Title: Fire and biodiversity in the Anthropocene

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Abstract: Fire has been a source of global biodiversity for millions of years. Yet, 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 include the combined effects of human activities and fire regimes. Improved forecasts for biodiversity must also integrate the connections between 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.

One Sentence Summary: Conservation of Earth's biodiversity demands recognition of, and response to, the critical role of fire.

Main Text:

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 occurred more frequently in areas with a long history of recurrent fire, including the boreal forests of Canada and Russia *(11, 12)*, and the mixed forests and shrublands of Australia, southern Europe and western USA *(13–15)*. Conversely, fire-dependent grassland and savanna ecosystems in countries such as Brazil, Tanzania and USA have had fire activity reduced and even excluded *(16–18)*. These changes pose a global challenge for understanding how to sustain biodiversity in a new era of fire. This requires improved knowledge of the interactions between 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. 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 plants to mature and re-establish 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 29,201 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 4,391 (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 a stratified sampling approach, from dragonflies, freshwater fishes 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).

[Fig. 1 here]

Changes in fire activity threaten biodiversity in habitat types and biogeographic realms worldwide (Fig. 1b). Proportionally, the threat from changed fire activity to species at risk of extinction is greater for savannas (27%), closely followed by grasslands (25%), rocky areas (25%), shrublands (25%) and forests (19%) (Fig. 1b). Across nine taxonomic groups that have been assessed systematically (Fig. 1a), we found that at least 1,074 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 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 species threatened by changed 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 Mountain Ash forests of Australia *(25)*. Many biodiversity hotspots remain inadequately studied, and unprecedented recent fires such as the 12.6 million ha of vegetation burnt in 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; Table S1), as well as indirect socio-economic 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.

[Fig. 2 here]

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 causing 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 re-shaping the species composition of temperate forests in Australia *(35)*, subalpine forests in the USA *(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, including deforestation fires used 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 decline 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 Orangutan (*Pongo borneo*) *(8)*.

In contrast, fire has been severely 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 hyper-diverse 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)*.

[Fig. 3 here]

Urbanization and habitat modification are important drivers of fire regimes *(13)* and of biodiversity *(44)* in Mediterranean-type and temperate ecosystems. In southern California, USA, 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: following 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 fire *(47)*. In temperate Mountain Ash (*Eucalyptus regnans*) forests of Australia, cumulative impacts of logging and extensive wildfire 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 post-fire 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 western USA, 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 temperate forests to shrublands *(55)*. Invasive animals can also affect biodiversity through their influence on the post-fire 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 post-fire 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 fossorial marsupials in Australia whose digging activity influences fire regimes *(58)*.

Socio-economic 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. Yet, 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 *(32)*, cessation of traditional fire practices in many parts of the world transformed landscapes. For example, colonialism in southwestern USA 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 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 modelling. 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, and 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 species richness was 27% greater for mammals and 40% greater for birds in areas with large variation in fire size, intensity and timing *(68)*. Studies in California, USA, 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, modelling 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 modelling 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 socio-economic 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)*.

[Fig. 4 here]

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, post-fire recruitment, and shortened fire intervals *(72)*. Modelling 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, while 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 due to heritable genetic variation between individuals has been assessed only for a small number of plant species but indicates significant evolutionary potential *(77)*. There are exciting opportunities to apply models and tools developed by evolutionary biologists – such as the breeder's and Price equations *(66)* - to forecast fire-driven evolutionary changes in the Anthropocene.

Feedbacks between 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, homeowners) taking actions such as prescribed burning. In mountain forests in the USA, 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 global ecosystems is a 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 novel and innovative, could be effective in promoting biodiversity in a new era of fire (Table 1). We summarize these (non-mutually exclusive) actions under three themes: (i) managing fire regimes 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.

[Table 1 here]

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 USA, 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, USA, a policy of permitting lightning-ignited fires to burn has created more diverse landscapes *(81)* which support a high species richness of plants and their pollinators *(69)*. Some fire-excluded forests, in southern Australia, southern Europe and western USA, 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)*.

