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Principles of fire ecology

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Abstract

Fire ecology is a complex discipline that can only be understood by integrating biological, physical, and social sciences. The science of fire ecology explores wildland fire's mechanisms and effects across all scales of time and space. However, the lack of defined, organizing concepts in fire ecology dilutes its collective impact on knowledge and management decision-making and makes the discipline vulnerable to misunderstanding and misappropriation. Fire ecology has matured as a discipline and deserves an enunciation of its unique emergent principles of organization. Most scientific disciplines have established theories, laws, and principles that have been tested, debated, and adopted by the discipline's practitioners. Such principles reflect the consensus of current knowledge, guide methodology and interpretation, and expose knowledge gaps in a coherent and structured way. In this manuscript, we introduce five comprehensive principles to define the knowledge fire ecology has produced and provide a framework to support the continued development and impact of the fire ecology discipline.

Resumen

La ecología del fuego es una disciplina compleja que solo puede ser comprendida mediante la integración de las ciencias biológicas, físicas, y sociales. La ciencia de la ecología del fuego explora los mecanismos y efectos de los fuegos de vegetación a través de escalas espaciales y temporales. Sin embargo, la falta de conceptos definidos y organizativos en ecología del fuego diluye su impacto colectivo en el conocimiento y en el proceso de toma de decisiones de manejo, haciendo esta disciplina vulnerable a desentendimientos y uso indebido. La ecología del fuego ha madurado como disciplina y requiere de una articulación de sus principios de organización únicos y emergentes. La mayoría de las disciplinas científicas han establecido teorías, leyes y principios que han sido probados, debatidos y adoptados por los practicantes de esas disciplinas. Estos principios reflejan el consenso sobre el conocimiento actual, guían su metodología e interpretación, y exponen los vacíos del conocimiento de una manera coherente y estructurada. Es este trabajo, introducimos cinco principios comprehensivos que definen el conocimiento que la ecología del fuego ha producido, y provee de un marco conceptual para apoyar el desarrollo continuo e impactos de la ecología del fuego como disciplina.

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Introduction

Fire ecology is the study of fire as an ecosystem process. Fire's relationships with living organisms and the physical environment include its integral coupling with human system evolution. Fire sustains or alters ecosystems through direct and indirect ecological effects that result from the interactions between fire energy exchange and the abiotic and biotic components and functions of an ecosystem. Its ecological roles vary across a broad range of temporal and spatial scales, and its effects range from being predictable to including stochastic processes. Fire and its feedbacks with terrestrial, aquatic, and atmospheric systems have attracted attention from a diversity of scientific disciplines. Even in fire-suppressed ecosystems or ecosystems where fire is rare, the lack of fire is a consideration of fire ecology, and virtually all biomass is combustible under the right conditions. Increasingly, this includes situations where climate change is altering fuel availability through decreasing fuel moisture consequent of increased temperatures and changes in seasonal patterns. That a field of fire ecology exists is a deliberate recognition of fire's role as a dominant factor in regulating ecosystem processes, in driving trajectories of ecological function, composition, and structure, and in mediating interactions between the environment and human systems. Fire has been central to the evolution, patterns, and functioning of life on our planet since at least the Silurian Period, ~ 420 million years ago, when the atmosphere accumulated sufficient oxygen for terrestrial biomass combustion to occur and plants colonized the terrestrial environment (Scott and Glasspool 2006).

Fire ecology necessarily draws from and integrates theories and principles of multiple disciplines, including ecology, evolution, physics, and chemistry, and social sciences such as behavioral science, environmental planning, and human geography, among others. Fire ecology was neglected in many general ecology textbooks for most of the twentieth century, and it was not treated independently from general terrestrial ecology until the 1970s and 1980s (e.g., Whelan 1995; Bond et al. 1996; Agee 1996). Until then, mentions of fire ecology might have been found in a book chapter along with climate and soils, in classroom lessons about ecosystem succession, or in conference sessions on natural disturbances. Bond and Keeley (2005) suggested that fire might be considered as an analog of vertebrate herbivory. Like herbivores (but unlike floods, earthquakes, cyclones, etc.) fire selects and transforms its 'food' (fuel, or organic compounds in vegetation and soils) to energy and complex organic and inorganic substances and gases (Pausas and Bond 2020a, b). By consuming the fuel that feeds them, both fire and herbivory experience strong reciprocity between disturbance frequency and intensity. Yet, fire differs from herbivory as a consumer in that it is generally less selective and more episodic, with the probability and severity of biomass consumption depending on immediate and only partly predictable weather and fuel conditions. With no top predator—and in some cases few limits to its contagion and impacts (e.g., abiotic and biotic, atmospheric, terrestrial, and aquatic impacts alike)—fire is an extraordinarily influential global consumer. Fire also interacts with grazed ecosystems and agroecosystems in culturally complex ways leading to outcomes that drive ecosystem trajectories (Collins and Calabrese 2012; Larson et al. 2013; Harris et al. 2007). Removal of fire or its addition, as with herbivory, can lead to cascading changes in ecosystem structure, composition, function, and overall biome shifts. The analogy with herbivory may help place fire in the context of scientific disciplines with older lineages, but this characterization of fire in earth systems is only partially satisfying given fire's unique characteristic as a process where subject (i.e., fire) and object (i.e., fuel) distinctions are blurry.

As a discipline, fire ecology has also suffered from a widespread perception, especially in western cultures, that fires are inherently destructive and undesirable events, rather than natural ecosystem processes (Donovan and Brown 2007). This prejudice reflects a recognition that fire can be dangerous to humans, leading to the addition of the qualifier of the untamable "wild" to arrive at "wildfire," akin to characterizing animals outside of human control as "wildlife." In some areas of the globe, fire was not perceived as a natural process for another somewhat paradoxical reason: long-held traditions of pastoral and indigenous burning signaled that fire was a tool wielded by humans, rather than being "natural" (Kimmerer and Lake 2001). The predominantly 20th Century efforts to eradicate fire from both unmanaged and managed ecosystems, and the ensuing controversy about re-introducing it where it has been suppressed, parallels the history of catastrophic eradication and reluctant re-introduction of large carnivores perceived as dangerous despite being a critical component of the functioning of ecosystems (Cronon 1996). A transition beyond these prejudices and cultural impasses in understanding fire's longstanding ecological and social significance has gained traction over the last few decades, and in response, research in fire ecology has grown exponentially (McLauchlan et al. 2020; Hiers et al. 2020; Neger and Rosas-Paz 2022). This has spurred the emergence of broadly consistent and globally applicable fire ecology concepts that have yet to be comprehensively distilled.

The very act of distillation and declaration of disciplinary principles has greatly impacted related fields, even causing "paradigm shifts" across ecology (e.g., in landscape ecology or applications of information theory to ecology principles; Wiens et al. 1993; O'Connor et al. 2019). Here, we define principles as qualitative and fundamentally true statements about the empirical patterns and processes that govern a discipline. Principles of fire ecology should have relevance both internally (i.e., to fire ecologists), as well as to the students, collaborators, and stakeholders of the knowledge fire ecology produces (i.e., all ecologists and beyond). They are meant to confer a common theoretical vocabulary that can improve communicating fire ecology to broader audiences, including those without a scientific background, which is a general need in ecology (Enquist et al. 2017) but especially critical in fire management (Glenn et al. 2022). This is vital for confronting a rapidly changing, no-analog world (Hiers et al. 2016) where people grapple with the complexity of emotions fire inspires (Ladino et al. 2022) without a clear understanding of what the distinct discipline of fire ecology has to offer.

Fire ecology principles can also serve as the foundation of educational approaches, increasing transferability across locations, educators, and instructional methods, thus enabling convergence across institutional and cultural boundaries. Reflecting the complex and unique theoretical underpinnings that fire ecology requires, we propose five organizing principles to initiate and structure a dialog for further refinement. Our intent is to advance fire ecology science and to translate research into appropriate fire management, policy, and social actions with salience, credibility, and legitimacy. These principles reflect our collaborative effort to recognize and reconcile fire ecology as a subdiscipline of ecology *and* a unique discipline inextricable from the social drivers of fire patterns and effects. Although there may be some conceptual overlap with previously identified principles of ecology (e.g. O'Connor et al. 2019), the principles presented here were developed independent of any existing frameworks with the goal of identifying governing, emergent ideas specific to fire ecology. The principles articulated in this manuscript are the product of years of discussion within this group. We acknowledge that other fire ecologists undertaking this same exercise might identify a different number or organization of principles, although the scope and areas of focus should be similar. We chose to identify five principles that each capture a unique and provocative attribute of fire ecology and its mechanisms that set the discipline apart from others. Collectively, the set of principles aims to be comprehensive. We believe these principles will prove useful for those outside the discipline, to understand fire ecology, and for current and future students and researchers within the discipline, to continue to advance fire ecology discoveries. We hope the illustrative examples we provide for the principles will inspire the reader's support for the notion that: "a world without fires is like a sphere without roundness—i.e., we cannot imagine it" (Pausas and Keeley 2009).

Our goals include:

- To address the barriers to advancing fire ecology that result from a lack of integrated thinking among the various disciplines that address fire as an earth system process;
- To underscore that fire is a keystone biophysical process that influences ecosystem composition, structure, and function in multiple ways and at multiple scales;
- To provide a framework for identifying knowledge gaps and prioritizing research directions among the various disciplines that address fire;
- To encourage a holistic, multi-disciplinary approach to hypothesis development and interpretation of fire ecology research; and
- To provide fire ecology with a consistent, translatable identity for understanding, framing communications, and policies in the future.

Importantly, the practice of science in accordance with the principles of fire ecology must also adhere to the standards, values, and practices of responsible and ethical research for our discipline to continue to make sound and defendable contributions to knowledge. We encourage readers to refer to and carefully apply the guidelines developed by the National Academy of Sciences and others when practicing fire ecology (Responsible Science: Ensuring the Integrity of the Research Process: Volume I 1992).

