# Wildfires as an ecosystem service

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**Wildfires are often perceived as destructive disturbances, but we propose that when integrating evolutionary and socioecological factors, fires in most ecosystems can be understood as natural processes that provide a variety of benefits to humankind. Wildfires generate open habitats that enable the evolution of a diversity of shade-intolerant plants and animals that have long benefited humans. There are many provisioning, regulating, and cultural services that people obtain from wildfires, and prescribed fires and wildfire management are tools for mimicking the ancestral role of wildfires in an increasingly populated world.**

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Humans gain a variety of benefits from the proper functioning of natural ecosystems, commonly referred to as "ecosystem services" (MA 2005). Wildfires are a globally important and integral part of many ecosystems, playing key roles in ecosystem dynamics and the retention of species that have evolved in response to fire (Pausas and Keeley 2009). We contend that most wildfires are natural processes that provide a variety of benefits to humankind, and that in wildfire-dependent ecosystems, disturbance is manifested by disruptions in the natural fire regime, often when fires are eliminated or the frequency of burning increases (Keeley and Pausas 2019). Although conservation of natural processes should not be strictly tied to their usefulness (Silvertown 2015), it is important to review the services that wildfires provide, given that they are often seen, incorrectly, as destructive disturbances.

Fire was certainly used by early hunter–gatherer societies, although there is evidence that the use of fire originated with even earlier hominids (Burton 2011; Gowlett 2016). Ancestral hominids were frequently exposed to fire from the time they moved into open savanna environments more than 2 million years ago. Eventually, humans learned to control fire and it became embedded in human behavior; as such, use of fire may be considered an outgrowth of far older, natural fire regimes (Gowlett 2016). In addition to cooking, as a means of improving the digestibility of plant and animal foods, early human societies used fire for many other purposes, including removal of pests from campsites, provision of heat and light, and for social events (eg bonfires, rituals). Indeed, evening campfires likely played a key role in the development of communication among early humans. Agricultural societies later used fire for deforestation to create farmland and, more recently, for forest management (eg slash-and-burn). Although learning how to use and control fire is considered to be a key step in the evolution of both humans and human societies (Wrangham 2009; Burton 2011), and being a pyrophilic (fire-dependent) species radically changed the ecological niche of humans, most people today have a negative perception of wildfires.

> ### In a nutshell:
>
> - We live in a flammable world and humans have benefited from fires for millennia
> - Wildfires generate open habitats for a diversity of light-loving plants and animals; these species offer a range of goods and services (food, fiber, pollination, tourism, hunting) to humans
> - Additionally, wildfires help to control pests and catastrophic fires, contribute to the regulation of biogeochemical cycles, and can benefit plants in adapting to novel climates
> - Prescribed fires can sometimes be used to replace the original role of wildfires

We aim to summarize the benefits to humans of living in a flammable world – that is, in a world that experiences recurrent wildfires. The multiple benefits (including direct fitness benefits) of fire use for early humans are not discussed here (see Wrangham 2009; Burton 2011); instead, we focus on wildfires. Prescribed fires are often intended to mimic the benefits of wildfires, so they are also briefly discussed below, but we focus primarily on the benefits of natural (ie historical) wildfire regimes. Perturbations in these fire regimes (eg an exclusion policy, or increase in the frequency or intensity of fires) would feed back to the functioning of the ecosystem and reduce these services in the same way that major anthropogenic changes in a rainfall regime would reduce the services that precipitation provides to humans. We believe that a thorough understanding of the benefits of wildfires requires a framework that describes impacts at the evolutionary scale (at which recurrent fires shape landscapes and the biodiversity they support), as well as at the socioecological scale (at which anthropogenic modifications of fire regimes feed back to humans; Figure 1). In this framework, we define "historical fire regimes" as those in which human influence is absent (including those before humans evolved; ie those operating on evolutionary scales; Figure 1), and "anthropogenic fire regimes" as