While 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 western USA, 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 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 re-wetting 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 significant 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 like 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 management of fire will likely 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, whereby invasive grasses replace woody plants, relies on coordination among fire managers, conservation practitioners and local communities to not only reduce ignitions but to also detect and remove invasive species as early as possible. In other cases, hotter burns may be applied to tackle encroachment by woody plants through judicious use of ‘fire storms’, such as in temperate grasslands of central USA 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 unburnt refuges while also controlling introduced mammalian predators is expected to benefit diverse populations of native wildlife across Australia *(56)*.

Evolutionary-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 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. Modelling 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 they remain connected to secure habitats now and in the future *(89)*.

Immediate measures to promote post-fire recovery are crucial for whole-ecosystem management. Yet, there is much to learn about the most effective actions for rapid recovery. Following mega-fires in eastern Australia in 2019-2020, large-scale efforts are underway 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 post-fire 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 western USA 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)*.

[Fig. 5 here]

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 *(46)*. 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 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 *(21)*. 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 fire 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 policy makers. Developing strategies and actions that enhance diverse social and ecological values is not necessarily straight-forward, 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, non-government 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.

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 *(46, 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 4,300 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 novel 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.

References and Notes:

1. T. He, B. B. Lamont, J. G. Pausas, Fire as a key driver of Earth's biodiversity. *Biol. Rev.* **94**, 1983–2010 (2019).
2. P. W. Rundel *et al.*, Fire and Plant Diversification in Mediterranean-Climate Regions. *Front. Plant Sci.* **9**, 1–13 (2018).
3. L. T. Kelly, L. Brotons, Using fire to promote biodiversity. *Science.* **355**, 1264–1265 (2017).
4. J. G. Pausas, W. J. Bond, Alternative Biome States in Terrestrial Ecosystems. *Trends Plant Sci.* **25**, 250–263 (2020).
5. M. S. Fletcher, T. Hall, A. N. Alexandra, The loss of an indigenous constructed landscape following British invasion of Australia: An insight into the deep human imprint on the Australian landscape. *Ambio* (2020). doi:10.1007/s13280-020-01339-3.
6. S. Archibald, Managing the human component of fire regimes: lessons from Africa. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150346 (2016).
7. D. M. J. S. Bowman *et al.*, The human dimension of fire regimes on Earth. *J. Biogeogr.* **38**, 2223–2236 (2011).
8. R. A. Chisholm, L. S. Wijedasa, T. Swinfield, The need for long-term remedies for Indonesia's forest fires. *Conserv. Biol.* **30**, 5–6 (2016).
9. J. Barlow, E. Berenguer, R. Carmenta, F. França, Clarifying Amazonia's burning crisis. *Glob. Chang. Biol.* **26**, 319–321 (2020).
10. F. S. Hu, P. E. Higuera, P. Duffy, M. L. Chipman, A. V. Rocha, A. M. Young, R. Kelly, M. C. Dietze. Arctic tundra fires: natural variability and responses to climate change. *Front. Ecol. Environ.* **13**, 369-377 (2015).
11. E. Whitman, M. A. Parisien, D. K. Thompson, M. D. Flannigan, Short-interval wildfire and drought overwhelm boreal forest resilience. *Sci. Rep.* **9**, 1–12 (2019).
12. K. Barrett *et al.*, Postfire recruitment failure in Scots pine forests of southern Siberia. *Remote Sens. Environ.* **237**, 111539 (2020).
13. T. Schoennagel *et al.*, Adapt to more wildfire in western North American forests as climate changes. *Proc. Natl. Acad. Sci.* **114**, 4582–4590 (2017).
14. M. M. Boer, V. Resco de Dios, R. A. Bradstock, Unprecedented burn area of Australian mega forest fires. *Nat. Clim. Chang.* **10**, 171–172 (2020).
15. F. Moreira *et al.*, Wildfire management in Mediterranean-type regions: Paradigm change needed. *Environ. Res. Lett.* **15**, 011001 (2020).
16. D. Twidwell, C. H. Bielski, R. Scholtz, S. D. Fuhlendorf, Advancing Fire Ecology in 21st Century Rangelands. *Rangel. Ecol. Manag.* (2020). doi:10.1016/j.rama.2020.01.008.

17. N. Andela *et al.*, A human-driven decline in global burned area. *Science.* **356**, 1356–1362 (2017).

18. J. R. Probert *et al.*, Anthropogenic modifications to fire regimes in the wider Serengeti-Mara ecosystem. *Glob. Chang. Biol.* **25**, 3406–3423 (2019).