Principle #1: fire is key to understanding the evolution and distribution of life on earth at all temporal and spatial scales of observation

> *Over scales of time ranging from dozens to millions of years and from microscopic to landscape scale, wildland fire serves to structure ecological assemblages and individual species traits. The understanding of fire in any landscape—especially increasingly managed environments of the modern world—benefits from a knowledge of fire in deep time and species' eco-evolutionary relationships with fire. Although ecologists have long held that soils and climate can explain ecosystem distributions across space and time, fire ecology reveals that fire has long been a keystone ecological process driving the distribution, evolution, and assembly of life on Earth.*

Interactions among fire, the atmosphere, and the evolution of major land plant groups

The Earth system's relationship with fire has been built over at least 420 million years, with fossil evidence of fire appearing approximately contemporaneously with plants colonizing land surfaces (Scott and Glasspool 2006). Wldfires have acted at the landscape scale since the evolution of the first forests more than 380 million years ago in the Devonian (Belcher et al. 2013). The evolution of the Earth's biosphere is a product of the interplay between vegetation and fire over deep time; vascular plants seem to have been predisposed to burn as soon as they appeared on the evolutionary stage. Far from being the "threat" to ecosystems as it is often perceived, fire and plants have "co-evolved". Over these long timescales, fire has interacted with land plants that fuel fires, but plants concurrently altered fire regimes and adapted to shifting fire frequencies and fire behavior (Belcher and Hudspith 2017; Baker et al. 2022). Over geologic time, biomes have shifted through climatic zones and fires have shifted with them, driven over long timescales by feedbacks among shifting climate, atmospheric oxygen levels, fire, and life on Earth. Most recently, since the late Pleistocene, as glaciers and ice sheets receded, fire has continually shaped assembly of novel plant communities in regions expected to be further impacted by anthropogenic climate changes (Gill et al. 2009). The earliest land plants evolved in a world where atmospheric CO_2 levels were seven times higher and oxygen levels were 1.4 times lower than today (Lenton et al. 2018). As plants spread and evolved, withdrawing CO_2 from the atmosphere and releasing oxygen, they dramatically changed the biochemistry of the planet (Beerling et al. 2001). By 380 million years ago in the Devonian, CO_2 levels in the atmosphere had halved and oxygen reached levels similar to today (Beerling et al. 2001; Lenton et al. 2018) and wildfires began to become a frequent feature of the Earth's land (Scott 2000). By the late Permian (~ 250 Ma), oxygen levels had risen due to the proliferation of plants across Earth's surface, facilitating ignitions and rendering vegetation flammable at higher fuel moistures, and fires began to occur in numerous ecosystems (Scott and Glasspool 2006; Glasspool et al. 2015). Because Earth rotates on a tilted axis, seasonal dryness that facilitates fire occurs annually (Pausas and Keeley 2009).

Not only does fire appear to be a key regulating process that moderates oxygen concentrations in the atmosphere by acting as a control on plant biomass (Belcher et al. 2021), but major oxygen-driven phases of fire appear to be linked to the acquisition of traits that aid plant survival in a highly flammable world. For example, during the Cretaceous period, (~ 66–145 Mya) atmospheric oxygen is likely to have been as high as 28% (compared to today's 21%; Belcher et al. 2021; Vitali et al. 2022). The earliest directly observable fossil evidence of the evolution of a plant trait characteristic of some present-day conifers found in fire-prone ecosystems is that of lower branch shedding, which evolved in a now-extinct group of Permian (~ 252–299 Mya) conifers (Looy 2013). However, reconstructions of the evolutionary history of the intrinsic structural states *required* for serotiny (canopy seed storage in closed woody cones) suggest that these characteristics may have emerged in early conifers 332 million years ago in the Late Carboniferous (He et al. 2016). These early conifers were short-statured trees, with spreading crowns and scale-like leaves enabling heat from surface fires to reach the cone-bearing crowns and promote seed dispersal. Reconstructions of the likely fire behavior indicate that their leaf and branchlet morphology would tend towards carrying fires of high intensity that burned with a rapid release of heat and quickly consumed the fuel (He et al. 2016). Spread probabilities during this period would have likely been between 90 and 100%; meaning that every ignition would likely lead to a spreading fire (Belcher et al. 2010). Fire return intervals in these forests are estimated to have been around 35 years (Falcon-Lang 2000). Therefore, conifers evolving in the Permo-Carboniferous period would have been challenged by frequent crown fires which can be seen as the driving force for the evolution of these early fire adaptations.

These fiery time periods were followed by a period in the early to Middle Triassic between 250–240 Ma where there is little fossil evidence for fire on the planet, known as the charcoal-gap (Belcher et al. 2010). However, by around 150 Ma atmospheric oxygen levels had risen to ~ 25% and were continuing to rise (Belcher et al. 2021). The *Pinus* clade evolved ~ 126 million years ago at a similar time as the planet appears to have become more fire-prone due to fuel-oxygen-induced changes in fire regimes (He et al. 2012). At the same time, the most dominant plant group in the modern world evolved: the angiosperms, plants that flower and create seeds, which altered fire regimes significantly (Bond and Scott 2010; Belcher and Hudspith 2017). The earliest angiosperms are believed to have been herbaceous and small in stature (Feild et al. 2004) with easily dryable and ignitable leaves (Bond and Scott 2010) that supported surface fire spread (Belcher and Hudspith 2017). Frequent fires would favor fire adaptations such as resprouting and seeds that readily germinated post-fire across the lifeforms of angiosperms, from herbs to trees. Around the same time, the *Pinus* clade of trees evolved thick, insulative bark for the first time (He et al. 2012). By around 100 million years ago, angiosperms were present as small trees and shrubs (Feild et al. 2011), capable of sustaining rapidly spreading and intense fires with a high probability of transitioning to crown fires (Belcher and Hudspith 2017). It is with this increased crown fire threat that some members of the genus *Pinus* appear to have evolved pyriscent serotiny (closed cones with fire-cued seed release), about 89 Ma (He et al. 2012).

The emergence of new angiosperm-driven fire regimes set amidst a background of rising oxygen seems to have enhanced the overall fire regulation of vegetation (Belcher et al. 2021; Vitali et al. 2022). Bond and Midgley (2012) hypothesized that some members of the angiosperms are the first plant lineage to have produced forests capable of suppressing fires owing to their closed structure. The suggested changes in forest structure, hydrology (Boyce et al. 2010), and the angiosperm-driven decline in atmospheric oxygen allowed some angiosperms to evolve as the Earth's first self-sustaining pyrophobic communities from ~ 58 Ma. Indeed, during the warm early Eocene (~ 34–56 Mya), vegetation similar to modern angiosperm tropical and paratropical forests extended up to 45–55° paleolatitudes north and south (Burnham and Johnson 2004; DeVore and Pigg 2010) and global charcoal compilations appear to indicate a > 50% decline in the amount of charcoal found in mire settings from ~ 60 Ma onwards to the present day compared to 90–60 Ma (Glasspool and Scott 2010). Fire during this period of the Oligocene (~ 23–34 Mya) also drove species diversification of *Pinus* (Jin et al. 2021).

As these events and innovations were occurring a new fuel type was emerging: the grasses. Grasses with the C3 photosynthetic pathway evolved in the Late Cretaceous associated with forested ecosystems (Strömberg 2011). The grasses gradually moved out of the forest, forming open habitats from 40 Ma during the Eocene, set against a global cooling trend (Strömberg 2011). However, it is the grasses with the C4 photosynthetic pathway that dominate within vast tropical savannas of the world today and fire has been hypothesized to have played a role in their expansion about 7 Ma. This idea is supported by sedimentary ocean cores from low latitude sites in the North Pacific that show a sharp increase in flux of charcoal between 10 and 1 Ma (Herring 1985). Beerling and Osborne (2006) proposed that fire initiated and has since maintained the C4 savanna biome via fires that occur as frequently as annually, discouraging establishment of forests. Models have indicated that C4 grasses can invade C3 grasslands and outcompete them in hot open environments, but C4 grasslands cannot invade forests without the aid of fire (Scheiter et al. 2012). Hence, fire appears to have been critical to the establishment of savanna grasslands and the expansion of C4 grasses in the Miocene (~ 5–23 Mya).

The formation of the savanna biome during this time is also supported by time-calibrated phylogenetic analyses of the expansion of savanna trees that appears to have happened between 10 and 3 Ma (Davies et al. 2020). These dates may support the savanna hypothesis of early hominin evolution. The most ancient hominin lineages date to 6–7 Ma near the equator, where a change from forest to savanna may have provided the driving force for a shift from an arboreal habitat to one that favored bipedalism (Davies et al. 2020). The spread of early hominins to higher tropical latitudes appears to have occurred around 3 million years ago (Parker et al. 2016). Fire has therefore been linked to the expansion and evolutionary success of humans. Anthropologists have proposed that early human pyrophilia resulted from living in increasingly fire-prone savanna environments, where they exploited frequent fire's foraging benefits and soon learned how to spread fire, by moving smoldering fuels to unburned patches and even across the landscape (Parker et al. 2016).

Fire and global vegetation distribution

Theory about biome distribution is being revised in response to new observations about fire's role in vegetation distributions. Climate has long been thought to primarily determine global vegetation patterns, with local modification by soils. The major biomes were thought to be a product of climate selecting for the best physiological fit to the challenges to plant growth and survival in the different physical environmental settings (Schimper et al. 1903). This view of the organization of life has changed rapidly in the last few decades. It has been challenged by the presence of alternative ecological states, such as mosaics of closed forests and open grassy ecosystems sharing the same climate and physical soil substrates (Pausas and Bond 2020a, b; Staver et al. 2011; Hirota et al. 2011; Bond 2019; Dantas et al. 2016). Until fire was added, global vegetation modelers could not predict certain vegetation assemblages such as the grasslands of the Great Plains of the USA, Kalahari grasslands, or the Russian steppe using only climate and soils. The idea of growth forms being the optimal fit for a given climate has also been undermined by the spread of invasive plant species into ecosystems with quite different plant forms. Among the most transformative invasives are those that alter the fire regime (Brooks et al. 2004). Flammable grasses have changed numerous invaded ecosystems (D'Antonio and Vitousek 1992). They have invaded succulent shrublands in the Sonoran Desert, grasslands and heathlands in central and Western Australia (Marshall et al. 2012; Fisher et al. 2009) and seasonally dry tropical forests in the New World, despite the supposed barrier of colonizing extremely nutrient-poor soils. Regardless of the extreme climate and soil conditions, the productivity of the invasive grasses has been sufficient to support frequent fires and alter other important aspects of the fire regime, such as seasonality. These frequent fires have transformed these complex ecosystems and their mix of growth forms, challenging the notion that the native species are optimally suited to the extreme environmental conditions.