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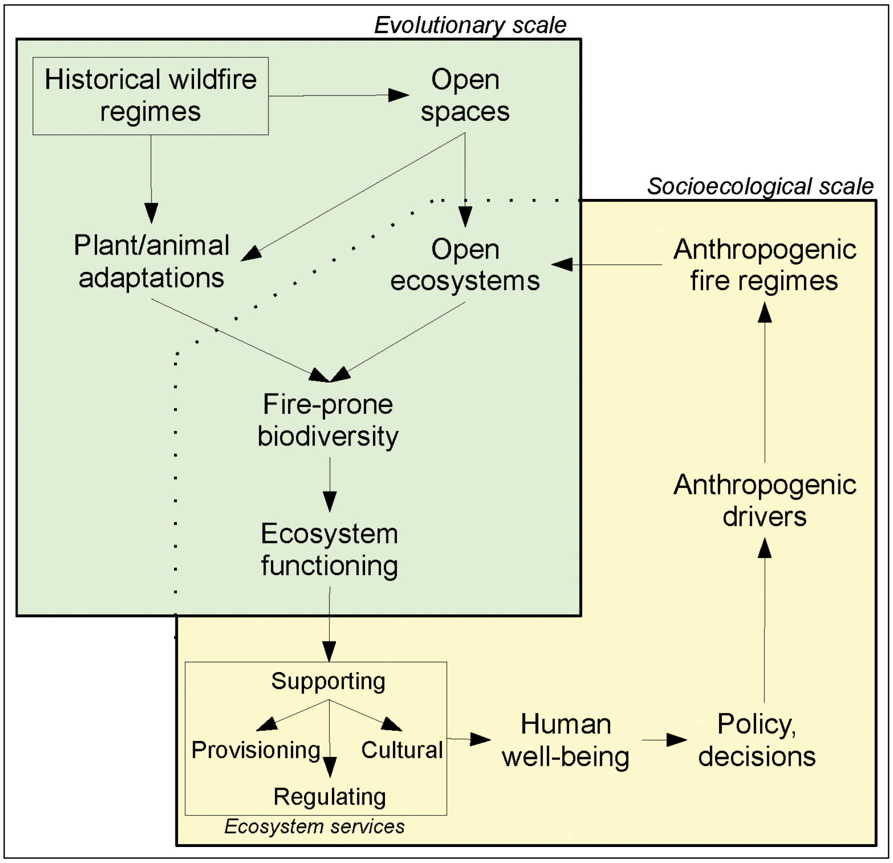


**Figure 1.** Schematic representation linking factors occurring at the evolutionary (green square) and at the socioecological (yellow square) scale associated with fire regimes and ecosystem services. Natural (historical) wildfire regimes create open habitats that can promote specific adaptations, biodiversity, and overall functioning in fire-prone ecosystems; these are the supporting services necessary for the production of all other services (Table 1). Decisions and policies may modify fire regimes (anthropogenic fire regimes) modulating ecosystem functioning and services (socioecological feedback); that is, policy decisions may switch between maintaining ecosystem services (stabilizing feedback) and generating unsustainable fire regimes (disruption of the feedback). Decisions and policies (bottom-right corner) include fire and landscape management decisions but also socioeconomic changes that have implications for fire regimes (eg rural abandonment; Pausas and Fernández-Muñoz 2012).

those modified by human activities (ie those operating on socioeconomic scales; Figure 1). Ecosystem services deriving from wildfires are grouped into four broad categories (MA 2005), consisting of supporting, provisioning, regulating, and cultural services (Figure 1). Several of these services have been poorly studied and as such are presented here as hypotheses to be tested. We also separate the services that were important to early societies (eg hunter–gatherer societies) from those that are relevant to contemporary societies (Table 1).

## Supporting services

Supporting services are usually defined as those necessary for the production of all other ecosystem services (MA 2005). The most basic ecosystem service provided by wildfires is the formation of open habitats that enable the evolution of a diversity of shade-intolerant plants and animals (Keeley *et al.* 2012, Parr *et al.* 2014; Andersen 2019). Fire is likely to contribute to a range of ecosystem services (Figure 1), given that biodiversity provides many services to humans (Isbell *et al.* 2017) and fire explains a major proportion of the variability in biodiversity (Ponisio *et al.* 2016; Pausas and Ribeiro 2017). Two general processes associated with fire are known to enhance biodiversity: evolutionary processes (via natural selection and evolution) and ecological processes (via habitat heterogeneity). The biodiversity effects of both types of processes occur because fire generates vegetation gaps.

Fires create new habitat with increased resources and reduced competition. To take advantage of such fire-generated habitat, many plants have evolved a diversity of adaptive strategies for persistence under recurrent fires (Keeley *et al.* 2012). Because fire often shortens generation time and reduces the overlap between generations (in non-resprouting plants), it promotes evolutionary novelties (Pausas and Keeley 2014). Ecologists increasingly recognize that fire may also influence several traits in animals, though these effects are less studied (Koltz *et al.* 2018; Pausas and Parr 2018).