19. A. M. Gill, Fire and the Australian flora: a review. *Aust. For.* **38**, 4–25 (1975).

20. R. G. Miller *et al.*, Mechanisms of Fire Seasonality Effects on Plant Populations. *Trends Ecol. Evol.* **34**, 1104–1117 (2019).

21. J. E. Keeley, J. G. Pausas, Distinguishing disturbance from perturbations in fire-prone ecosystems. *Int. J. Wildl. Fire*. **28**, 282–287 (2019).

22. J. E. Keeley *et al.*, in *Fire in Mediterranean ecosystems: ecology, evolution and management* (Cambridge, UK: Cambridge University Press, 2012).

23. D. G. Nimmo *et al.*, Animal movements in fire-prone landscapes. *Biol. Rev.* **94**, 981–998 (2019).

24. International Union for the Conservation of Nature (IUCN), The IUCN Red List of Threatened Species. Version 2019-3. Downloaded 14 Febr. 2020. www.iucnredlist.org (2019).

25. Internation Union for the Conservation of Nature (IUCN), The IUCN Red List of Ecosystems. Accessed 14 April 2020. https//iucnrle.org/ (2020).

26. B.A. Wintle, S. Legge, J. C. Z. Woinarski, After the megafires: what next for Australian wildlife? *Trends Ecol. Evol.* **35**, 753-757 (2020).

27. W. Steffen *et al.*, Trajectories of the Earth System in the Anthropocene. *Proc. Natl. Acad. Sci.* **115**, 8252–8259 (2018).

28. D. M. J. S. Bowman *et al.*, Fire in the Earth system. *Science.* **324**, 481-484 (2009).

29. S. Archibald, C. E. R. Lehmann, J. L. Gómez-dans, R. A. Bradstock, Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 6445–6447 (2013).

30. B. Rogers *et al.*, Focus on changing fire regimes: Interactions with climate, ecosystems, and society. *Environ. Res. Lett.* **15**, 030201 (2018).

31. S. Díaz *et al.*, Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, **366**, eaax3100 (2019).

32. R. A. Bradstock, A biogeographic model of fire regimes in Australia: Current and future implications. *Glob. Ecol. Biogeogr.* **19**, 145–158 (2010).

33. E. Batllori *et al.*, Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. *J. Ecol.* **107**, 1187–1198 (2019).

34. P. M. Brando *et al.*, Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis. *Annu. Rev. Earth Planet. Sci.* **47**, 555–581 (2019).

35. T. A. Fairman, C. R. Nitschke, L. T. Bennett, Too much, too soon? A review of the impacts of increasing wildfire frequency on tree demography and structure in temperate forests. *Int. J. Wildl. Fire*. **25**, 831–848 (2016).

36. M. G. Turner, K. H. Braziunas, W. D. Hansen, B. J. Harvey, Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl. Acad. Sci. U. S. A.* **166**, 11319–11328 (2019).

37. S. R. Holden, B. M. Rogers, K. K. Treseder, J. T. Randerson, Fire severity influences the response of soil microbes to a boreal forest fire. *Environ. Res. Lett.* **11**, 035004 (2016).

38. K. Joly, P. A. Duffy, T. S. Rupp, Simulating the effects of climate change on fire regimes in Arctic biomes: implications for caribou and moose habitat. *Ecosphere.* **3**, 1-18 (2012).

39. M. A. Cochrane, C. P. Barber, Climate change, human land use and future fires in the Amazon. *Glob. Chang. Biol.* **15**, 601–612 (2009).

40. L. N. Paolucci, J. H. Schoereder, P. M. Brando, A. N. Andersen, Fire-induced forest transition to derived savannas: Cascading effects on ant communities. *Biol. Conserv.* **214**, 295–302 (2017).

41. R. B. De Andrade *et al.*, The impacts of recurrent fires on diversity of fruit-feeding butterflies in a south-eastern Amazon forest. *J. Trop. Ecol.* **33,** 22–32 (2017).

42. M. P. Veldhuis *et al.*, Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science.* **363**, 1424–1428 (2019).

43. R. C. R. Abreu *et al.*, The biodiversity cost of carbon sequestration in tropical savanna. *Sci. Adv.* **3**, e1701284 (2017).