Where wildland fires have occurred for millennia, shade-intolerant biota evolved very differently from those of closed forests at the climate "potential" (Bond 2019). They include the fire-maintained shrublands of southwestern Africa and Australia, the richest temperate floras in the world. These systems have lineages dating back to the initial spread of angiosperms from ~ 90 Ma (He and Lamont 2018). Fire-dependent biota also include savanna ecosystems, such as the species-rich Brazilian Cerrado. Here, phylogenetic analyses have shown that the *Mimosa* species are closely related to forest sister species but diverged concurrently with the rise of flammable C4 grasses within the last five or six million years (Simon et al. 2009).

Based on the percent area burned and frequency, the tropical and sub-tropical savannas and those of the Mediterranean climate regions (MCRs) are among the most fire-prone biomes. Overall, both support relatively high biomass production during the wet season followed by a long dry season (the cool season in the tropics and the warm season in the MCRs). In savannas, fires occurring early in the dry season tend to support greater tree densities and diversity compared to fires in the late dry season (before the rains), which are generally of higher severity, killing fire-sensitive woody species and top-killing shoots of saplings, thereby creating more open, grassy ecosystems (e.g., Laris and Wardell 2006; Williams et al. 1999). Differences in fire severity combined with changes in fire frequency have also been linked to changes in woody ecosystems (Bowman and Wood 2009; Paritsis et al. 2015; Wood and Bowman 2012). High-severity fires in mixed-conifer forests of the North American MCR may be followed by the growth of highly flammable shrubs, which can promote repeated high-severity fires, thus blocking forest recovery (Coppoletta et al. 2016; Tepley et al. 2017). The shrubs tend to support shrub-crown fires whereas the forests historically burned with lower-intensity surface fires. Many of these historical low-intensity regimes have now transitioned to a fire regime characterized by higher severity fires, driven by heavy fuels and high tree densities promoted by a century of fire suppression (Safford et al. 2021). The development of alternative stable states implies some negative feedbacks occurring within each ecosystem that can maintain that state (Principle 3); however, transitions to a different stable state are possible through positive feedbacks.

Fire adaptive traits

Wildland fires can injure or kill plants and animals, yet fire-prone ecosystems are often highly diverse and include global biodiversity hotspots (Noss et al. 2015). This is because many species have acquired fire-adaptive traits that enable survival and reproduction under recurrent fires. Different fire regimes exert different evolutionary pressures, mainly depending on the frequency, intensity, and seasonality of fires, and thus plants have generated a diversity of fire adaptive traits (Keeley and Pausas 2022). In fire-prone ecosystems, fire explains a significant part of the genotypic and phenotypic variability within species and of the diversity of communities. Fire is a major agent of natural selection (He et al. 2019). Many plant species use multiple strategies to survive or to increase in abundance post fire.

Plant traits adaptive to recurrent fires can broadly be classified into two types: those that confer survival, and those that allow quick recruitment/regrowth in the post-fire environment. Plant strategies for survival include protected buds, meristematic tissues, and xylem conduits from heat during a fire. For instance, recurrent surface fires often select for trees with a thick insulating bark and with self-pruning of the lower branches, as in the case of many *Pinus* species (Keeley and Zedler 1998; Pausas 2015; Varner et al. 2022). The thick bark and the vertical fuel discontinuity make those pines tolerant of lower-intensity surface fires characteristic of the conditions under which the traits were selected (Gill 1975). Fires can also select for plants with protected bud locations, as in the case of those deep in the trunk of the tree as demonstrated in many eucalypts and savanna trees (Burrows 2002; Charles-Dominique et al. 2015); when they burn at high intensity, they resprout from those protected stem buds (epicormic resprouting; (Pausas and Keeley 2017). The buds of many grasses, forbs, and shrubs are protected if they are located belowground (Pausas et al. 2018), as soils are poor heat conductors. Plants often accumulate buds (i.e., forming a bud bank) in the base of the stem, sometimes forming large burls (lignotubers), or in belowground organs such as roots, rhizomes, underground stems, and tubers, which allows survival through resprouting of the protected buds (Pausas et al. 2018). The cost of resprouting is the accumulation of carbohydrates (starch) for growing new shoots when the plant is defoliated by fire (i.e., without photosynthetic capacity), and the maintenance of a bank of dormant buds. This cost would only benefit a plant under recurring selective forces, and it is likely that for some lineages, fire has played this role, in concert with herbivory and some other disturbances (e.g., flooding, wind).

Fire adaptive traits also include those that allow recruitment in postfire conditions, often enabling plants to take advantage of novel postfire conditions with high resources and low competition, thereby increasing their population size. In many MCRs, gaps are generated by crown fires, and many shade-intolerant plants have evolved mechanisms to detect new open conditions created by fire that are suitable for germination. These strategies include formation of a soil seed bank of dormant seeds, where the heat or chemicals from combustion can break seed dormancy (i.e., fire-stimulated germination; Pausas and Lamont 2022), generating a massive postfire recruitment. Other postfire seeders store seeds in the canopy instead of in the soil; these types of trees and large shrubs have cones or fruits that remain closed for years, until being opened by a fire which disperses the seeds in the postfire bed (pyriscent serotiny; Lamont et al. 2020). Typical examples of serotinous plants are closed-cone pines in the Northern hemisphere (e.g., *Pinus contorta* and *Pinus clausa*) and many Proteaceae (e.g., *Banksia*) in the Southern hemisphere. Postfire seeders also benefit from being flammable to ensure as fire ensures dormancy release (in species with soil seed bank) or seed dispersal (in serotinous species) and the recruitment in the postfire environment with high resources and low competition (Bond and Midgley 1995; Pausas et al. 2017). Populations of many plants increase rapidly after fire when surviving plants and initial colonizers, including many herbaceous plants and geophytes, flower in abundance (fire-stimulated flowering; Hiers et al. 2003, Lamont and Downes 2011) to benefit from the high-resource and low-competition environment for their offspring. Many plant species use multiple strategies to increase in abundance post fire.

Fire-prone ecosystems also harbor a rich fauna assembly. Because animals are mobile organisms, their adaptive traits are often behavioral and thus more difficult to depict than in plants (Pausas and Parr 2018; Pausas 2019). Many animals survive fires by moving to a refuge (e.g., hiding belowground, in cracks, among roots, in unburned patches) or moving away from the fire (for animals with high mobility). Thus, for those animals, it is adaptive to quickly detect the coming fire to react accordingly (Pausas and Parr 2018; Nimmo et al. 2021). For example, there is evidence that some animals from fire-prone ecosystems have an enhanced capacity to detect fire through smelling the smoke or hearing the fire (Álvarez-Ruiz et al. 2021a, b; Álvarez-Ruiz et al. 2023). Among the few morphological adaptations in animals is the occurrence of infrared (fire) detectors in some pyrophilous beetles (Buprestids, Coleoptera; Evans 1966); they use burned areas as mating sites and an ideal environment for reproductive success. Animals are not only affected by the fire itself, they also need to survive the postfire environment, which is quite different from the pre-fire. Thus, some animals acquire cryptic dark colors (Lillywhite et al. 1977; Forsman et al. 2011) or have the capacity to enter in torpor after fire (Stawski et al. 2015). Interestingly, the postfire environment may also provide some benefits, as it is an environment with fewer parasites for vertebrates (the "cleaning effect" of fire; Álvarez-Ruiz et al. 2021a, b). Overall, the dominant fire adaptive strategies in animals are different from those plants and our understanding of the diverse examples and mechanisms of animal fire adaptations has only just begun (Pausas 2019).

Principle #2: fire integrates biotic and abiotic, above- and below-ground components and processes

> *Wildland fire may appear to be an external agent acting upon the landscape it burns, but it is an emergent property of the ecosystem itself. It integrates abiotic and biotic components and processes both immediately and for some time after fire. Fire greatly influences biogeochemical cycling across scales, as well as feedbacks on the biota, which in turn serve as drivers of fire. Along with its scale and global extent, the rate at which fire converts matter into energy with impacts across above- and below-ground, atmospheric, and aquatic boundaries make fire a uniquely impactful and integrative process.*

Abiotic-biotic integration

While other processes such as herbivory act to integrate biotic and abiotic factors (Bond and Keeley 2005), the process of rapid oxidation and extremes of energy release make fire unique in both intensity and degree in its influence over other ecological and atmospheric processes. After ignition, fire behavior, including its ability to spread (or be extinguished) is determined by the structure, arrangement, chemistry, pattern (e.g., topographic positioning), and moisture content of biotic material acting as fuel (organic compounds in vegetation, soils, or structures; Van Wagtendonk 2006; Dickman et al. 2023; Parsons et al. 2017). Fire behavior is further influenced by antecedent and concurrent local abiotic conditions, especially wind speed and direction, precipitation, and atmospheric stability, which in turn are characteristic of other abiotic factors, such as time of day and year and associated incident radiant heat, cloudiness, or topography (Johnson and Miyanishi 2001; Riley et al. 2013a, b). The relative strength of each of these drivers can change over time and across space and due to their interactions, as well as the scale of observation. Thus, each fire, and even each moment of fire, represents a unique combination of environmental factors intersecting fuel to produce heterogeneous impacts on the systems in which it occurs.

Abiotic weather patterns also influence fuel moisture (and thus combustion characteristics) at various spatial and temporal scales. These can range from hourly changes driven by diurnal cycles or changes in synoptic weather affecting moisture content of fuels (Kreye et al. 2018) and organic soils (Reardon et al. 2009), to monthly cycles of vegetation growth and senescence, hydrology, and deviations from average conditions (Dickman et al. 2023). On longer timescales, annual-decadal patterns such as drought and modes of ocean circulation (e.g., El Nino, Pacific Decadal Oscillation, and Atlantic Multidecadal Oscillation) and even longer-term fluctuations such as global climate change influence fuel moistures (Resco de Dios et al. 2021; Ellis et al. 2022; Abatzoglou and Williams 2016). The combustion of biotic material subsequently has the potential to influence abiotic factors, including both local meteorological conditions and global weather immediately and for months after a fire (Liu et al. 2014; Yu et al. 2019). For example, wildland fire is responsible for a significant portion of aerosolized global particulate matter including black and brown (pyrogenic) carbon, which have climate-forcing impacts globally that in turn affect biotic components and processes (Zhang et al. 2017) and influence fire occurrence. For example, soot that lands atop snow or ice dramatically reduces albedo and can result in higher rates of melting than during non-wildfire years (Aubry-Wake et al. 2022). Both biotic and abiotic (e.g., soot) ice nucleation particles are emitted during biomass fires (Moore et al. 2020; Barry et al. 2021; Kobziar et al. 2022) and can be transported in the free atmosphere around the globe. Coupled with black and brown carbon, these particles are known to influence cloud radiative properties, cloud glaciation, and precipitation patterns downwind (Petters et al. 2009; DeMott et al. 2010; Kanji et al. 2017), which in turn drive flammability and fuel distribution over larger spatial and temporal scales. Gaseous products of combustion including CO_2 and CH_4 further influence overall greenhouse gas abundance and its effects on global climate and biota (Liu et al. 2014), with varying impacts on the availability of fuels and patterns of present and future wildland fires (Westerling et al. 2003; Hurteau et al. 2019).