At the ecological scale, fires generate habitat heterogeneity by opening gaps and creating snags and deadwood patches; as such, fires increase the number of potential ecological niches, which enhances evolutionary processes. There is plenty of evidence that under natural conditions many species require the open habitats that are formed and maintained by recurrent fires and grazing, with the species-rich savannas and prairies serving as obvious examples. The "pyrodiversity begets diversity" hypothesis is based on this idea (Martin and Sapsis 1992), and many prescribed fire programs focus on species conservation, including the conservation of some ecological processes (eg pollination; Brown *et al.* 2017).

## Provisioning services

Wildfires were the primary natural agent for generating and maintaining the open spaces that were often used by early human societies for gathering food and for hunting, and later for farming. Wildfires still sustain open grazing areas and create wildlife habitat, both of which benefit recreational activities such as tourism and hunting. Anthropogenic fire regimes, including the prescribed burning programs commonly used to enhance pasture quality or to facilitate hunting, have replaced many historical regimes (Figure 2).

Wildfires maintain diversity and genetic variability, thereby also contributing to the creation of a range of natural products for human consumption. For instance, to be able to resprout

 

**Table 1. Examples of ecosystem services provided by recurrent wildfires to both early and contemporary human societies**

| Type | Service | Society type |
|---|---|---|
| Provisioning | Provide open spaces for pastures, agriculture, and hunting | Early, contemporary |
| | Stimulate germination of desirable annual “crops” post-fire | Early |
| | Provide carbohydrates from underground plant organs | Early |
| | Provide craft and basketry material (resprouts) | Early |
| | Maintain open spaces for grazing and hunting | Early, contemporary |
| | Provide essences, medicines, and flowers (ornamental) | Contemporary |
| Regulating | Pest control for humans and livestock | Early, contemporary |
| | Reduce catastrophic wildfires | Early, contemporary |
| | Accelerate species replacement under changing conditions | Early, contemporary |
| | Enhance flowering and pollinator activity | Contemporary |
| | Water regulation | Early, contemporary |
| | Carbon balance | Early, contemporary |
| Cultural | Spiritual | Early |
| | Ecotourism in open ecosystems | Contemporary |
| | Recreational hunting | Contemporary |
| | Scientific knowledge about the origin of biodiversity | Contemporary |
| | Information about ancestral fire management techniques | Contemporary |

**Notes:** “Contemporary” refers mainly to Western societies; services listed as “early” may also be “contemporary” to some indigenous or rural societies.

following a fire, fire-prone ecosystems harbor a rich flora with a diversity of underground plant structures (Pausas *et al.* 2018); these species typically protect themselves from fire by storing buds and carbohydrates belowground, which humans use for food (Figure 3). Examples include many bulbs, tubers, and rhizomes that were consumed by early hominids (Dominy *et al.* 2008), and it has been suggested that dependence on these widely spaced plant resources contributed to the evolution of bipedalism (Lieberman 2013). Today, highly selected versions of these plant structures are commonly employed in gardening and horticulture. In addition, post-fire resprouts of several species were used extensively in the past as craft and basketry material, and are still in use in many rural populations and indigenous societies (eg hazel [*Corylus* spp], willow [*Salix* spp], and beargrass [*Xerophyllum tenax*] reprouts are often used by tribes in Northern California).

For plants, an annual (as opposed to perennial) life cycle is also an adaptive strategy for persisting in disturbed ecosystems, and many annual food crops originated from open, fire-prone ecosystems (Khoury *et al.* 2016). Moreover, open habitats are rich in flowers, pollinators, and herbivores, which led to the evolution of different chemical compounds to attract pollinators and deter herbivores; chemical compounds may have also evolved to enhance flammability (Pausas *et al.* 2016). Many of these compounds are now the basis for large industries (eg perfumes, drugs). All of these services would be drastically limited in a world without a long history of wildfires.

## Regulating services

### Regulation of pest populations

Early human societies used fire to clear campsites of pest species. For example, the first Europeans to explore what is now California reported that Native Americans commonly burned campsites when flea infestations became intolerable (Bolton 1927). Parasites are still a problem for humans and livestock, and fire has often proven effective in reducing parasite


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**Figure 2.** (a) Wildfires and burns have been used to facilitate hunting for millennia; here, Nola Taylor, a member of the Martu People in Western Australia, burns spinifex grass (*Spinifex* sp) to flush out small game during a hunt. (b) In forests, frequent understory wildfires reduce vertical fuel buildup and prevent the occurrence of large, high-intensity fires that are often catastrophic to both the forest and human communities (shown here is a mixed *Pinus ponderosa* and *Calocedrus decurrens* forest in California's Sequoia National Park).

