REVIEW

FIRE ECOLOGY

Fire and biodiversity in the Anthropocene

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Fire has been a source of global biodiversity for millions of years. However, interactions with anthropogenic drivers such as climate change, land use, and invasive species are changing the nature of fire activity and its impacts. We review how such changes are threatening species with extinction and transforming terrestrial ecosystems. Conservation of Earth's biological diversity will be achieved only by recognizing and responding to the critical role of fire. In the Anthropocene, this requires that conservation planning explicitly includes the combined effects of human activities and fire regimes. Improved forecasts for biodiversity must also integrate the connections among people, fire, and ecosystems. Such integration provides an opportunity for new actions that could revolutionize how society sustains biodiversity in a time of changing fire activity.

Fire has shaped the diversity of life on Earth for millions of years (*1*). Variation in fire regimes enables many plants to complete their life cycles (*2*), creates habitats for a range of animals (*3*), and maintains a diversity of ecosystems (*4*). Although people have used fire to modify environments for millennia (*5*–*7*), the cumulative effects of human activities are now changing patterns of fire at a global scale—to the detriment of human society, biodiversity, and ecosystems.

Many recent fires have burned ecosystems where fire has historically been rare or absent, from the tropical forests of Southeast Asia (*8*) and South America (*9*) to the tundra of the Arctic Circle (*10*). Large, severe fires have also been observed in areas with a long history of recurrent fire, and this is consistent with predictions of increased wildfire activity in the boreal forests of Canada and Russia (*11*, *12*) and the mixed forests and shrublands of Australia, southern Europe, and the western United States (*13*–*15*). Conversely, fire-dependent grassland and savanna ecosystems in countries such as Brazil, Tanzania, and the United States have had fire activity reduced and even excluded (*16*–*18*). These emerging changes pose a global challenge for understanding how to sustain biodiversity in a new era of fire. This requires improved knowledge of the interactions among fire, biodiversity, and human drivers and new insights into conservation actions that will be effective in this changing environment.

In this review, we explore the causes and consequences of fire-induced changes to biodiversity in the Anthropocene, the current era characterized by the prominent role of human activity in shaping global ecosystems. We start by synthesizing how changes in fire activity threaten species with extinction across the globe. Next, we examine how multiple human drivers are causing these changes in fire activity and biodiversity. We then highlight forward-looking methods for predicting changes in ecosystems and forecasting the positive and negative effects of fire on biodiversity. Finally, we foreshadow emerging actions and strategies that could revolutionize how society manages biodiversity in ecosystems that experience fire. Our review concludes that conservation of Earth's biodiversity is unlikely to be achieved without incorporating the critical role of fire in national biodiversity strategies and action plans and in the implementation of international agreements and initiatives such as the UN Convention on Biological Diversity.

Extinction risk in a fiery world

A central concept in fire science is the fire regime, which describes the type, frequency, intensity, seasonality, and spatial dimensions of recurrent fire (*19*). Many species are adapted to a particular fire regime, so substantial changes to these fire characteristics can harm populations (*20*) and shift ecosystems (*21*). For example, plants that require fire to release seeds can be threatened by fire intervals shorter than the time needed for them to mature and reestablish a seed bank or by fire intervals longer than seed and plant life spans (*22*). For animals, changes in the frequency and intensity of fire can reduce the availability of key resources for foraging and shelter, limit the capacity to recolonize regenerating habitats, and, in the case of severe fires, directly increase mortality (*23*).

We reviewed the 29,304 terrestrial and freshwater species categorized as threatened with extinction by the International Union for the Conservation of Nature (IUCN) (*24*) and found that for at least 4403 (15%), modification of fire regimes is a recorded threat. Changes in fire activity threaten a range of taxonomic groups that have been assessed comprehensively or through sampling representative species or multiple regions, from birds, dragonflies, and mammals to gymnosperms, legumes, and monocots (Fig. 1A). Some groups, such as gymnosperms, are at greater risk of fire-driven extinction: Changed fire activity is a threat to 28% of these taxa classified as critically endangered, endangered, or vulnerable (Fig. 1A).

Changes in fire activity threaten biodiversity in habitat types worldwide (Fig. 1B). Proportionally, the threat from changed fire activity to species at risk of extinction is greater for savannas (28%), closely followed by grasslands (26%), rocky areas (26%), shrublands (26%), and forests (19%) (Fig. 1B).

Across nine taxonomic groups that have been assessed systematically (Fig. 1A), we found that at least 1071 species are categorized as threatened by an increase in fire frequency or intensity and 55 species by exclusion of fire. This delineation, however, oversimplifies the nature of threats; for example, it masks the relationship in some ecosystems