44. D. A. Driscoll *et al.*, Resolving future fire management conflicts using multicriteria decision making. *Conserv. Biol.* **30**, 196–205 (2015).

45. A. D. Syphard, T. J. Brennan, J. E. Keeley, Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Divers. Distrib.* **25**, 90–101 (2019).

46. F. Moreira, G. Pe'er, Agricultural policy can reduce wildfires. *Science.* **359**, 1001–1001 (2018).

47. A. Regos *et al.*, Trade-offs and synergies between bird conservation and wildfire suppression in the face of global change. *J. Appl. Ecol.* **55**, 2181–2192 (2018).

48. D. B. Lindenmayer, C. Sato, Hidden collapse is driven by fire and logging in a socioecological forest ecosystem. *Proc. Natl. Acad. Sci. U. S. A.* **115**, 5181–5186 (2018).

49. G. T. Pecl *et al.*, Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science.* **355**, eaai9214 (2017).

50. J. G. Pausas, J. E. Keeley, Abrupt Climate-Independent Fire Regime Changes. *Ecosystems.* **17**, 1109–1120 (2014).

51. M. L. Brooks *et al.*, Effects of Invasive Alien Plants on Fire Regimes. *Bioscience.* **54**, 677–688 (2004).

52. E. J. Fusco *et al.*, Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 23594–23599 (2019).

53. C. Riginos *et al.*, Potential for post-fire recovery of Greater Sage-grouse habitat. *Ecosphere.* **10**, e02870 (2019).

54. C. N. Foster *et al.*, Animals as Agents in Fire Regimes. *Trends Ecol. Evol.* **35**, 346–356 (2020).

55. G. L. W. Perry, J. M. Wilmshurst, J. Ogden, N. J. Enright, Exotic Mammals and Invasive Plants Alter Fire-Related Thresholds in Southern Temperate Forested Landscapes. *Ecosystems*. **18**, 1290–1305 (2015).

56. B. A. Hradsky, Conserving Australia's threatened native mammals in predator-invaded, fire-prone landscapes. *Wildl. Res.* **47**, 1–15 (2020).

57. C. N. Johnson *et al.*, Can trophic rewilding reduce the impact of fire in a more flammable world? *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20170443 (2018).

58. C. M. Ryan, R. J. Hobbs, L. E. Valentine, Bioturbation by a reintroduced digging mammal reduces fuel loads in an urban reserve. *Ecol. Appl.* **30**, e02018 (2020).

59. M. A. Moritz *et al.*, Learning to coexist with wildfire. *Nature*. **515**, 58–66 (2014).

60. A. D. Syphard, J. E. Keeley, A. H. Pfaff, K. Ferschweiler, Human presence diminishes the importance of climate in driving fire activity across the United States. *Proc. Natl. Acad. Sci.* **114**, 13750–13755 (2017).

61. C. A. Nobre *et al.*, Land-use and climate change risks in the amazon and the need of a novel sustainable development paradigm. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 10759–10768 (2016).

62. A. Brinkert, N. Hölzel, T. V. Sidorova, J. Kamp, Spontaneous steppe restoration on abandoned cropland in Kazakhstan: grazing affects successional pathways. *Biodivers. Conserv.* **25**, 2543–2561 (2016).

63. M. J. Liebmann *et al.*, Native American Depopulation, Reforestation, and Fire Regimes in the Southwest United States, 1492-1900 CE. *Proc. Natl. Acad. Sci. U. S. A.* **113**, E696-704 (2016).

64. A. Holz *et al.*, Population collapse and retreat to fire refugia of the Tasmanian endemic conifer Athrotaxis selaginoides following the transition from Aboriginal to European fire management. *Glob. Chang. Biol.* **26**, 3108–3121 (2020).

65. R. E. Keane *et al.*, Representing climate, disturbance, and vegetation interactions in landscape models. *Ecol. Modell.* **309**, 33–47 (2015).

66. M. C. Urban *et al.*, Improving the forecast for biodiversity under climate change. *Science.* **353**, aad8466 (2016).

67. P. H. Verburg *et al.*, Methods and approaches to modelling the Anthropocene. *Glob. Environ. Chang.* **39**, 328–340 (2016).