 


**Figure 3.** Fire-prone ecosystems are rich in geophytes that flower very quickly after a fire event (fire-stimulated flowering). These species are the first to enhance pollination activity; their underground organs were also an important source of carbohydrates for early humans, and they are the ancestral species of many common contemporary garden plants. Pictured here are geophytes native to Spain that flower quickly after a wildfire: (a) *Narcissus triandrus pallidulus*, (b) *Asphodelus cerasiferus*, (c) *Gladiolus illyricus*, and (d) *Iris lutescens*.

loads. In British Columbia, Canada, for instance, lungworm (*Protostrongylus* spp) loads were up to 10 times smaller in native Stone's sheep (*Ovis dalli stonei*) that had access to recently burned areas than in sheep that did not (Seip and Bunnell 1985). There is evidence that fire suppression increases the risk and transmission of infectious disease pathogens (eg including those carried by organisms such as ticks, chiggers, fleas, lice, mosquitoes, and a diversity of flies) and modifies host–parasite dynamics in a range of systems (Scasta 2015). For instance, burns are currently used to control the spread of some pest-related problems, such as mosquito-borne diseases. Scasta (2015) referenced 24 studies that document the effects of fire, 23 of which demonstrate fire as an effective tool for managing vegetation, parasites, and disease. Wildfires therefore often serve as a natural control for many diseases and pests that affect wildlife, forests, livestock, and human populations.

## Regulation of catastrophic fires

In many forest types, frequent surface fires reduce the probability of large, high-intensity wildfires that can be catastrophic to ecosystems and human societies (Figure 2). This issue emerged after the highly successful fire suppression policy that was introduced in the US in the 20th century (eg in many coniferous forests in western states), and that contributed to dangerous increases in understory fuels. This novel fuel accumulation is driving the conversion from frequent, low-intensity surface fire regimes to large high-intensity crown fires (Covington and Moore 1994; Allen *et al.* 2002; Keeley and Pausas 2019). The high frequency of natural wildfires in these forests had resulted in less hazardous fires (Walker *et al.* 2018). Elimination of this important ecosystem service increased the fire hazard and, due to the massive increase in tree density, is likely to have led to the extensive dieback of trees following the extreme 2012–2014 drought in the Sierra Nevada Mountains of California (Keeley and Syphard 2016). Both the "natural burn" policy (allowing wildfires to burn naturally and suppressing them only under defined management conditions; Boisramé *et al.* 2017) and prescribed fires are often designed to reduce the frequency of catastrophic fires.

## Role in ecosystem water regulation

The smaller amount of woody vegetation after a wildfire event greatly reduces water consumption by plants and thereby increases water availability in wells and springs, which several researchers consider to be an important reason for the traditional use of fire by Native Americans in California (Anderson and Keeley 2018). More recently, local farmers in Chile reported increased stream flow following large fires in January 2017 that mainly burned large forest plantations. This is consistent with observations that burned forests are less susceptible to drought mortality than unburned forests (van Mantgem *et al.* 2016; Boisramé *et al.* 2017), and that surviving trees grow faster (Alfaro-Sánchez *et al.* 2016). In addition, forest clearings created by fires often support deeper winter snowpacks, which melt later in spring than snow in densely forested areas (Lundquist *et al.* 2013); this means that water is released more slowly in the spring and summer as opposed to rushing down as winter floods. Wildfires can therefore help to alleviate water shortages for humans in dry years.

### Acceleration of species replacement in changing conditions

In response to a warming world, many plant species may need to shift to sites where environmental conditions are more suitable (eg moving poleward or uphill). However, long-lived plants (eg trees) are unlikely to relocate quickly enough because of the difficulty of colonizing areas that are already occupied by other plant species (low population turnover). By opening gaps, wildfires may help species replacement to occur more quickly than in closed conditions, especially in ecosystems dominated by non-resprouting (fire-killed) species (eg Wang *et al.* 2019). In addition, these new gaps for recruitment select for individuals (ie genotypes) better suited to the new climate, thereby enhancing adaptation to drier conditions. We suggest that recurrently burned ecosystems may be better positioned for tracking global warming than non-fire-prone ecosystems, although this hypothesis requires further testing.