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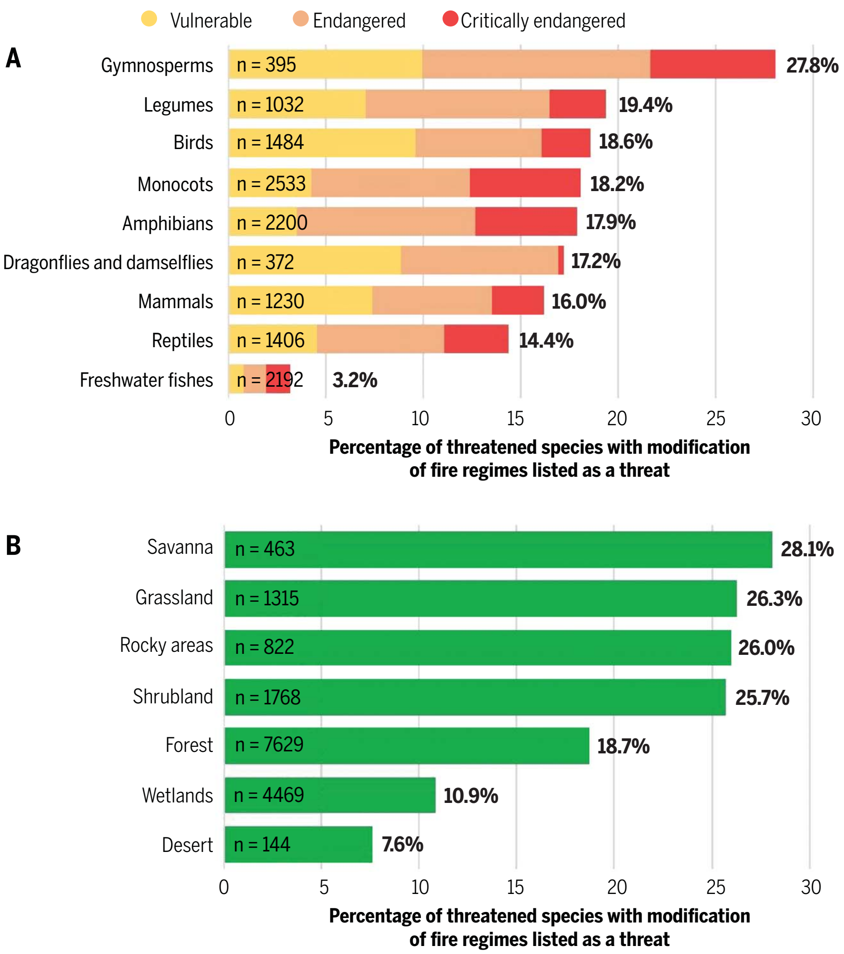


Fig. 1. Fire-driven extinction risk by taxonomic group and habitat type. (**A**) The percentage of threatened species (those classified as critically endangered, endangered, or vulnerable) for which modification of fire regimes is a threat (defined as threat type "Natural system modifications - Fire and fire suppression" in the IUCN Red List) for nine taxonomic groups. *n* is the total number of threatened species within each taxonomic group. Selected species include those globally assessed for the IUCN Red List, from groups assessed either comprehensively (amphibians, birds, gymnosperms, mammals), through a sampled approach of global data (dragonflies and damselflies, legumes, monocots, reptiles), or across several regions (freshwater fishes). The estimated percentages of species in each group that has been assessed include: gymnosperms, 91%; legumes, 17%; birds, 100%; monocots, 10%; amphibians, 84%; dragonflies and damselflies, 72%; mammals, 90%; reptiles, 71%; and freshwater fishes, 61%. (**B**) The percentage of threatened species for which modification of fire regimes is a threat for seven selected habitat types. *n* is the total number of threatened species, of the nine taxonomic groups within each habitat type [as defined in the IUCN Red List (24)].

between fire exclusion and subsequent intense wildfire from fuel accumulation. Nevertheless, important differences within and between habitat types emerge when the direction of fire regime change is considered. For example, of the species categorized as threatened by an increase or decrease in fire activity in forests (Fig. 1B), exclusion of fire is a threat to 17% of those in temperate forests and only 1% of those in tropical moist montane forests.

Changes in fire activity also threaten other levels of biodiversity. Assessments undertaken through the IUCN Red List of Ecosystems show that altered fire regimes, in combination with other drivers, threaten whole ecosystems with collapse, including the Cape Flats Sand Fynbos of South Africa and the mountain ash (*Eucalyptus regnans*) forests of Australia (25). Many biodiversity hotspots remain inadequately studied, and unprecedented recent fires such as the 12.6 million ha of vegetation burned in eastern Australia from late 2019 to early 2020 (26) mean that numerous species may have declined since their status was assessed. Thus, we are likely underestimating the total number of species threatened by ongoing changes in fire regimes.

Drivers of change in the Anthropocene

Among the profound consequences of the Anthropocene is the acceleration of Earth toward a hotter climate and a markedly different biosphere (27). Fire is both a consequence of and a contributor to this acceleration (28) but it is not acting alone: Interactions between fire and anthropogenic drivers such as global climate change, land use, and invasive species are reshaping ecosystems worldwide. Recent work describing global fire regimes has shown that patterns of fire are closely linked to climate, vegetation, and human activity (7, 17, 29, 30). Here, we synthesize linked changes in biodiversity and fire regimes and how they are shaped by three groups of direct drivers arising from human actions (Fig. 2 and table S1), as well as indirect socioeconomic drivers that underpin them (31). Our focus is on taxa and ecosystems likely to be threatened by the pace and magnitude of such change while recognizing that some taxa stand to benefit from these changes.

Global climate change

Anthropogenic climate change, including rising atmospheric CO_2 and a hotter global climate, modifies fire regimes by changing fuels, ignitions, and fire weather (32). These changes in turn alter the composition of ecosystems and the nature of species interactions. A prime example is fire interacting with more-severe droughts. In the Mediterranean Basin, abrupt shifts in ecosystems from forest to shrubland are triggered by large fire events followed by at least one extreme drought year (33). Elsewhere, intensifying droughts are contributing to more widespread fires in tropical forests in Amazonia, the Congo Basin, and Southeast Asia, with high mortality of thin-barked trees (34). More frequent or more intense climate-induced fires even threaten forests with a long history of high-intensity fire. For example, successive fires that occur before trees can set seed and reproduce are reshaping the species composition of temperate forests in Australia (35), subalpine forests in the United States (36), and boreal forests in Canada (11) and Russia (12). Such changes have cascading effects on the biota. For example, high-intensity fires in boreal forests in Alaska negatively affect microbes and fungi through soil heating (37) and by reducing the cover of lichens, a critical food source for caribou (*Rangifer tarandus*) (38).

Land-use change

Humans alter fire regimes through land-use changes associated with agriculture, forestry, and urbanization and by intentionally starting or suppressing fires (6, 7, 13). How changes in land use affect fuels, fire, and biodiversity varies depending on the type of activity and ecosystem.