Fire-generated winds can also be viewed as a driver of biological dispersal on both a macro- and microscopic scale. These winds transport soils, seeds, and pollen kilometers from the combustion source (Bormann et al. 2008). Millions of living microbes per hectare burned are transported in smoke to be deposited, and to potentially colonize, the downwind environments in which they land (Kobziar et al. 2022, 2024; Kobziar and Thompson 2020). Both abiotic and biotic smoke constituents have clear impacts on terrestrial biota, including humans and wildlife through inhalation, allergic response, or infection (Liu et al. 2015; Kobziar and Thompson 2020; Sanderfoot et al. 2021; Zhou et al. 2021), lake and stream ecosystems through particulate matter (PM) deposition and shading (Lynch et al. 2004; David et al. 2018), and through ecological cascades by affecting photosynthetically active radiation (PAR; Scordo et al. 2021). For example, vegetation and crop growth can be both positively and negatively impacted by suspended PM impacts on incident diffuse PAR affecting light use efficiency (Hemes et al. 2020). Our current understanding of fire effects as channeled through the atmosphere has benefited from novel, cross-disciplinary approaches such as large prescribed fire experiments leading to new fire ecology disciplines (e.g., "pyroaerobiology"; Prichard et al. 2019; Hiers et al. 2020; Kobziar et al. 2018) and continue to yield evidence for fire's uniquely integrative role.

Fire's integration of abiotic and biotic factors is exemplified by fire's effects on soils and aquatic systems which can have profound impacts on soil biota and freshwater and oceanic ecosystems (Riera and Pausas 2024). In infrequently burned ecosystems, fire removes understory and overstory vegetation as well as litter and duff, increasing with fire severity (Hyde et al. 2016b). Soil can then be exposed directly to rainfall and runoff during subsequent high-intensity storms and dramatically increase erosion rates (Spigel and Robichaud 2007). Increased dry ravel also plays a role in post-fire erosion (Roering and Gerber 2005). Following fires where significant reduction of vegetation and organic soil layers has occurred (i.e., high-severity fires), large changes in hydrological patterns and soil movement have been observed, especially in steep terrain (Shakesby and Doerr 2006). Increases in erosion following fire can greatly exceed background rates; in one Oregon Coast Range ecosystem, USA, rates increased by six-fold after fire accounting for up to 50% of the erosion impacting the system (Roering and Gerber 2005). Stream morphology can change after fire, including through aggradation of debris flow fans, channel infilling, and sediment fining following fire, especially in areas of higher-severity fire (Hoffman and Gabet 2007; Riley et al. 2013a, b; Wilson et al. 2021). Thus, in mountainous or hilly areas that regularly experience fire, a pulsed rhythm of sediment production and erosion may ensue that over time demonstrates the influence of fire on soil conditions (Roering and Gerber 2005). Episodic events such as debris flows following fire contribute the majority of sediment transport in mountainous terrain (Dietrich and Dunne 1978). Thus, post-fire debris flows can subsequently alter stream course and morphology (Hoffman and Gabet 2007). Fire can also change soil physical and chemical properties, for example by inducing hydrophobicity or increasing water availability due to reductions in live vegetation. Commensurate impacts include increases in surface water flow and decreases in infiltration, affecting local-scale biota, overall watershed function, and provision of ecosystem services (Roces-Díaz et al. 2022), and altering biogeochemical processes which govern, e.g., the levels of P, N, and C in soils (Dove et al. 2020). Pyrogenic horizons can be a key diagnostic characteristic for soil classification, leading to proposals that fire be considered a sixth soil-forming factor (Certini 2014).

Influx of charcoal, sediments, nutrients, and other fire-derived elements into adjacent streams can increase following fire, impacting water quality and its dependent ecosystems and ecosystem services (Lynch et al. 2004; Smith et al. 2011). Stream temperatures may increase following fire due to the removal of overstory vegetation, with these effects persisting for years, which may translate into additional stress for fish populations already stressed by high water temperatures due to climate change (Mahlum et al. 2011). Because fire decreases both above-ground and below-ground vegetation cover and root strength, increased erosion often occurs after fire, with mass wasting events such as post-fire debris flows becoming more common in the months and years after a fire (Wondzell and King 2003; Cannon et al. 2010).

Wildfire byproducts enter the oceans via terrestrial (e.g., sediments) and atmospheric (smoke, aerosols, ash) routes (Riera and Pausas 2024). Thus, wildfires enhance the land-sea interaction by altering marine chemistry and carbon and nutrient cycling. These changes have been shown to enhance phytoplankton productivity which can cascade to other trophic levels with both positive and negative effects on the oceanic biota (Riera and Pausas 2024). The enhanced primary productivity is also a way to sink carbon into the deep sea. For example, researchers estimated that carbon loss from megafires in Australia was balanced by smoke-induced phytoplankton blooms where aerosols were deposited (Wang et al. 2022). This emphasizes the importance of fire as a key component of the global biogeochemical cycles in our Earth system (Pausas and Bond 2020a, b).

Above-below ground integration

While combustion of biotic fuels is most frequently an above-ground (or above-water) process requiring oxygen from the atmosphere, fire also occurs at or below the soil interface, as in the case of burning of organic soil horizons, roots, and other below-ground vegetation or buried woody debris (Watts and Kobziar 2013; Busse et al. 2013; Kreye et al. 2017; Rein et al. 2008). The magnitude of heat produced from fire whether from burning fuels above, on, within, or pulsed through the soil profile determines the magnitude and duration of impact on the biotic and abiotic components of soil which in turn drive the soil processes which support the overall ecosystem functioning (Kreye et al. 2013; Rein et al. 2008; Busse et al. 2013). It is through complex biochemical mechanisms that fire integrates above-ground and below-ground processes and components. For example, above-ground plant mortality eventually releases both labile and recalcitrant carbon into soils while root availability to microbial decomposition increases, changing soil carbon efflux and nutrient content (Adkins et al. 2019) as well as impacting soil microbial community composition (Fox et al. 2022). The symbiotic relationship between mycorrhizal fungi and many tree species can be critical to post-fire vegetation survival and regeneration (Fox et al. 2022). Key soil-dwelling organisms are known to benefit from fire's effects, including some mycorrhizal fungi and bacteria (Whitman et al. 2019; Fox et al. 2022), although effects on many other groups of soil biota remain poorly understood (Pressler et al. 2019), in part owing to an incomplete understanding of their tolerance to soil heating (Pingree and Kobziar 2019).

Along with effects on soil hydraulic conductivity (Quigley et al. 2021), hydrophobicity levels (Doerr et al. 2006), and runoff and erosion (Bodí et al. 2014; Balfour et al. 2014), fires that burn below-ground (i.e., within organic soils such as peatlands) can have important biogeomorphic feedbacks including hydrological cycling and its many impacts, such as water quality and amount (Shakesby and Doerr 2006). For example, in intermittently dry wetlands, the loss of organic soil from combustion leads to water-induced weathering of bedrock, expanding wetland patches and driving landscape-scale vegetation patterns and subsequent flammability mosaics (Watts et al. 2014; Watts and Kobziar 2015).

As one of the three major pathways for carbon and nutrient cycling (also including herbivory and microbial decomposition; Pausas and Bond 2020a, b), fire plays both direct and indirect roles in integrating above and below-ground resources. While herbivory decomposes green biomass and soil microbes decompose dry biomass (litter), fire decomposes both green and dry biomass in an abrupt manner, and distributes the resulting inorganic matter at broad spatial scales though aerosols (Pausas and Bond 2020a, b). Plant nutrients essential for the growth and functioning of ecosystems ultimately come from the atmosphere (N) and the weathering of rock and soil (P, K, Mg, Ca, micronutrients). Nitrogen is incorporated into the soil through deposition and nitrogen-fixing through symbiotic relationships between certain plants and bacteria. Plants derive nutrients directly from the soil (or other organisms through symbiotic relationships) and incorporate them into organic chemicals compositing biomass. Nutrients are further transferred through herbivory or microbial decomposition, with nutrients ultimately being returned to the soil, where they might be taken up by plants, leached, or moved by runoff to water bodies (Larson et al. 2013). Fire redirects these pathways, directly by volatizing nitrogen and carbon compounds to the atmosphere and redepositing mineral nutrients through ash (Bodí et al. 2014; Quigley et al. 2019), typically intermixed with other products of combustion such as pyrogenic organic matter (Maestrini et al. 2017; Pingree and DeLuca 2017). Indirect effects on nutrient cycling result from potentially persistent impacts on the below-ground microbial communities and their metabolic substrates (Pietikäinen et al. 2000; Adkins et al. 2020), as well as to root abundance or biomass (Johnson and Matchett 2001; Kitchen et al. 2009). Depending on the severity of fire, these soil components are also influenced by changes to above-ground plant community composition and productivity which determines the quality of herbivore habitat (Murphy et al. 2018). Nutrient redeposition via herbivores may temporarily increase resources for and diversity of certain organisms, including surviving plants and microbes (Hawkins and Zeglin 2022). For example, fire indirectly provides habitat for some legume species which are essential for nitrogen fixing to complete the nitrogen cycle (Hiers et al. 2003; Peterson et al. 2007).