68. C. M. Beale *et al.*, Pyrodiversity interacts with rainfall to increase bird and mammal richness in African savannas. *Ecol. Lett.* **21**, 557–567 (2018).

69. L. C. Ponisio *et al.*, Pyrodiversity begets plant-pollinator community diversity. *Glob. Chang. Biol.* **22**, 1794–1808 (2016).

70. M. W. Tingley *et al.*, Pyrodiversity promotes avian diversity over the decade following forest fire. *Proc. R. Soc. B Biol. Sci.* **283**, 20161703 (2016).

71. P. D. Bentley, T. D. Penman, Is there an inherent conflict in managing fire for people and

conservation? *Int. J. Wildl. Fire*. **26**, 455–468 (2017).

72. J. Henzler *et al.*, A squeeze in the suitable fire interval: Simulating the persistence of fire-killed plants in a Mediterranean-type ecosystem under drier conditions. *Ecol. Modell.* **389**, 41–49 (2018).
73. A. I. T. Tulloch *et al.*, Fire management strategies to maintain species population processes in a fragmented landscape of fire-interval extremes. *Ecol. Appl.* **26**, 2175–2189 (2016).
74. H. M. Regan, C. I. Bohórquez, D. A. Keith, T. J. Regan, K. E. Anderson, Implications of different population model structures for management of threatened plants. *Conser. Biol.* **31**, 459-468 (2017).
75. T. C. Bonebrake *et al.*, Fire management, managed relocation, and land conservation options for long-lived obligate seeding plants under global changes in climate, urbanization, and fire regime. *Conserv. Biol.* **28**, 1057–1067 (2014).
76. S. Gómez-González, C. Torres-Diáz, C. Bustos-Schindler, E. Gianoli, Anthropogenic fire drives the evolution of seed traits. *Proc. Natl. Acad. Sci. U. S. A.* **108**, 18743–18747 (2011).
77. M. C. Castellanos, S. C. González-Martínez, J. G. Pausas, Field heritability of a plant adaptation to fire in heterogeneous landscapes. *Mol. Ecol.* **24**, 5633–5642 (2015).
78. S. Archibald *et al.*, Biological and geophysical feedbacks with fire in the Earth System. *Environ. Res. Lett.* **13**, 033003 (2017).
79. D. M. J. S. Bowman *et al.*, Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **371**, 20150169 (2016).
80. T. A. Spies *et al.*, Using an agent-based model to examine forest management outcomes in a fire-prone landscape in Oregon, USA. *Ecol. Soc.* **22** (2017). doi:10.5751/ES-08841-220125.
81. G. Boisramé, S. Thompson, B. Collins, S. Stephens, Managed Wildfire Effects on Forest Resilience and Water in the Sierra Nevada. *Ecosystems*. **20**, 717–732 (2017).
82. S. L. Stephens *et al.*, Is fire "for the birds"? How two rare species influence fire management across the US. *Front. Ecol. Environ.* **17**, 391–399 (2019).
83. A. Morton. 'Dinosaur trees: firefighters save endangered Wollemi pines from NSW bushfires'. (2020), (available at https://www.theguardian.com/australia-news/2020/jan/15/dinosaur-trees-firefighters-save-endangered-wollemi-pines-from-nsw-bushfires).
84. R. E. Keane, Managing wildfire for whitebark pine ecosystem restoration in western North America. *Forests*. **9**, 648 (2018).
85. G. Granath, P. A. Moore, M. C. Lukenbach, J. M. Waddington, Mitigating wildfire carbon loss in managed northern peatlands through restoration. *Sci. Rep.*, **6**, 1-9 (2016).
86. T. E. Lovejoy, C. Nobre, Amazon tipping point: Last chance for action. *Sci. Adv.* **5**, 4–6 (2019).
87. I. P. J. Smit *et al.*, An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas. *J. Appl. Ecol.* **53**, 1623–1633 (2016).
88. C. M. Sgrò, A. J. Lowe, A. A. Hoffmann, Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* **4**, 326–337 (2011).

89. A. J. H. Meddens *et al.*, Fire refugia: What are they, and why do they matter for global change? *Bioscience*. **68**, 944–954 (2018).