Until recent decades, tropical broadleaf forests of the Afrotropical, Indomalayan, and Neotropical realms rarely experienced large fires (8, 39). Contemporary land use,

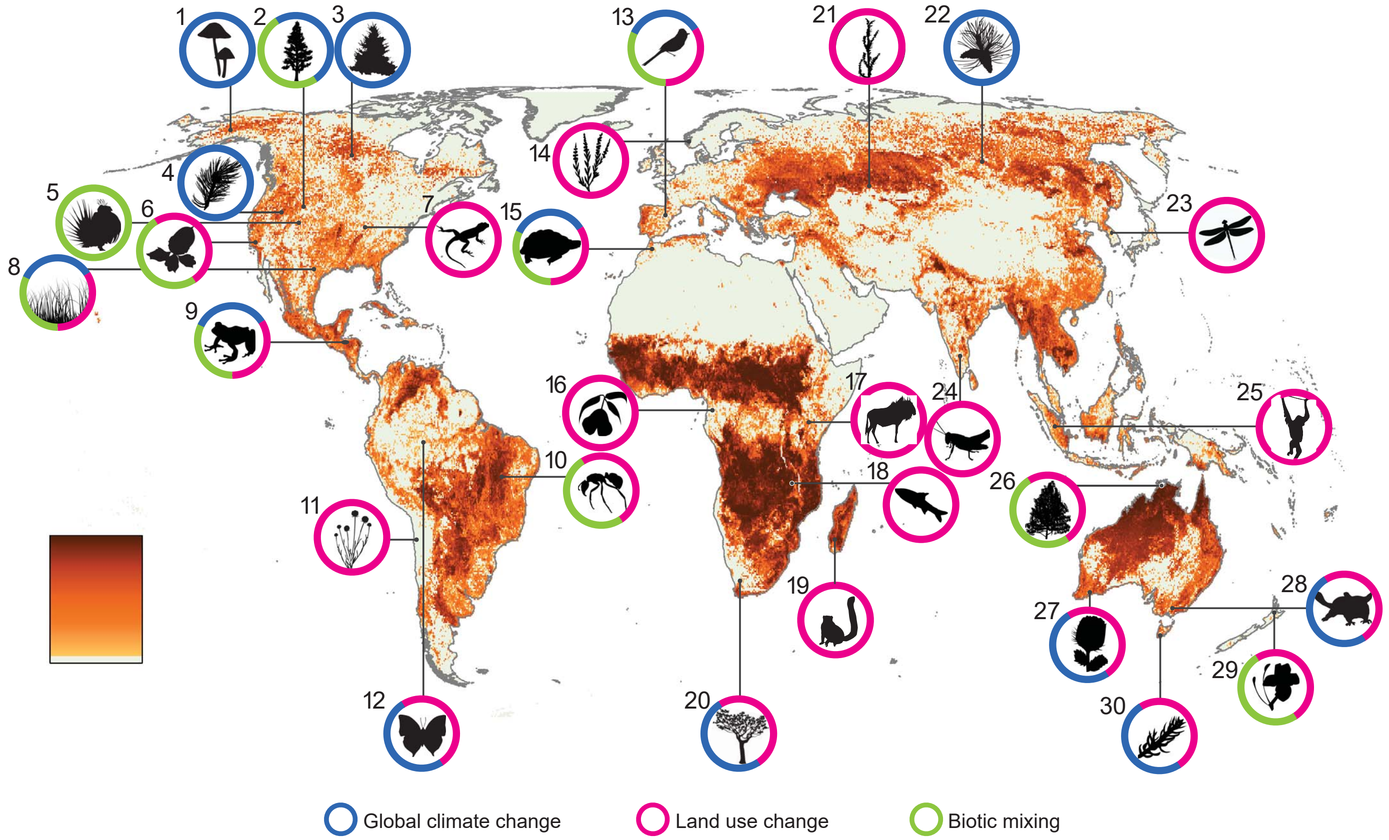


Fig. 2. Global portrait of linked changes in fire and biodiversity. Examples of documented and predicted fire-driven changes in biodiversity are shown. Details of the anthropogenic drivers associated with each of these changes are provided in the main text or table S1, following the numbered key. Examples are overlaid on a map of the number of times a fire was recorded from 2000 to 2019 in a given 500 m by 500 m MODIS pixel averaged across the 10 km by 10 km pixels displayed on the map.

including deforestation fires to clear primary forest for agriculture, often promotes more frequent and severe fires. In the Amazon basin, logging, habitat fragmentation, and climate change act synergistically to increase the risk of larger and more severe fires (*39*). This can drive abrupt change from forest to derived savannas (*40*). Cascading effects on a host of forest fauna have been observed, including declines in ant and butterfly communities (*40*, *41*) (Fig. 3). In tropical forests in Indonesia, massive wildfires caused by land clearing threaten some of the world's most biodiverse ecosystems and emblematic species such as the orangutan (*Pongo borneo*) (*8*).

By contrast, fire has been markedly reduced and almost eliminated from some grassy ecosystems, such as the Serengeti-Mara savanna of Tanzania, through increased livestock grazing and habitat fragmentation (*18*). This has led to woody encroachment, which threatens wild populations of large herbivores (Fig. 3) (*42*). Fire exclusion in the hyperdiverse Brazilian Cerrado is threatening biodiversity in areas where recurrent fire, which limits woody encroachment, has been impeded by habitat fragmentation and fire suppression policies. Where forests have encroached into unburned Cerrado, plant species richness has declined by 27% and ant richness by 35% (*43*). In other areas, such as parts of the Great Plains of North America, a century or more of active fire suppression has led to the replacement of grassland with juniper (*Juniperus* spp.) woodland (*16*).

Urbanization and habitat modification are important drivers of fire regimes (*13*) and of biodiversity (*44*) in Mediterranean-type and temperate ecosystems. In Southern California, native chaparral shrublands support exceptionally high plant diversity. Short intervals between fires, associated with increased ignitions near urban areas, trails, and roads, are converting chaparral into vegetation dominated by exotic herbs (*45*). In the Mediterranean Basin, expansion of urban areas is linked with agricultural land abandonment: After rural depopulation, mosaics of farmland and open forest have shifted to more fire-prone shrublands and forests (*46*). Larger and more severe wildfires are expected to negatively affect forest-dwelling birds, but some open-country species will benefit from more frequent fires (*47*). In temperate mountain ash forests of Australia, the cumulative impacts of logging and extensive wildfires have removed large trees, placing populations of arboreal mammals that nest in old trees, such as Leadbeater's possum (*Gymnobelideus leadbeateri*), at increased risk of extinction (*48*).