Energy flow

Fire acts to redirect, rather than sequester, the flow of energy in the development and function of an ecosystem. As recognized in classical ecology, fire strongly influences the pathways of energy flow in ecosystems that facilitate the spread of fire (Odum 1969). Energy derived from solar radiation is converted to chemical energy through photosynthesis. Combustion results in the rapid transformation of chemical energy in plant biomass to heat energy through exothermic reactions that can cause the heating and combustion of more biomass, sustaining the fire feedback and spread of fire. Johnson and Miyanishi (2001) emphasized the critical connection of measuring energy release for fire-prone ecosystems, as variation in energy transfer is key to a mechanistic understanding of ecological outcomes (O'Brien et al. 2018). Due in part to the challenges of predicting fire or observing active fire, a limited number of ecological studies measure combustion or show an appreciation for the variation in the phases (i.e., flaming or smoldering) and characteristics of the combustion process (Hiers et al. 2020; Bonner et al. 2021). Combustion is most often incomplete, such that resulting substances, composed mostly of carbon (i.e., incompletely burned vegetation or aerosolized pyrogenic organic matter), retain some energy and may either be locally deposited or translocated by aerial convection as mixtures of soot, ash, plant materials, organic smoke content, and other substances including living organisms (Bodí et al. 2014; Yu et al. 2019; Moore et al. 2020; Kobziar et al. 2022). Water, either via ground or atmospheric pathways (e.g., rainfall deposits of smoke constituents) transports ash and living/non-living carbonaceous content to waterways and the ocean, at times producing massive increases in the biomass and function of resident biota such as phytoplankton (Tang et al. 2021). Influxes of sediments and removal of overstory vegetation can also result in changes in stream chemistry and temperature from increased insolation, suppressing fish populations after fire (Rieman and Clayton 1997).

Plants with traits to survive fire often have a repository of chemical energy that allows for rapid recovery of ecological processes following fire (Starr et al. 2015). Post-fire alterations in herbivore and microbial habitat, availability of and competition for resources, vectors of microbe, and seed dispersal and pollination, are some factors that can be strongly influenced by fire-induced changes in the distribution of energy, further illustrating the degree to which fire integrates biotic and abiotic processes. Fires and effects are dynamically linked in multifaceted ways, reflective of both the individual and collective influence of plant life history traits (Principle 1) and post-fire energy exchange and biochemical fire effects.

Principle #3: recurring fires result in dynamic feedbacks which serve to organize ecosystem structure, composition, and function

> *Although ecologists long considered fire to be an acute disturbance that altered a natural succession of ecosystem states, all fire-prone ecosystems are the product of community reassembly following multiple fires over time and are inherently non-stationary. Fire is a highly variable process driving heterogeneous effects, which when intersecting repeated fires over time, create feedbacks of self-sustaining ecological trajectories, non-linear outcomes, landscape-scale patterning, and alternative stable states. These cumulative fire effects can maintain ecological communities, result in alternative ecological states, or cause dynamic transitional change. This principle adds the necessary context of the variability of fire behavior and vegetation feedbacks across temporal and spatial scales that make fire a necessary and often inevitable emergent process rather than a perturbation of the system.*

The fire regime

The fire regime concept has dominated our understanding of cyclical fire effects on ecosystem processes and community assembly (Krebs et al. 2010; Keane 2015). Fire regime attributes characterize repeated fires over time, and often include mean fire return interval (MFRI, or the average number of years between fires for a given location), seasonality, severity, and intensity (Gill 1975; Bergeron et al. 2002; Archibald et al. 2013; He et al. 2019). Such historical perspectives are often referred to as "natural" fire regimes, which presuppose evolutionary timescales and stable conditions, shown in Principle 1 to only be stable for a given time. The reliance on mean characteristics—such as the MFRI—has limited understanding of variation as a critical attribute of repeated fire that drives ecosystem distribution on multiple continents (Hiers et al. 2016; Keane 2017). Similarly, the desire in many locations to work towards ecosystem "restoration" implies a static ecological baseline as the goal- which is most often a Holocene baseline fire regime when the ecology of fire has a much longer Earth history. In addition to temporal variation, spatial heterogeneity of fire regime factors can be a driving force in fire's effects on ecosystem patterns and processes (Keeley and Stephenson 2000; Collins and Stephens 2010; Freeman and Kobziar 2011) but this is inconsistently included in the traditional description of fire regimes or application of fire regimes to related scientific fields (Boisramé et al. 2019) or management decision-making (Flatley and Fulé 2016; Freeman et al. 2017). Importantly, the contribution of Indigenous cultural fire practitioners to "natural" fire regimes is often omitted. For example, conceptualizing fire regimes as "lightning regimes" may erase and obscure the contribution of Indigenous peoples to human-mediated fire regimes (Kimmerer and Lake 2001). In addition, anthropogenic fire suppression has drastically reduced the frequency of fires on many continents, as well as changing its seasonality, restricting fires in essence to the times of year when they cannot be extinguished due to extreme fire behavior (Calkin et al. 2015). The result has predictably shifted many fires regimes effectively toward higher-intensity conditions, and altered spatial patterning and impacts.

While ecosystem states and transitions among states (Pausas and Bond 2020a, b) are well established as a fundamental ecological concept, fires are often considered catalysts between states rather than more complex processes within and among ecosystem states that have variable spatial and temporal outcomes. In both frequent and infrequent fire systems, an example of this is the spatial patterning in fires, both in terms of burned vs. unburned areas as well as variation within the burn, that become "legacies" that drive ecosystem recovery specific to the patterns of severity (sensu Franklin et al. 2007). For example, the distance from low-severity patches with intact seed sources to severely burned patches influences the trajectory of vegetation post burn (Tangney et al. 2022), which in turn impacts subsequent fire probability and patterns of consumption and ecological trajectory across the landscape (Nemens et al. 2022). The focus on "within-fire" variability allows that not all fire has the same effects within a single burned area or between fires in the same fire regime, and that ecosystems are the result of the composite and inherent variability, or "pyrodiversity" (He et al. 2019; Steel et al. 2021) of fire regime factors and their feedbacks at multiple scales.

The critical distinction between fire as an evolving component of ecosystems rather than an external driver with predictable outcomes is most often misunderstood in restoration applications of the historical fire regime concept, where recommendations to recreate mean fire regime characteristics are presumed to sustain the biodiversity and desired compositional and structural elements of a given ecosystem and its services (Freeman et al. 2017). However, the long history of climate and humans interacting with fire has shown the critical importance of fire in evoking non-linear outcomes (Flatley and Fulé 2016; Jones et al. 2022). Interactions between sequential fires can drive changes outside the boundaries ("envelope" as per Keane 2017) or historical range and variability (Keane et al. 2002) of a defined fire regime (Hu et al. 2010; Prichard et al. 2017; Tangney et al. 2022). This potential for non-linearity is increased with the arrival of exotic species (e.g., cheatgrass and cogongrass; Balch et al. 2013, Estrada and Flory 2015), unprecedented climate changes (Jones et al. 2022), or unintended interactions of anthropogenic disruptions to land use and ignition patterns and other conditions that linked ecosystems with particular fire regimes and effects of the past (Varner et al. 2005; Freeman et al. 2017; Brando et al. 2020).

Because of its reliance on historical boundaries defining "natural fire," the fire regime concept does not intuitively reflect the non-stationarity of how repeated fire interacts with vegetation responses. This is an important consideration in a no-analog future, where unique species compositions and novel climates create conditions outside those historical boundaries (Freeman et al. 2017). This is partly because fire regimes are often defined by a chosen historical context of ecosystem response to fire or present-day fire practices (Miller and Safford 2020). Instead, a focus on what drives both positive and negative feedbacks of recurring fires better enables projecting future ecological trajectories in a rapidly changing world (Riley et al. 2019). To provide for a more nuanced and less hegemonistic representation of these feedbacks, the "Ecology of Fuels" (Mitchell et al. 2009) concept was introduced as an alternative to the focus on fire regimes. The Ecology of Fuels represents greater theoretical flexibility and understanding of the role of repeated fire. This concept underscores the recognition that fire ultimately links vegetation through space and time and drives structure and function in predictable ways in frequently burned ecosystems (McLauchlan et al. 2020; Loudermilk et al. 2022). For example, the type and amount of fuel developing after a fire dictates the time in which the next fire can occur (i.e., "reburns"), and short reburn intervals will result in vastly different vegetation development pathways than long reburn intervals (Prichard et al. 2017; Stevens-Rumann et al. 2020; Jaffe et al. 2023). In some cases, variability in fire regimes is actively employed in large-scale fire management programs. For example, in the nearly 2 M ha Kruger National Park in South Africa, after decades of fixed fire intervals, intentionally diverse frequencies and seasons of prescribed fire combined with lightning ignitions are used to achieve a range of desired ecological and social benefits that were not resulting via adherence to the mean historical fire regime metrics (Govender et al. 2006; Van Wilgen et al. 2011).

Alternative stable states and feedbacks

Traditional ecosystem ecology afforded the concept of stability to systems that appeared to retain consistent structure and composition in the face of "external" stressors such as fire. Ecosystems were considered "stable" when they are not significantly altered by biotic or abiotic disturbances. Current understanding, however, shows that the complex interplay of fire regime characteristics, climate and weather, and land cover conditions across spatial and temporal scales results in alternative stable states that are natural expressions of ecosystem nonstationarity. Many frequently burned ecosystems represent one of multiple alternative stable states as a result of fire and tend to exhibit particular ecosystem structures and vegetation composition that is conducive to fire, with examples including most grasslands, some shrublands, and many woodlands. These frequently burned systems often contain exceptionally high levels of biodiversity (e.g., African, South American, and USA savannas, many Mediterranean ecosystems globally, pine woodlands in North America, tallgrass prairies/grasslands globally). Their structure and composition deteriorate functionally when fire is removed even for as little as a decade. Frequency is not the only factor driving fire-maintained stability. Seasonality plays an important role, since vegetation phenology interacts with fire to drive moisture conditions during the fire (Loudermilk et al. 2022) and can determine the composition of post-fire communities and their resulting flammability characteristics (Balch et al. 2013, Kane et al. 2021). Even in ecosystems that are the expressions of low-frequency, high-severity fires, such as stand-replacing fire-dominated ecosystems (e.g., *Pinus pungens*, some *Populus tremuloides*, serotinous *P. contorta*, *P. clausa*, some Mediterranean ecosystems), fire is a process that must happen (albeit infrequently) to maintain ecological function of these ecosystems and the often critical habitat they provide.

Repeated fires can create negative feedbacks generating ecosystem stability (stabilizing feedbacks). However, abrupt fire changes may generate positive feedbacks driving the system to an alternative state (Pausas and Bond 2020a). Loudermilk et al. (2016) describe a positive feedback process where the facilitation effect of xeric sub-canopy *Quercus* species on *Pinus* regeneration is essential in *P. palustris* ecosystems following the loss of pine overstory. Here, frequent fires maintain a soil and light environment for successful pine regeneration and keep the otherwise dominant sub-canopy oaks in shrub form. These and other shrubs can be teleologically viewed as "nurse plants" for pine regeneration by reducing solar heat exposure and desiccation between fires, which promotes pine seedling survival (Marsh et al. 2023). Consequently, pines contribute to fuelbeds that are more flammable than those of many *Quercus*. This positive feedback is found at the local scale, within small forest gaps, but has landscape-scale implications for ecosystem distribution and pattern. Similarly, stand-replacing fires in forests such as *P. rigida* (Givnish 1981; Clark et al. 2015) and *P. canariensis* can have feedbacks that maintain system attributes over repeated fire through resprouting and serotiny.