90. O. D. Bassett *et al.*, Aerial sowing stopped the loss of alpine ash (Eucalyptus delegatensis) forests burnt by three short-interval fires in the Alpine National Park, Victoria, Australia. *For. Ecol. Manage.* **342**, 39–48 (2015).

91. F. K. Lake, A. C. Christianson, Indigenous Fire Stewardship. *Encycl. Wildfires Wildland-Urban Interface Fires*, 1–9 (2019).

92. R. Bliege Bird, D. Nimmo, Restore the lost ecological functions of people. *Nat. Ecol. Evol.* **2**, 1050–1052 (2018).

93. J. Mistry, B. A. Bilbao, A. Berardi, Community owned solutions for fire management in tropical ecosystems: Case studies from Indigenous communities of South America. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150174 (2016).

94. J. R. Welch, E. S. Brondízio, S. S. Hetrick, C. E. Coimbra Jr, Indigenous burning as conservation practice: Neotropical savanna recovery amid agribusiness deforestation in Central Brazil. *PloS One*, **8**, e81226 (2013).

95. X. Cui *et al.*, Green firebreaks as a management tool for wildfires: Lessons from China. *J. Environ. Manage.* **233**, 329–336 (2019).

96. A. D. Barnosky *et al.*, Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science.* **355**, eaah4787 (2017).

97. J. G. Pausas, J. E. Keeley, Wildfires as an ecosystem service. *Front. Ecol. Environ.* **17**, 289–295 (2019).

98. Conservation Biology Institute, The Nature Conservancy, and Paradise Parks and Recreation, *Paradise nature-based fire risk resilience project* (Tech. Rep. Corvallis, Oregon, 2020).

99. https://www.cbd.int/

100. B. W. Van Wilgen, N. Govender, I. P. J. Smit, S. MacFadyen, The ongoing development of a pragmatic and adaptive fire management policy in a large African savanna protected area. *J. Environ. Manage.* **132**, 358–368 (2014).

101. A. R. Templeton, H. Brazeal, J. L. Neuwald, The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology*. **92**, 1736–1747 (2011).

102. V. Vandvik, J. P. Töpper, Z. Cook, M. I. Daws, E. Heegaard, I. E. Måren, L. G. Velle, Management-driven evolution in a domesticated ecosystem. *Biol. Lett.* **10** (2014), doi:10.1098/rsbl.2013.1082.

103. B. Chergui, R. C. Rodríguez-Caro, E. Graciá, S. Fahd, X. Santos, Population density of the spur-thighed tortoise Testudo graeca declines after fire in North-western Africa. *PLoS One*. **14**, 1–12 (2019).

104. G. Walters, Customary fire regimes and vegetation structure in Gabon's Bateke Plateaux. *Hum. Ecol*. **40**, 943–955 (2011).

105. J. D. M. White, S. L. Jack, M. T. Hoffman, J. Puttick, D. Bonora, V. Visser, E. C. February, Collapse of an iconic conifer: Long-term changes in the demography of Widdringtonia cedarbergensis using repeat photography. *BMC Ecol.* **16**, 1–11 (2016).

106. D. Bhaskar, P. S. Easa, K. A. Sreejith, J. Skejo, A. Hochkirch, Large scale burning for a threatened ungulate in a biodiversity hotspot is detrimental for grasshoppers (Orthoptera: Caelifera). *Biodivers. Conserv.* **28**, 3221–3237 (2019).

107. D. M. Bowman, H. J. MacDermott, S. C. Nichols, B. P. Murphy, A grass–fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecol. Evol.* **4**, 4185-4194 (2014).