Biotic mixing

Humans have redistributed species across the globe (*49*) and, in doing so, have created novel assemblages that modify fuels, fire regimes, and postfire dynamics (*50*). In many parts of the world, invasive plants have increased flammability and fire frequency (*22*, *51*). For example, in deserts and shrublands of the western United States, invasive cheatgrass (*Bromus tectorum*) increases fuel loads and continuity, which alters regional fire regimes (*52*). In turn, increased fire frequency reduces habitat for the greater sage-grouse (*Centrocercus urophasianus*), a bird that prefers to forage in dense sagebrush (*53*). Invasive animals can also modify fire regimes by altering fuels (*54*). The introduction of exotic vertebrate herbivores to New Zealand generated open conditions favorable for frequent low-intensity fires and contributed to the conversion of

A Exclusion of fire threatens wild herbivores in savanna ecosytems in the Serengeti-Mara, Tanzania.

B Deforestation fires cause shifts in vegetation with cascading effects on fauna in Amazonia, Brazil.

Fig. 3. Some tropical ecosystems are experiencing too much fire and others not enough. (**A**) Frequent fires are a key aspect of African savanna ecosystems that support a large portion of the world's remaining wild large mammals. However, fire activity in the Serengeti-Mara of Tanzania has been reduced, and some areas no longer experience fire. This could increase shrub encroachment (top left; photo by S. Archibald) and the displacement of wild herbivores that prefer open areas (top right; photo by D. D'Auria) (*18*, *42*). (**B**) The Amazon basin is home to ~10 to 15% of the world's terrestrial biodiversity. In southeast Amazonia (bottom left; photo by P. M. Brando), human drivers increase deforestation fires and uncontrolled fires. This is driving shifts from humid forest to drier forests or derived savannas. Cascading effects on fauna include the decline of forest butterfly species such as the leaf wing butterfly (*Zaretis itys*) [bottom right; photo by Morales/agefotostock (*40*)].

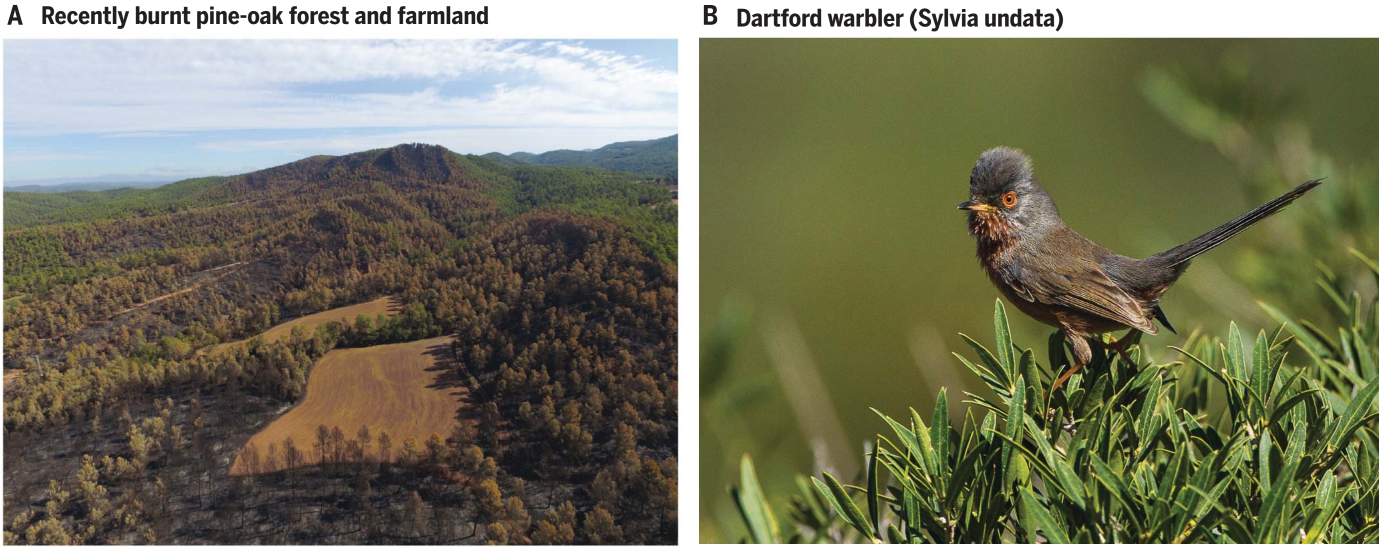
temperate forests to shrublands (*55*). Invasive animals can also affect biodiversity through their influence on the postfire recovery of species: In Australia, an increase in the activity of the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*), as well as their greater hunting success in postfire environments, increases mortality of native animals (*56*).

Disruption of biotic interactions and the removal of species can also shape fire and biodiversity associations. Experimental evidence indicates that removal of large grazing mammals in Africa and North America alters ecosystem structure and increases fire activity (*57*). Indeed, our review of IUCN Red List data indicates that modification of fire activity has contributed to the recent extinction of 37 species, including a suite of marsupials in Australia whose digging and foraging activity may have influenced fire regimes (*58*).

Socioeconomic drivers

Demographic, economic, political, and institutional factors underpin changes in land use and other direct drivers of fire regimes and their impact on biodiversity (*6*, *15*, *59*). Contemporary changes in human population size and distribution shape fire regimes worldwide, with corresponding pressures on biodiversity and ecosystems (*17*, *60*). In the Amazon basin, increases in deforestation and uncontrolled fires have underlying societal causes, including market demand for beef, soybean, and timber, as well as transportation and energy projects and weak institutional governance (*9*, *61*). Political and social institutions also are important. After the collapse of the Soviet Union, the abandonment of large areas of cropland in Kazakhstan provided opportunities for the restoration of steppe grasslands. However, in some recovering grasslands, the removal of grazing animals and the subsequent increase in fire activity has reduced plant species richness. (*62*). Conflicts are a largely unrecognized driver of changes in fire regimes: An endangered dragonfly, *Asiagomphus coreanus*, inside the demilitarized zone between South Korea and North Korea is threatened by anthropogenic fire used to reduce vegetation for increased visibility (*24*).