Rather than an isolated event triggering a set vegetation trajectory, fire is a highly variable, complex process that can have non-linear or unexpected influences on ecological trajectories. For example, in a system that normally experiences frequent fires with a constrained range of low-intensity surface fire behavior, the reintroduction of fire after a long fire-free period will likely produce different effects since the fire behavior and severity may change (Varner et al. 2005). Another example is the effects from overstory canopy loss (death/removal), which increases solar radiation penetration, and vegetative growth and regeneration response of certain sub-canopy species: these all cause fine to coarse-scale changes in subsequent fuel conditions and fire behavior (Loudermilk et al. 2022). Alternatively, canopy increases resulting from a decreased fire frequency can increase fuel moisture conditions to such an extent that fire can no longer propagate through the altered fuel beds and fire-adapted species no longer proliferate (Nowacki and Abrams 2008). For example, *Quercus-Carya* forests of the Southern Appalachian mountains of the USA have been altered through the exclusion of fire, which has led to a multidecadal transition from *Quercus* and *Carya* dominance to *Acer rubrum* and other fire-intolerant species through a process termed "mesophication" (Nowacki and Abrams 2008). Mesophication resists fire through the development of less-flammable litter (Kane et al. 2021) and a more humid microclimate (Nowacki and Abrams 2008). When fires are reintroduced to these stands under conditions extreme enough to allow spread, expectations were that mesic species would decline. However, recent work points to changed microbial communities and decomposition patterns that place fire-tolerant species at greater risk of post-fire mortality than their mesic counterparts, due to an increase in fine-root encroachment in the enhanced soil organic layer (and therefore higher potential for consumption by fire; Carpenter et al. 2021). This feedback of altered fire regimes over time could accelerate the state change to the mesophication trend despite reintroduction of fires, underscoring the complexity of fire's role and representing a negative feedback loop.

There are many other examples of feedback loops, including in tropical systems where fires alter structure and composition in such a way to make re-occurrence of fire more likely (Brando et al. 2020) leading to alternative states. For example, in the Amazon, road construction and agricultural activities can initiate positive feedbacks at both regional and local scales that increase fuel amount, availability, and likelihood of ignition (Nepstad et al. 2001). Repeated fires in these ecosystems have persistent effects on forest structure with reduced biomass and lianas (vines), as well as strong impacts on species richness and composition relative to single fires (Silveira et al. 2016). The trajectory of repeated fire in rainforests represents divergent pathways for ecosystem responses and a long-term transition away from closed-canopy forest, changed microclimate, and altered composition. Such a trajectory can drive existing feedbacks by contributing to global climate change via releasing large amounts of stored carbon in rainforests to the atmosphere, further exacerbating climate change (Riley et al. 2019).

These pathways and trajectories are created by multiple fires over time that interact at timescales that are finer than what are typical of evolutionary time as described in Principle 1. The inherent non-stationarity of ecosystems, however, doesn't remove repeated fire from time horizons needed for fire management and ecosystem management planning. Rather it highlights the need to understand how repeated fires do ecological work and how to predict their effects in non-linear and no-analog futures, particularly in human-dominated ecosystems and those responding to climate change.

Principle #4: fire behavior and effects derive from a continuum of deterministic to stochastic process elements at all spatial and temporal scales

> *The prediction of fire effects occurs along a gradient from deterministic to stochastic causal mechanisms. This includes mechanisms driving deterministic effects (e.g., effects of heating on fuel moisture) to random or probabilistic processes (e.g., post-fire rainfall patterns or seed dispersal by wildlife). Probabilistic effects occur when a mechanism, while known in theory, anecdotally, or with partial empirical evidence, must be represented but cannot be entirely measured due to lack of detail or logistical or technological difficulty. Probabilistic elements also derive from chaotic effects that cannot be known but can be better understood through approaches such as scenario planning. Accounting for both knowable (epistemic) and unmeasurable (aleatory) uncertainty in the underlying processes driving fire effects is critical for predictive modeling and achieving desired managed fire effects.*

Fire is at times simplified as the result of the combination of three factors: heat, oxygen, and fuel- leading to the reductionist supposition that understanding these components can explain the drivers of fire's immediate effects. However, fire effects are ultimately driven by the complex variability in spatial–temporal patterns, quantities of heat transferred into organisms and the physical environment, and subsequent effects of that energy transfer (Johnson and Miyanishi 2001; O'Brien et al. 2018; Atchley et al. 2021). Ecological responses to this energy transfer occur along a spectrum of interacting stochastic-to-deterministic mechanisms, both intrinsic and extrinsic to fire. For example, individual plant mortality can be driven by the variation in fire intensity that is the result of millions of consecutive fluctuations in fire-atmosphere coupling (Kobziar et al. 2006; Trouvé et al. 2021) or fine-scale variation in surface fuel characteristics driven by, for example, the random location where a pine needle falls and settles against a blade of grass (Loudermilk et al. 2014; O'Brien et al. 2018; Ritter et al. 2020). Alternatively, some fire effects are more predictable and the result of innate characteristics of species such as heat-stimulated seed germination or protective bark (see traits in Principle 1). These types of ecological drivers can occur independently or interact to shape fire-driven ecological outcomes at various scales of observation.

Stochastic fire effects can occur through variation in fire energy release driven by random or quasi-random processes, such as air turbulence or spatial arrangement and condition of vegetation at the moment a fire passes through. These stochastic elements can be captured using probabilities bounded by empirical evidence. For example, Loudermilk et al. (2019) showed that the influence of fire on plant community assembly was driven by random birth and mortality of individual plants caused by spatial variation of fire energy release, that itself was the result of random vegetation and fuel distribution (O'Brien et al. 2016). The spatial arrangement of fuels at fine scales has deterministic (e.g. falling foliage driven by tree size, type, shape, and gravity) and random properties, such as the final resting spot of foliage or cones after falling from a tree. Although each tree defines the larger domain of where a cone may fall, climate, plant productivity, animal behavior, and weather variables define when and where each cone falls within that domain. These impacts can also extend beyond plant community dynamics to explain patterns in insect and interaction diversity, all driven by the fine-scale variation in heat dose-dependent mortality (Dell et al. 2017; 2019).

The complex dynamics of fire-atmosphere coupling can also result in stochastic differences in fire energy release that can drive local variation in vegetation interactions with fire behavior (Jonko et al. 2021) and resulting plant injury and mortality (Wiggers et al. 2013). For example, turbulence and entrainment of air are based on variations in local vegetation structure, such as canopy gaps or thinning. Opening of the canopy also increases the penetration of solar radiation, causing a drying effect on surface vegetation that was previously shaded. The interaction of these two phenomena can create a heterogeneous fuel moisture environment, and complex interactions with climate, weather, and topography that drive positive and negative feedbacks with fire behavior and effects (Matthews et al. 2012; Marshall et al. 2020; Banerjee et al. 2020b, a). Stochasticity in flame patterns is also seen at small scales (e.g. cm to m) due to turbulent flame dynamics driven by structures such as Gortler vortices; these structures are visible only recently due to new technologies such as high-speed thermal imagery (e.g. Katurji et al. 2021).

Deterministic responses to fire are often more easily observed and have been the focus of most fire effects research. Species traits help predict fire effects and are often linked to the magnitude of fire energy release in an ecosystem and/or frequency of repetitive fires (Stevens et al. 2020; Burton et al. 2021). For example, ants sometimes form mutualistic relationships with trees in frequent-fire ecosystems, with the payoff for the ants driven by protection or enhancement of resources or habitat, and the payoff for the tree driven by ant modification of surrounding fine fuels (Janzen 1967; Dalrymple and Safford 2019). As illustrated in Principle 1, high-severity fires that remove overstory biomass favor reproductive strategies such as serotinous cones and recovery of aboveground tissue from underground tissues or epicormic buds. Alternatively, traits such as thick bark and self-pruning limbs are attributed to low rates of and total energy release fires where overstory trees escape most damage (Bond and Keeley 2005). While immediate fire effects can at times be deterministic with respect to fire energy, the post-fire responses may still be heavily influenced by less predictable events. These include short-term climate variation, local weather, other change agents such as fungal pathogens or bark beetles, and local variation in fire behavior and intensity, notwithstanding ignition patterns and topography.

Research on fire effects through the lens of dose–response relationships is useful along the entire continuum of causal drivers. For example, lethal energy dose for individual organism mortality is best characterized as a probabilistic function of the dose–response relationship (Smith et al. 2016; Sparks et al. 2017). Plant tissues likely have discrete or discernible thresholds for mortality (Lodge et al. 2018), where mechanisms for mortality and dose dependence can be quantified (O'Brien et al. 2018; Partelli-Feltrin et al. 2023). However, interactions among fire and non-fire drivers of ecological responses can alter the magnitude of heat dose-dependent thresholds. For example, the threshold heat dose for plant mortality is heavily influenced by pre- and post-fire drought, beneficial or pathogenic insect or microbial presence, temperature extremes, and other non-fire events (Hood et al. 2018). The relative importance of damage to different plant tissues is only beginning to be examined (Partelli-Feltrin et al. 2023). Traditional assumptions of "lethal dosages" such as 60 °C for 1 min are increasingly being challenged as fire effects studies expand to include diverse lifeforms beyond or mutualistic/symbiotic with plants (Pingree and Kobziar 2019). For example, many fungal and bacterial species demonstrate extraordinary tolerance to even long-duration high-temperature heating in some soil environments (Pingree and Kobziar 2019; Gow 2009; Whitman et al. 2019). Understanding the nature of each causal mechanism, i.e., random or deterministic or some combination of the two, is critical for developing better predictions of ecosystem responses to fire. Fire has been described as being a dynamic system with characteristics of a steady state (Finney et al. 2021). Decoupling direct, indirect, and interacting mechanisms will likely be essential for a clearer understanding of causal drivers of fire effects, which can in turn increase a broader understanding of the evolution of species traits and their relationship to fire. In this way, impacts can be better understood even as novel post-fire conditions emerge through accelerating global change.

