changes difficult. This knowledge gap is occurring not only in little studied areas (e.g., Asia, tropical ecosystems) but also in areas that were not subject to fires until recently, and fire ecology therefore has had a limited tradition (e.g., Central Europe). So, plant trait databases that include fire traits need to be expanded in the number of species and geographically. There is also a bias toward woody plants in most databases. Databases may also need to include the fire characteristics (e.g., intensity, season, fire interval, fire type), because responses may be quite different depending on them. Trait databases, together with the increasing availability of phylogenetic information would also allow us to make more accurate estimations of the origin and evolutionary pathways of fire traits and, therefore, to better reconstruct the evolutionary fire history of our planet. A limitation of the phylogenetic approach is that early extinctions makes inferring deep patterns of character evolution rather difficult. For instance, fires were common in the Carboniferous, but we have been unable to trace back fire adaptations to that period. Is the abundance of rhizomes in ferns a response to those fires? (Pausas et al. 2018).

Another relevant question is how does evolution inform our predictions about how novel fire regimes will affect species and ecosystems. We have evidence that many fire related plant traits can evolve relatively rapidly under different fire regimes (e.g., Gómez-González et al. 2011, Pausas et al. 2012, Hernández-Serrano et al. 2013, Vandvik et al. 2014, Guiote and Pausas 2023, Keeley 2023). What are the limits of those evolutionary changes in the framework of our current fire regime changes? The ecoevolutionary feedback loops are also little explored; that is, plants can modify fire regimes, and these modifications can feed back to the plants with evolutionary consequences (Pausas and Bond 2022).

There is still little understanding of the evolutionary response to fire in the animal kingdom, especially because their responses are often behavioral rather than morphological, and it is therefore more difficult to pinpoint fire as a selective factor (Pausas and Parr 2018). However, changes in color, not only in invertebrates (Forsman et al. 2011), is still a research area as those changes may improve camouflage and thermoregulation in postfire conditions. Another little explored research area is how fire affects biotic interactions (e.g., García et al. 2016) and the evolutionary consequences and vice versa—that is, how biotic interactions affect the evolution of plant traits in interaction with fire (e.g., Talluto and Benkman 2014). For instances, how does fire temporarily disassembles the network of plant–animal interactions, and what are the consequences on the fitness of the interacting species? And how and to what extent do postfire dynamics reassemble those interactions?

Sequencing techniques that provide wide genome coverage are quickly advancing as their prices are plummeting, and they are therefore becoming more accessible to ecologists. This should allow us to explore the genetic footprint of traits selected by fire, as well as to study fire-driven population divergence and field heritability of fire traits (e.g., Castellanos et al. 2015). Epigenetics is also quickly advancing, and chances are that some of the fire products (smoke, ash) could produce some adaptive epigenetic changes; even processes such as postfire resprouting are likely to affect the epigenetic mosaicism with fitness consequences (Herrera et al. 2022). Therefore, epigeneitcs may be a fruitful research area for understanding quick postfire changes. Collectively, these advances should contribute to showing that fire has played an important evolutionary role.

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Author contributions

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