Even before the acceleration of social and ecological changes in the mid-1900s (*31*), cessation of traditional fire practices in many parts of the world transformed landscapes. For example, colonialism in the southwestern United States disrupted fire-dependent human cultures with cascading effects for ecosystems, including dense stands of conifer forests replacing previously open vegetation (*63*). In Australia, changes arising from the displacement of Indigenous peoples and their purposeful



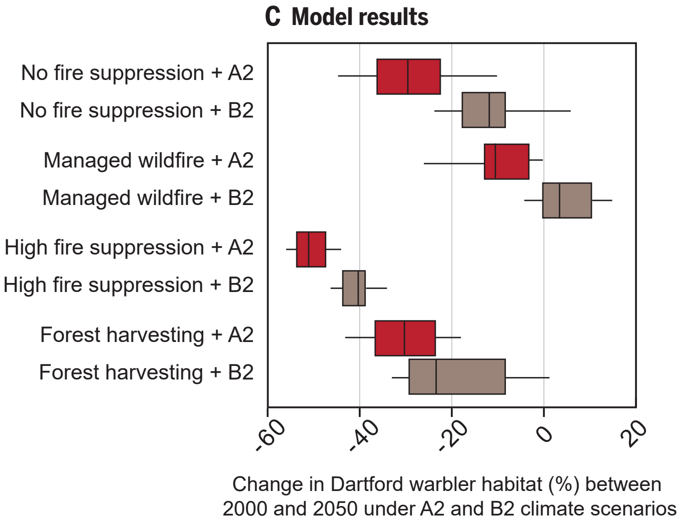


Fig. 4. Modeling ecosystems in transition in the Mediterranean Basin. Integrating data on land use, climate change, and fire dynamics [(**A**); photo by L. Brotons] with empirical bird occurrence data [(**B**); photo by F. Veronesi, Francesco Veronesi from Italy/CC BY-SA (https://creativecommons.org/licenses/by-sa/2.0)] is helping to predict the impact of social and ecological changes on species distributions. (**C**) Comparison of management actions showed that the Dartford warbler, an open-country species, will benefit from managed wildfire that creates new open spaces (*47*). Box plots show the median change in Dartford warbler habitat and the interquartile range from 10 simulations. A2 climate scenarios were associated with a lower number of large wildfires than B2 climate scenarios.

use of fire have been linked with extinctions of mammals (*24*), transformation of vegetation types (*5*), and decline of species such as the endemic Tasmanian pine (*Athrotaxis selaginoides*) (*64*). Cessation of traditional fire practices continues to affect species and ecosystems today (*5*).

Improving the forecast for biodiversity

To underpin new and emerging approaches to conservation in the Anthropocene, an urgent task is to better quantify how biodiversity responds to changing fire regimes. This requires a mix of empirical studies, manipulative experiments, and modeling. Various methods are available to predict changes in fire behavior and fire effects (*65*), changes to biodiversity (*66*), and anthropogenic drivers (*67*). Here, we focus on methods that couple information on fire and biodiversity, particularly those that incorporate human drivers.

A surge of empirical studies has explored the relationship between biodiversity and the spatial and temporal variation in fire regimes (sometimes called "pyrodiversity") (*3*). For example, a continent-wide assessment of savanna ecosystems in Africa showed that pyrodiversity was important in wet savannas, where areas with large variation in fire size, intensity, and timing had 27% more mammal species and 40% more bird species than areas with low variation in fire regimes (*68*). Studies in California found that the diversity of pollinators, plants, and birds in mixed-conifer forests was higher in areas with greater spatial variation in fire interval and severity (*69*, *70*). Linking such information on fire patterns and biodiversity with projections of future wildfires or management actions provides a powerful way to forecast future changes to ecosystems. For example, modeling has been used to identify alternative strategies for prescribed burning to reduce wildfire risk for populations of the iconic koala (*Phascolarctos cinereus*) in southeastern Australia (*71*).

Advances in predictive modeling also deliver new opportunities to couple fire and biodiversity data with likely trajectories of multiple drivers. For instance, coupling a dynamic fire-succession model with species distribution models enabled projection of the impact of alternative management and climate change scenarios on bird communities in northeastern Spain (*47*). Letting some wildfires burn in mild weather conditions was predicted to create new open spaces that would benefit open-habitat species (*47*) (Fig. 4). Forest harvesting for bioenergy production, an important socioeconomic consideration, also benefited some species by offsetting the loss of open habitats through a reduction in severe fires. Integrating projections of climate, wildfires, and species distributions offers an opportunity to design nature reserves that are effective now and in the future (*47*).

Process-based models that incorporate biological mechanisms such as demography and dispersal offer a robust way to model potential relationships between fire and biodiversity that may be outside the range of past conditions (*66*). For example, an individual-based model was used to examine the response of Hooker's banksia (*Banksia hookeriana*), a shrub species in southwestern Australia, to climate-mediated shifts in seed production, postfire recruitment, and shortened fire intervals (*72*). Modeling revealed that the effects of multiple stressors will threaten population persistence; a drier climate reduces the range of fire intervals that enable seed production and seedling recruitment, and the intervals between fires are projected to become shorter (*72*). Process-based models can also guide strategic management of populations of tree and shrub species when changes in fire regimes interact with habitat fragmentation (*73*), pathogens (*74*), and urban growth (*75*).