Further complexity arises from the impacts of important non-fire drivers on ecological responses after fire. For example, links between fire energy transfer and fire effects can be decoupled by extrinsic interactions such as the impact of a post-fire drought on a plant's ability to recover from crown damage (Barker et al. 2022). Some interactions generate feedback loops that sustain ecosystem properties, while others can create unpredictable, non-linear, or state-changing outcomes. As with feedbacks of multiple fires (Principle 3), a dramatic shift away from a fire-maintained plant community could result from the loss of a single foundation species if that species also serves to produce the fuel that carries fire- a situation observed with the complete loss of *Pinus caribaea* overstory as a result of an introduced insect pathogen (Dani Sanchez et al. 2019). Such extrinsic factors will require coupling variation in fire behavior to climate and ecological process modeling to understand non-linear or novel outcomes.

Spatial heterogeneity in fire effects results from pre-fire characteristics of the landscape (including variations in fuel arrangement and antecedent fuel moisture across topographic gradients) as well as conditions that occur during the fire. These conditions include variations in weather and the way wind moves across dissected topography, fuel moisture fluctuations in response to weather, and the direction fire enters vegetation (e.g., heading, flanking, or backing). The spatial heterogeneity results from characteristics of the landscape that could be measured or known (deterministic) intersecting with chaotic factors such as weather (stochastic). Fire is thus an important player in the field of landscape ecology, which studies interactions and diversity of lifeforms and the natural environment at a landscape scale. Fire effects often occur in patches of low, moderate, and high severity dispersed across the burned area, with the size and proportion of these patches (an element of "pyrodiversity"; Steel et al. 2021) varying from fire to fire, even within the same fire regime (Collins and Stephens 2010). Fire patch size can greatly affect post-fire vegetation trajectories, as distance to seed source is a major factor in whether an area experiences post-fire tree regeneration (the closer a burned area is to seed source, the more likely it is to regenerate; Stevens-Rumann and Morgan 2019). Fire patch size also links to post-fire abiotic factors, with areas with larger patches and higher proportion of moderate and high-severity fire and higher slope more likely to experience debris flows than areas of low severity and lower slope (Gartner et al. 2015; Hyde et al. 2016a, b). Patchiness of a landscape is related to post-fire outcomes, as recently burned areas tend to slow fire spread (Parks et al. 2015) and may also act as areas where firefighters can pursue suppression tactics. Fire generates complexity in both vertical (e.g., removal of ladder fuels) and horizontal (e.g., variation in fire severity patches) directions. Each of these mechanisms for fire effects across a landscape represents a complex combination of deterministic and stochastic elements.

Predicting post-fire outcomes in a rapidly changing climate future depends on understanding of causal mechanisms to improve parameterization of ecosystem process models (Dickman et al. 2023). Despite the long-standing recognition that fire effects must be understood in the context of climate change (Flannigan et al. 2009), some models fail to capture fire as a physical process of interacting atmosphere-vegetation-fire feedbacks as well as resulting fire effects. Instead, many vegetation models use indirect scale-dependent ecological phenomena influenced by fire, such as estimates or thresholds of fire effects on seed dispersal and recruitment ability and limitations, mortality and re-sprouting patterns, post-burn depredation, and cumulative soil impacts, but still treat each fire as an event with predetermined behavioral characteristics and ecological responses (Fisher et al. 2018, Keane et al. 1996, Scheller et al. 2019, Sturtevant et al. 2009). It is important to note that integrating complexity into ecological models does not always translate into greater accuracy and precision—it only ensures important processes are accounted for in the computation of fire effects.

Including fire-atmospheric feedbacks and better understanding of the physics of fire behavior in models will fill an important need for mechanistically linking dynamic fire behavior to feedbacks with fire effects, vegetation response, and future fire conditions, as well as helping to guide effective fire management. The coupling of mechanistic models with models that incorporate a range of variability within the stochastic to deterministic continuum can be used to identify unknowns and test whether they affect underlying processes that occur at different scales. In addition, techniques such as scenario planning can be used in models to address phenomena for which the probability of stochastic events (e.g. weather) is not known (Riley and Thompson 2016). As our current climate-fire interactions disrupt ecosystem trajectories and create novel conditions, a more mechanistic understanding of the relationships between fire behavior and its impacts from the sub-meter to the landscape scale can improve our ability to predict and plan for both stochastic and deterministic fire effects.

Principle #5: human ideas, institutions, and impacts are key drivers of historical, contemporary, and future fire

> *The inextricable human relationship with fire has a long and complex history. Unlike most other natural disturbances, fire has a broad range of human uses and can be applied intentionally as an ecological forcing agent with reasonably predictable results. Although humans are one of many regulators of fire, uniquely sentient human ideas, morals, ethics, and policies drive decisions that affect fire across the globe and at scales ranging up to the entirety of the Earth system. This makes the human regulation of fire a fundamentally different process requiring a diversity of scientific approaches (e.g., anthropology, geography, behavioral science, policy etc., integrated with natural sciences). Fire is and always has been a tool for achieving human objectives, be they biological, ecological, cultural, or combinations thereof. At the same time, some uncontrolled fires are having devastating impacts on humans and their environment. Ultimately, the human relationship to fire will continue to be a major driver of fire ecology research and of societal capacity to adapt to ongoing environmental and climatic changes.*

Early human use of fire

Early hominids observed and experienced fire for millennia, often taking advantage of naturally ignited fire for foraging (Glikson 2013). Human control of fire for domestic purposes can be confidently dated to the Middle Pleistocene Epoch, between 300,000 and 400,000 years before present (James et al. 1989; Roebroeks and Villa 2011; Agam et al. 2021; James et al. 1989). There is some evidence of potentially much earlier fire control (Hlubik et al. 2017). By the middle of the Middle Paleolithic (c. 150,000 ybp), humans in many parts of the globe were regularly harnessing fire. As suggested by the large increase in fire-related deposits and artifacts in Europe between 130,000 and 70,000 years ago (Roebroeks and Villa 2011), uses evolved gradually, beginning with the provision of warmth, light, protection, and the ability to live in colder climes; to the increased efficiency of hunting tools and practices; to the ability to cook meat for easier ingestion of protein, the manufacture of more sophisticated tools, and the production of materials like adhesives (Carmody and Wrangham 2009; Clark and Harris 1985).

This extended history of fire usage reflects and can be considered a driver of the evolution of human society and culture, leading to technological and cultural advancement. This is evidenced by ideological and religious belief systems from around the world (Frazer 2019). Examples include the ancient Greek myth of Prometheus' theft of fire from Zeus; the exploits of the Polynesian mythological hero Maui, who stole the ability to make fire from the goddess Mahuika; Mixcoatl's gift of fire to humans in Aztec mythology; and Manco Cápac, at once the Incan god of fire and sun and founder of Incan society, who is credited in Incan mythology with introducing humanity to technology (Frazer 2019). These mythologies capture the transition of the human relationship with fire from a natural force to be reckoned with to a highly valuable tool. For millennia, and continuing still today, Indigenous communities actively use fire to manage vegetation for numerous purposes, such as providing protection from predators and other humans, preparing land for agriculture and grazing, and promoting the growth of plants for food, medicine, shelter, basket making, and other practical uses (Kimmerer and Lake 2001; Lake et al. 2017; Lake and Christianson 2019; Greenwood et al. 2022).

The dawn of "bad" fire

Unlike the above examples, the Judeo-Christian conception of Hades and Hell can be seen as a platform supporting largely fearful and antagonistic views of fire in many European traditions. European colonization of much of the world in the 17th–nineteenth centuries was accompanied by the exportation of such pyrophobic attitudes to newly inhabited continents that soon became a dominant paradigm (Pyne 1997). This shift in perspective was driven by several factors that include the predominant use of wood in European-built structures and perceptions that demonized fire itself (e.g., religious linkages to hell, racist viewpoints, destruction of nature, etc.). Development of progressively more effective fire control technologies soon followed. Often, this promoted the design of public information campaigns that criminalized cultural burning (Seijo 2009). In many colonized regions—Australia and North America are the best-known examples—Indigenous peoples were forcibly removed from their ancestral lands and prevented from conducting traditional practices, including cultural burning (Cronon 1996). Large landscapes were set aside in national parks and other reserves to preserve their "pristine" nature and protect them from human depredations (Stamou 2002; Laris and Wardell 2006; Seijo et al. 2020; Ladino et al. 2022; Armenteras and de la Barrera 2023). European-derived models of forest management, which were adopted by most colonies, ex-colonies, and other Europeanized societies in the late 19th and early twentieth centuries, narrowly defined the value of forests as sources of timber, and perceived fires as wasteful, destructive, and unnatural (Safford and Stevens 2017; Pausas and Bond 2019). The rise of modern fire-fighting technologies—trucks, planes, helicopters, professional wildland fire-fighting organizations—and tactics increased fire suppression effectiveness and reduced risk, and led to delusions that absolute control of fire was in reach (Pyne 1997). Today, in the early twenty-first century, most nations on Earth continue to strongly discourage the use of fire as an ecosystem management tool.

Recognition of "good" fire

By the late 1960s, a growing body of research began to demonstrate that (1) fire, including cultural burning, plays an important ecological role in natural ecosystems, and (2) fire exclusion has resulted in a series of detrimental ecological impacts (Leopold et al. 1963). This research was originally centered in South Africa, but soon expanded to other nations, including the USA, Australia, the Mediterranean Basin, east Africa, and Brazil (Pyne 1991; Van Wilgen et al. 2011; Welch et al. 2013; Pooley 2022). In the USA, the rise of fire ecology research was coincident with—and influenced—the environmental movement. By the mid-1970s, all the US federal land and resource management agencies had stepped away from full fire suppression as a policy and embraced the notion of "ecological fire management" (Stephens and Ruth 2005). It has only been more recently that European-centric viewpoints have begun to shift to acknowledge that Indigenous peoples and cultural burning are intrinsically part of the social-ecological system and fire regimes rather than separated from lightning-ignited fires (Whitlock et al. 2010; Lake et al. 2017; Larson et al. 2021; Copes-Gerbitz et al. 2022). However, a number of causes contribute to continued fire suppression, including public misperception of fire's role in ecosystems and institutional causes such as inertia and the transference of blame to fire managers (Calkin et al. 2015). For many reasons, fire suppression continues to dominate fire management in the US, such that approximately 98% of all wildland ignitions in the USA are extinguished before they reach 120 ha (Calkin et al. 2005).