### Carbon regulation

Although wildfires consume organic matter and release carbon (C) to the atmosphere, this occurs in the short term, whereas over the longer term C fixation can be high during post-fire regeneration. From a broader temporal perspective, fire emissions are balanced out by previous C sinks (Yue *et al.* 2016), and under a natural (sustainable) fire regime, long-term C balance should therefore be relatively stable. Given that charcoal is a very recalcitrant C contributor to the soil (ie resistant to microbial decomposition), fires could increase C-sink capabilities by increasing soil charcoal (Santín *et al.* 2015); however, the proportion of C retained in the soil – and its longevity – likely varies as a function of ecosystem type. Recurrent fires also enhance belowground C allocation in resprouting plants (Pausas *et al.* 2018), which is another way soil C can increase. Overall, frequent wildfires reduce very large and high-intensity fires, and thereby regulate the C cycle by smoothing C source–sink dynamics. However, gaining a better understanding of the conditions and thresholds whereby changes in fire regime could switch a system from C-source to C-sink, and to what extent prescribed fires could be used to modulate this switch, will require further research.

### Pollination enhancement

In many regions, a shortage of flowers limits natural pollinator abundance and therefore constrains the pollination service these species provide to crops (Goulson *et al.* 2015; Winfree *et al.* 2018). Populations of both flowers and pollinators are larger in open spaces than in forests and closed ecosystems (Campbell *et al.* 2007; Hanula *et al.* 2015), and people often generate disturbances (eg clearing) to enhance pollination activity (Goulson *et al.* 2015). In many ecosystems, however, wildfire is the primary natural factor that creates open ecosystems. There is increasing evidence that landscape mosaics with a diversity of fire regimes and post-fire ages (pyrodiversity) promote floral and pollinator diversity (Ponisio *et al.* 2016; Brown *et al.* 2017; Lazarina *et al.* 2019), which could enhance crop pollination (Winfree *et al.* 2018). Fire can also extend the flowering period, and therefore increase the frequency of pollination (Mola and Williams 2018). Given the current global pollination crisis, this service provided by wildfire may become more important; using prescribed fires to create clearings adjacent to crops may help to boost pollination by a wide variety of pollinators.

## Cultural services

By promoting biodiversity and habitat heterogeneity, wildfires generate opportunities for recreation and ecotourism; for instance, some savanna ecosystems are hotspots for ecotourism and hunting tourism. Wildfires also provide researchers with opportunities to study the way in which disturbance selects for adaptations and influences biodiversity (thereby contributing to scientific knowledge). Furthermore, many native and traditional societies have a long experience of living with fire (ie cultural knowledge) and may therefore be sources of knowledge for Western societies (Fowler and Welch 2018).

Bipedalism in humans evolved in open landscapes, and these types of environments are still preferred by many people and societies, who consider them to be more hospitable than closed forests (Buss 2015). However, this preference is often masked by more recent cultural values, at least in Western countries (eg the 19th-century timber culture; Marsh 1865; Pausas and Bond 2019). Despite such shifts in values, the preservation of natural open environments and their drivers may still provide an emotional and aesthetic service.

## Conclusions

Wildfires are natural phenomena, and are important for the distribution, biodiversity, and functioning of many ecosystems worldwide (Bond *et al*. 2005; Keeley *et al*. 2012; Pausas and Ribeiro 2017). Natural fire regimes also provide an assortment of ecosystem services, although many of these remain largely unnoticed (Table 1). However, it is also true that many current anthropogenic fire regimes are susceptible to catastrophic fires. This is especially relevant in ecosystems for which fire events were extremely rare throughout their evolutionary history (eg rainforests), and for which fire regimes fall outside of the range of their historical variability (Allen *et al*. 2002; Keeley and Pausas 2019). Fire management could focus on shaping fire regimes that provide balance between ecosystem services and natural resources protection, given that a variety of tools are available for fire management (eg prescribed fires, wildfire management, fire suppression, fuel treatments; Stephens *et al*. 2013; Boisramé *et al*. 2017) and that each one may be appropriate for different settings. Actively shaping fire regimes is becoming even more necessary as the planet becomes warmer and drier. However, in many fire-prone ecosystems, landscape development patterns put human communities at risk, and thus, even ecologically sustainable fire regimes can be socially unsustainable.

Fire regimes vary around the world, and the full range of services provided by fire within the diversity of global ecosystems remains to be quantified. Some services are well supported (eg regulation of fire intensity, pest control) but others require formal validation or quantification; for instance, can we design experiments to evaluate the role of fire in accelerating species replacement in a changing climate? To what extent have fire suppression policies increased the presence of pests? And can wildfires be managed to optimize ecosystem services? Addressing questions like these would greatly improve our understanding of the ecosystem services provided by wildfires.

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