Currently, predictive models of biodiversity do not incorporate empirical data on evolutionary responses to fire, yet some aspects of biodiversity are rapidly evolving in the face of changing fire regimes. In Chile, where shrublands have experienced human-driven increases in fire frequency, anthropogenic fires are shaping the evolution of seed traits in a native herb, including seed pubescence and shape, with fire selecting plants with thicker pericarps (*76*). Variation in fire-related traits caused by heritable genetic variation between individuals has been assessed only for a small number of plant species but indicates moderate evolutionary potential (*77*). There are exciting opportunities to apply models and tools developed by evolutionary biologists, such as the breeder's and Price's equations (*66*), to forecast fire-driven evolutionary changes in the Anthropocene.

Feedbacks among fire, biodiversity, and other natural and anthropogenic drivers of biodiversity are important and have been assessed using a variety of methods (*39*, *59*, *78*, *79*). However, new approaches to quantifying feedbacks between social and ecological systems are needed. A promising technique is the use of agent-based models that quantify how changes in the environment create feedbacks that influence the likelihood of human actions (*80*). Such models can incorporate feedbacks between fire-driven changes in vegetation and the likelihood of human actors (e.g., family forest owners and homeowners) taking actions such as prescribed burning. In mountain forests in the United States, incorporating social and environmental interactions that influence the probability of planned fire and wildfire helped to quantify the effect of alternative fire management strategies on wildlife such as birds and mammals (*80*).

Emerging strategies and actions

The prominent role of human activity in shaping ecosystems at planetary scales is the hallmark of the Anthropocene and sets the context for emerging strategies and actions. First, it demands that scientists, stakeholders, and decision-makers confront the diverse and often synergistic changes to the environment that are occurring worldwide and emphasizes the need for new, bolder conservation initiatives. Second, it places the increasingly important role of people at the forefront of efforts to understand and adapt to ecosystem changes. Third, by linking people and local land uses with ecosystems, there is a greater likelihood of finding effective, place-based solutions to suit species and ecosystems.

A suite of emerging actions, some established but receiving increasing attention, others new and innovative, could be effective in promoting biodiversity in a new era of fire (Table 1). We summarize these (nonmutually exclusive) actions under three themes: (i) fire regimes that are managed by being tailored to species or ecosystems, (ii) approaches that focus on "whole ecosystems" (and not just on fire), and (iii) approaches that recognize the critical role of people.

A first set of approaches involves actively managing fire to suit particular species or ecosystems. This means ensuring the right amount, pattern, and timing of fire in landscapes that need it and less fire in those that do not. Temperate forests in the western United States, for example, have had a century-long history of fire suppression. A new prospect in temperate ecosystems is forest managers letting wildfires burn when conditions are not extreme (*81*) to promote mixed-severity fires that advantage a range of species (*70*). For example, in Yellowstone National Park, a policy of permitting lightning-ignited fires to burn has created more diverse landscapes (*81*) that support a high species richness of plants and their pollinators (*69*). Some fire-excluded forests in southern Australia, southern Europe, and the western United States have such high levels of fuels that mechanical treatments combined with prescribed fire may be needed to reduce the potential for biodiversity losses associated with high-intensity wildfire (*15*, *82*).

For innovative fire management in the Anthropocene, careful planning and deep knowledge of an ecosystem and its biota will be important to ensure the appropriate fire regime to achieve conservation objectives (*3*, *68*), whether the aim is to promote critical habitat features such as hollow-bearing trees (*48*), functional resources such as seed banks (*20*), or landscapes with diverse fire histories (*70*).

Although fire suppression threatens some ecosystems, targeted suppression can be a positive strategy to protect vulnerable species and ecosystems in fire-dependent and fire-sensitive ecosystems alike. For example, the fire-sensitive Wollemi pine (*Wollemia nobilis*) is an endangered Gondwanan relic with less than 200 individuals in a single rainforest valley in eastern Australia. During extensive wildfires in 2020, firefighters used targeted suppression to save this species (*83*). In subalpine vegetation of the western United States, surviving trees in whitebark pine (*Pinus albicaulis*) forests devastated by an exotic pathogen are actively protected by targeted fire suppression because they represent the seed source for future populations (*84*). Active fire suppression also has benefits in areas where it can reduce an uncharacteristically high fire frequency arising from increased human-caused ignitions associated with urban expansion (*45*).

A second set of approaches focuses on whole ecosystems, not just fire. Ecosystems can be particularly vulnerable to changes in fire regimes when already stressed by other threats and the synergies emerging from these threats (*39*). For example, populations of plants and animals affected by extreme drought, or those that occur in disconnected patches or are under pressure from exotic predators, are more likely to be threatened by fire when it interacts with these other disturbances (*56*, *72*, *73*). A whole-ecosystem approach that manages fire in the context of wider restoration and conservation actions is more likely to be effective (*79*). For example, strategic rewetting of drained peatlands and replanting with fire-resistant mosses is a promising technique for reducing fire frequency and promoting biodiversity in boreal forests in Canada (*85*). In the Amazon rainforest, a large-scale restoration project involving local citizens and national actors has been proposed to increase the total area and connectivity of rainforest habitat (*86*).

Reintroduction of species that have key functional roles offers an innovative opportunity to promote ecological processes that moderate fire regimes (*57*). For example, the reintroduction of a digging marsupial (*Isoodon fusciventer*) in an urban reserve in western Australia led to reduction of surface fuel loads and the predicted rate of fire spread (*58*). Digging animals modify fuels by creating foraging pits and burrows; the reintroduction of previously common digging species is an exciting prospect for restoring fire-prone ecosystems (*58*). In Africa, reintroducing native grazing animals such as the white rhinoceros (*Ceratotherium simum*) creates patchy fire regimes (*57*). Habitats created by these native megaherbivores differ from areas heavily grazed by livestock and provide habitat for birds, insects, and plants (*57*). Reintroduction of species to assist in the management of fire will likely