Although US influence on many western nations' wildland fire policy and practice has been significant (e.g., fire-fighting technologies and the tacit focus on fire prevention and suppression), several Latin American nations have sought to adopt more liberal policies relative to fire use as a management tool. This more recent shift largely is based on findings from internal domestic science and influence by international non-governmental organizations (NGOs), like The Nature Conservancy and World Wildlife Fund. Mexico formally transitioned from full fire suppression to fire management in 2017 (see evidence of earlier unsuppressed wildfires in Baja California; Stephens, Fry, and Franco-Vizcaíno 2008; Murphy et al. 2021), and Brazil has been on the verge of making a similar change for at least a decade (L. Steil, FAO, pers. comm.). Colombia has also considered making changes to its current complete ban on fire use, but those efforts are currently stalled (S. Rodrigues-Buritacá, Instituto Humboldt, pers. comm.). Only a few nations in the rest of the world have formally adopted fire management policies that recognize the ecological importance of fire in some ecosystems; these include South Africa, Australia, Spain, Portugal, and a few nations in the Mediterranean Basin. However, as policies shift in relation to global climate change and other major drivers, advances towards fire management reform in many of these countries continue to be precarious (Seijo et al. 2015).

Confounding factors

The word "crisis" is being used to describe the current state of wildland fire with regard to impact on human communities (for example, the US Forest Service's *Wildfire Crisis Strategy*). The factors contributing to this characterization are difficult if not impossible to disentangle, as they include complex interactions between changes in fuels caused by decades of fire suppression, land use changes, expanding Wildland-Urban Interface (WUI), and changes in climate, along with shifting attitudes and philosophies about fire-human relationships (Ladino et al. 2022). There is evidence that at the global scale, area burned in the last few decades is actually decreasing rather than increasing (Doerr and Santín 2016; Andela et al. 2017; Giglio et al. 2013). Yet fire's impact on global human communities continues to grow with a rise in the intersection of human populations, fire, and more recently, intercontinental smoke. Both climate change and the long-distance transport of smoke from large, long-duration wildfires demonstrate that the effects of fire on humans extend beyond the fire perimeter and burn period.

The human relationship with fire has contributed to environmental challenges of the 20th and early twenty-first centuries. The combustion of vegetation and fossil fuels, including estimated biomass burning release of 2069 Tg C year^{-1}(van Wees et al. 2022), discharges more than 10 Pg of carbon per year—an overall carbon release rate (at least for the dominant fossil fuels emissions) that is unprecedented over at least the last 66 million years (Zeebe et al. 2016). Resulting climate change has compounded land use/fuels management impacts and contributed to changes in fire regimes that shift species composition and abundance, stimulate ecological invasion, and provoke changes in carbon and water cycling, wildlife habitat, ecosystem services, and climate resilience (Bowman et al. 2009; Johnstone et al. 2010;

McLauchlan et al. 2020; Rakhmatulina et al. 2021). In much of the world, changes have resulted in larger, more severe fires that can be destructive to ecosystem processes and human wellbeing (Bowman et al. 2017; Halofsky et al. 2020; Mueller et al. 2020).

Extreme weather-driven wildfire outbreaks have caused significant economic losses and human mortality (Moreira et al. 2020; Safford et al. 2022). Under warming and drying climates, fires set for agricultural purposes in tropical latitudes are more likely to escape and the scale of burning has amplified due to increased land ownership consolidation. Aside from the widespread loss of tropical forest, this has led to increased respiratory disease and related mortality in (mostly) rural human populations, and economic and livelihood losses to small landholders (Nepstad et al. 2001; Frankenberg et al. 2005). In subtropical savanna systems, institutional resistance to small-scale cultural fire use has resulted in social conflict, economic hardship, and stark contradictions between national policies and local practice (Kull 2004; Archibald 2016; Moura et al. 2019).

Rapid development spurred by the housing crisis and subsequent building in fire-prone areas in the wildland-urban interface (WUI) have exacerbated the conditions that can limit application of effective vegetation management practices (Syphard et al. 2012; Radeloff et al. 2018). Since 1990, tens of millions of new homes have been built in the WUI in countries like the USA, Australia, South Africa, and Chile, with hundreds of thousands of homes damaged by or lost to wildfire in the same period (e.g., Radeloff et al. 2018; Godoy et al. 2019). Since 2015, in California, USA alone, nearly 50,000 homes, commercial buildings, and other structures have been destroyed by wildfires, nearly 200 people have died, and insured economic losses have exceeded $50 billion (Safford et al. 2022). Direct fire-caused damage and death in the Mediterranean Basin, Chile, and Australia have been also centered on human populations in the WUI (Moreira et al. 2020; Filkov et al. 2020; Ganteaume et al. 2021). In addition, recent studies suggest that the impacts of smoke on respiratory and cardiovascular systems during and following major wildfire seasons cause morbidity and death for many thousands of people worldwide (O'Dell et al. 2021; Hahn et al. 2021; Akdis and Nadeau 2022).

Toward a paradigm shift

Conventional land and fire management may be ill-prepared to face the synergistic effects of legacy management policies and practices, climate change, and the expansion of ex-urban development in fire-prone landscapes (North et al. 2015; Moreira et al. 2020). Fire suppression usually begets higher fuel loadings and increased vegetation homogeneity that fosters subsequent larger, more intense, and dangerous fires. Arguably, novel applications of existing practices bode well for effectively facing these complex challenges. Many organizations and existing programs (e.g., Fire Learning Networks, cooperative extension programs, prescribed fire councils, prescribed fire training exchanges) are potential tools to address barriers that may hinder the broad use of intentional fire in vegetation management, particularly if they join forces to engage in coordinated and collaborative partnerships to evaluate novel approaches, not simply expand existing practice. Similarly, NGOs, government agencies, and academic institutions can play a key role in leading effective communications globally about the need for flexible fire management policies. These institutions are critical to educate the broader public about the intentional use of fire as a mechanism for dispelling common misconceptions surrounding the good fire-bad fire dichotomy. They also possess unique opportunities to promote concepts of ecological resilience, where the focus is less about recreating the pre-industrial past and more about using historical baselines as waypoints or roadmaps rather than endpoints (Safford et al. 2012; Freeman et al. 2017). Ideally, academic institutions, state and federal agencies, and NGOs will continue to build translational ecology and boundary-spanning capacities to address and convey the complex interdisciplinary nature of fire ecology (Enquist et al. 2017; Safford et al. 2017).

Opportunities to recognize, incorporate, and equally value traditional and diverse Indigenous knowledge systems and practices alongside other fire management approaches may improve and accelerate the capacity of forest and fire managers to meet the challenges of rapid climatic and land use changes (Seijo et al. 2015). This is particularly true with the current and growing interest in the traditional Indigenous use of fire around the globe (Yibarbuk et al. 2001; Hoffman et al. 2021). The recognition of the importance of cultural burning not only within Indigenous societies but for its broader landscape applications holds great promise for landscape stewardship, in addition to facilitating the establishment of community and ecosystem resilience to climate change (Hoffman et al. 2021; Long et al. 2021). This is consistent with recent research (Long et al. 2017; Marks-Block et al. 2021; Adlam et al. 2021) that conveys the current relevance of Indigenous knowledge systems that have evolved over millennia. Moreover, Indigenous approaches to fire often reflect a nuanced understanding of and relationship with fire that is based on respect-oriented stewardship of landscapes that comprise ancestral homelands. Such human connections to the land extend beyond the context of functional ecological processes and can serve to demonstrate the many dimensions of community well-being.

Finally, socio-ecological considerations of truly adaptive land and fire management require reconsidering common metrics, such as annual area burned. The standard use of area burned is no longer adequate for characterizing the growing impacts of climate change on humans and ecosystems (Hood et al. 2022; Macdonald et al. 2023), and suggests that any form of increased fire is necessarily negative. Some have argued that the focus should be on an assessment of the socio-ecological context and impacts of fire (or its absence; Moreira et al. 2020). This extends to our understanding of the efficacy of human intervention practices and policy in the context of scope, scale, improved ecological outcomes (per Moreira et al. 2020), and avoided socio-ecological damage. In sum, humans are inextricably connected to fire, both the good and the bad. Ultimately, the human relationship to fire will be a major determinant of our capacity to adapt to ongoing and intensifying environmental and climatic changes.

Conclusion

As these Principles demonstrate, fire ecology represents the nexus of many related fields, from ecology and biology to fluid dynamics and combustion science, from anthropology to behavioral science and public policy. Defining the key theoretical underpinnings of this integrated field helps ensure fire ecology's scientific rigor. For example, reporting fire effects in the context of measured abiotic conditions and/or fire behavior supports principles 2 and 3. By clearly articulating the conceptual foundation for the disciplinary space fire ecology uniquely occupies, we hope to set standards for hypothesis formulation, experimentation, observation, and interpretation. These principles can structure future development of theory and promote a holistic consideration of fire ecology's scope and relevance.

The five principles articulated here anchor fire ecology as a distinct discipline key to understanding life on Earth. Fire is now (and for a long time has been) part of human social systems, affected by human values, decisions, laws, and intent, which drive human-fire relationships and the ecological consequences of those relationships. This linkage to humans and human systems is inextricable and recognizes both evolutionary ties between fire and *Homo sapiens*, and the long cultural connections of fire to human societies that are often reflected in enduring Indigenous ecological knowledge. Understanding fire effects both as an integrated biophysical, chemical, and social phenomenon, and a complex interplay of biomass-mediated energy transfer, underscores the need for mechanistic understanding of fire and its effects on all ecosystem components. Such an understanding would bridge the two sub-disciplines that have traditionally bifurcated the discipline between combustion science and fire effects.

While our expectation is that these principles represent a comprehensive distillation of foundational knowledge for the field, we recognize that as knowledge grows, so too will our understanding of fire ecology principles. Our hope is that this effort allows for a continuing and robust conversation about what comprises the discipline of fire ecology, and better positions future fire research for rapid advances in knowledge and sustainable management of fire in an ever-changing world.

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Authors' contributions
Kobziar and Hiers contributed equally to the manuscript, conceiving of the original ideas and defining the final principles, writing the Introduction and Conclusion, leading or co-leading the writing of Principles 2, 3, and 4, and overall editing. Belcher, Bond, Enquist, Loudermilk, Miesel, O'Brien, Pausas, Riley, Safford, Wall, Watts, and Varner led the writing teams for different principles of the manuscript. The remainder of the authors plus the principle leaders provided intellectual and editorial input across the manuscript.

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