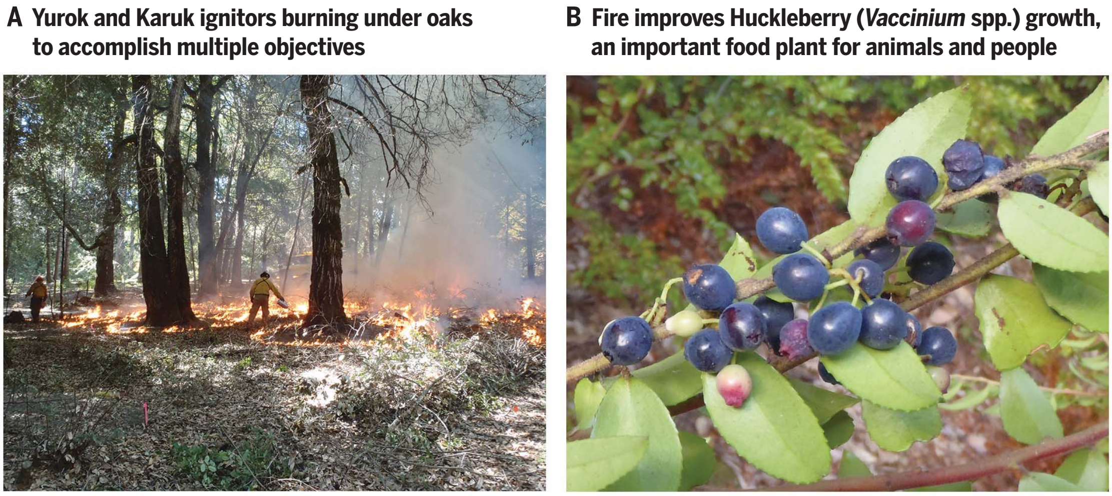


Fig. 5. Pyrodiversity with purpose in temperate forests of the western United States. (**A**) The Klamath-Siskiyou region is home to Indigenous peoples with different languages and histories. After more than a century of policies that promoted fire suppression, newly developed collaborations led by Indigenous communities and including scientists and local stakeholders are being formed to reinstate Indigenous fire practices. This cultural burning diversifies the frequency, seasonality, and intensity of fires and results in a fine-scale mosaic of disturbance history (photo by F. Lake). (**B**) Reinstating Indigenous burning, coupled with other cultural practices such as hunting, gathering, and tending of habitats for resources, supports a wide range of biodiversity, including species used for food, materials, medicines, and ceremonial purposes (*91*) (photo by F. Lake).

be most valuable in ecosystems that have experienced an increase in fire activity.

Many circumstances require the simultaneous management of multiple threats or drivers to achieve benefits for biodiversity. Invasion of highly flammable herbaceous species can exacerbate increased fire frequency, causing a positive grass-fire feedback cycle now evident across a range of deserts, shrublands, and savannas (*51*, *52*). Preventing or breaking this cycle in which invasive grasses replace woody plants relies on coordination among fire managers, conservation practitioners, and local communities to not only reduce ignitions but also to detect and remove invasive species as early as possible. In other cases, hotter burns may be applied to tackle encroachment by unwanted woody plants through the judicious use of "fire storms," such as in temperate grasslands of the central United States and savanna ecosystems in southern Africa (*16*, *87*). Simultaneous management of fire regimes and invasive animals can also be beneficial; for example, fire management to create unburned refuges while also controlling introduced mammalian predators is expected to benefit diverse populations of native wildlife across Australia (*56*).

Evolutionarily informed approaches for managing whole ecosystems are a newer prospect. Options for building ecological resilience to fire include managing for larger, better-connected populations to ensure the maintenance of genetic variation (*88*). A more radical approach is to use translocations to enhance gene flow and increase species' adaptability in fire-prone environments (*88*). For example, knowledge of within-species variation in plant traits, such as time to reproductive maturity, could be used by land managers to select populations for translocation that are better equipped to deal with changes in fire frequency. Modeling studies indicate that managed relocations outside of a species' known geographic range could also be effective in addressing population decline caused by high fire-frequency and land-use change (*75*). An increasingly important measure to increase ecosystem resilience to changes in fire regimes is to identify fire and climate refuges and ensure that they remain connected to secure habitats now and in the future (*89*).

Immediate measures to promote postfire recovery are crucial for whole-ecosystem management. However, there is much to learn about the most effective actions for rapid recovery. After the megafires in eastern Australia in 2019–2020, large-scale efforts are under way to assess the value of feeding stations, reducing browsing pressure by introduced herbivores, controlling invasive predators, and creating artificial shelters (*26*). For plants, rapid recovery actions include aerial seeding (*90*), seed collection (*75*), and restoration plantings (*84*). The benefits of restoration plantings are likely to apply to a range of taxa, including populations of freshwater fish and frogs threatened by postfire runoff of soil and sediments into streams (*24*).

A third set of approaches focuses on the critical role of people. Restoring and promoting landscapes that benefit people creates opportunities to balance biodiversity with other values in many regions of the world. Learning from previous and contemporary management by local and Indigenous people and promoting collaborative fire management are valuable steps in promoting fire regimes that benefit people and biodiversity (*91*–*94*). For example, reinstating Indigenous burning practices in the Klamath-Siskiyou bioregion in the western United States supports a wide range of species used as resources for food, materials, medicines, and ceremonial purposes (*91*) (Fig. 5). In the western deserts of Australia, hunting fires used by the indigenous Martu people increase vegetation diversity and support high populations of endemic mammals and reptiles. In the absence of the Martu, the more extensive lightning-ignited fires reduce biodiversity (*92*).

Diversified agriculture can also provide a range of habitats for plants and animals and shape fire regimes that benefit biodiversity. For instance, agricultural and forestry practices in the Mediterranean Basin that promote mosaics of low-flammability crops, orchards and oak trees reduce the risk of large, intense fires (*46*) and provide habitats for species-rich communities of birds (*47*). In China, more than 364,000 km of green firebreaks – strips of low flammability vegetation – have been planted in a range of terrestrial ecosystems and have the potential to promote biodiversity while reducing fire activity where it is unwanted (*95*).

Challenges and opportunities

Global changes in fire regimes will continue to amplify interactions between anthropogenic drivers and create challenges for biodiversity conservation and ecosystem adaptation. But

Table 1. New and emerging actions for sustaining biodiversity in ecosystems that experience fire.

Emerging approach	Reference
Managed wildfire whereby wildfires are allowed to burn naturally in fire-prone ecosystems and are suppressed only under specific conditions	(*81*)
Targeted fire suppression to protect vulnerable populations or ecosystems, aided by real-time data	(*84*)
Reintroduction of grazing and fossorial animals that regulate fire regimes for the benefit of threatened species or whole ecosystems	(*57*)
Simultaneous management of fire and other drivers such as invasive plants and animals	(*56*)
Use of extreme weather conditions to create “firestorms” that can be used to reduce woody plant encroachments in savannas and grasslands	(*87*)
Building evolutionary resilience by maintaining large and connected populations with genetic variation, identifying and protecting refuges, and increasing adaptability to future fire regimes by translocation	(*88*)
Rapid response and recovery teams that enact emergency conservation management including providing refuges for animals, planting and reseeding to promote rapid revegetation, and, in extreme situations, ex situ conservation	(*26*)
Indigenous fire stewardship and reinstatement of cultural burning in a modern context to enhance biodiversity, ecosystems, and human well-being	(*91*)
Diversified agricultural systems that moderate fire regimes and provide habitats for a range of species	(*46*)
Green firebreaks comprising low-flammability species planted at strategic locations to help reduce fire spread while providing refuges for biota	(*95*)

there are exciting opportunities for finding solutions that benefit both people and nature.

Historical or novel ecosystems

Restoring historical fire regimes is often regarded as the best approach for biodiversity and ecological resilience (*22*). However, recreating historical fire regimes in landscapes that are highly modified by climate change, new land-uses, and invasive species, will not necessarily lead to effective biodiversity conservation (*96*). Conserving organisms requires evidence of how ecosystems may respond to fires that are modified by, and subject to, new stressors. Direct measures of species, populations and ecosystems and their change through time, will help in identifying the fire characteristics that best promote biodiversity. The path forward requires deep knowledge of both historical and contemporary landscapes.

Linking biodiversity, ecosystem services, and human well-being

Promoting fire regimes that benefit biodiversity is difficult partly because of the need to simultaneously consider multiple values. In Mediterranean-type ecosystems, expansion of urban areas is bringing more people into proximity with wildfire activity, making human safety a priority in fire planning (*13*, *15*, *59*). Fires also sustain livelihoods (*92*, *94*) and influence ecosystem services such as water, climate, pest control and soil regulation (*97*), and these too are important considerations for local communities and policy makers. Developing strategies and actions that enhance diverse social and ecological values is not necessarily straightforward, but explicitly recognizing trade-offs and uncertainty between competing values can help navigate this complexity (*44*, *71*).

Creating innovative partnerships and policies

At local and regional scales, getting more of the ‘right’ type of fire in landscapes entails forging new alliances to build and apply knowledge. Indigenous-led fire stewardship is an example of a bottom-up approach to fostering partnerships between Indigenous and non-Indigenous institutions that aim to share and implement understanding of cultural burning practices which, in turn, can improve cultural connections and enhance ecosystems (*91*, *93*). Another example of forging new alliances comes from the city of Paradise, California, burned in 2018 in the catastrophic ‘Camp Fire’. Partnerships among scientists, conservation organizations and urban planners are redesigning the city by strategically locating less-flammable land-uses, such as orchards or parklands, and creating opportunities to achieve social and ecological goals (*98*). Sharing knowledge through training and education is crucial for integrating biodiversity into fire policy.

At national and global scales, biodiversity conservation will benefit from greater integration of fire into conservation policy. The United Nations Convention on Biological Diversity guides national and international efforts to protect species and ecosystems. A range of stakeholders, including signatory countries, nongovernment organizations and scientists, are currently negotiating a new Global Biodiversity Framework of goals and targets for the decade to 2030. Together with other drivers, changed fire regimes will affect proposed goals for increasing ‘the area, connectivity and integrity of natural ecosystems’ and reducing ‘the number of species that are threatened’ (*99*). Explicitly incorporating fire regimes in the formulation of the new Global Biodiversity Framework provides an opportunity to develop innovative policies to set and achieve biodiversity targets. Emerging global initiatives that bring together scientists with a wide range of stakeholders, such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), provide a foundation through which new biodiversity policies and scenarios could be developed and assessed. At the same time, international efforts to reduce greenhouse gas emissions, such as the Paris Agreement, remain crucial.

Monitoring and manipulating ecosystems

Assessing the effectiveness of conservation actions requires strategic collection of data on fire, biodiversity, and anthropogenic drivers. Data that inform a mechanistic understanding are essential for early warnings of regime shifts and their consequences (*48*, *66*). Experiments have provided a large body of knowledge, but more examples of large-scale manipulations of ecosystems are needed to assess new initiatives such as green fire breaks, and translocations aimed at increasing adaptive capacity. However, experiments that address ecological questions are not necessarily designed in ways that most effectively influence management (*100*). Adaptive management aims to resolve this dilemma by identifying a plan for addressing critical knowledge gaps, testing alternative actions and monitoring outcomes to improve future management (*100*).

Conclusions

Conservation of Earth's biological diversity will be achieved only by recognition of, and response to, the critical role of fire in shaping ecosystems. More than 4400 terrestrial and freshwater species, from a wide range of taxa and regions, face threats associated with inappropriate fire regimes. Innovative science and new partnerships across a range of sectors are crucial for navigating big decisions about new and changing ecosystems – whether it be consideration of fire in the context of meeting global biodiversity targets, safeguarding regional ecosystem services, or protecting homes and habitats. Placing the increasingly important role of people and their relationships with biodiversity at the forefront of efforts to understand and adapt to changes in fire regimes is central to these endeavors.

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SUPPLEMENTARY MATERIALS

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Table S1
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