Acknowledgments: We thank the Centre Tecnològic Forestal de Catalunya for hosting the workshop that led to this paper, and the people of Solsona for welcoming our international team: **Funding:** The workshop leading to this paper was funded by the Centre Tecnològic Forestal de Catalunya and the ARC Centre of Excellence for Environmental Decisions. LTK was funded by a Victorian Postdoctoral Research Fellowship (Victorian Government), a Centenary Fellowship (University of Melbourne) and an Australian Research Council Linkage Project (LP150100765). AR funded by the Xunta de Galicia (Postdoctoral Fellowship ED481B2016/084-0) and the Foundation for Science and Technology under the FirESmart project (PCIF/MOG/0083/2017). ALS was supported by a Marie Skłodowska-Curie Individual Fellowship (746191) under the European Union Horizon 2020 Programme for Research and Innovation. LB was partially funded by the Spanish Government through the INMODES (CGL2014-59742-C2-2-R) and the ERANET-SUMFORESTS project FutureBioEcon (PCIN-2017-052).; **Author contributions:** All authors contributed to the conceptualization of ideas and research goals during a one-week workshop in Solsona, Spain and/or follow up meetings in Tucson, USA. LTK, LB, AD and KMG led the workshop. LTK wrote the original draft. All authors contributed to reviewing and editing of the paper. LTK prepared visual material with assistance from ALS, EB and SA. JLS, KMG and LTK synthesized IUCN Red List data.; **Competing interests:** Authors declare no competing interests.; and **Data and materials availability:** All data are available in the main text or the supplementary materials.

Supplementary Materials:

Table S1 Details of linked changes in fire regimes and biodiversity documented in Figure 2.

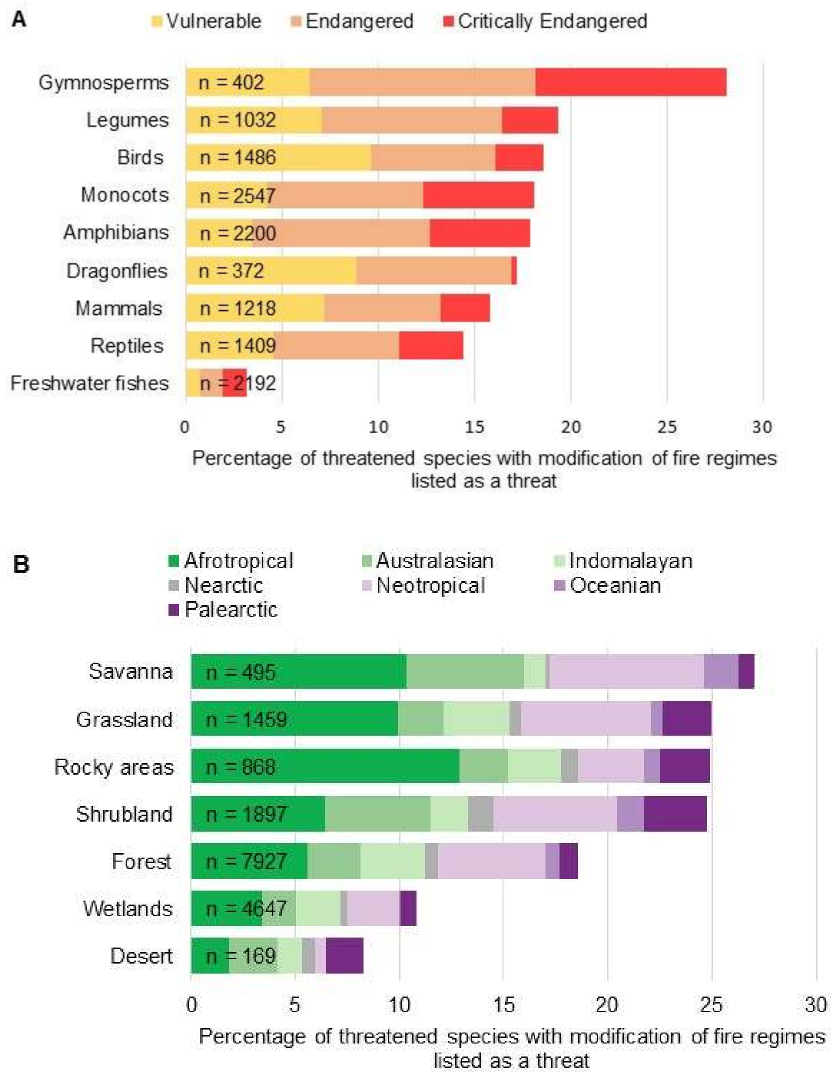

Fig. 1. Fire-driven extinction risk by taxonomic group and habitat type. **(A)** The percentage of threatened species (those classified as Critically Endangered, Endangered or Vulnerable) for which modification of fire regimes is a threat (defined as threat type 'Natural system modifications - Fire and fire suppression' in the IUCN Red List), for nine taxonomic groups. n is the total number of threatened species within each taxonomic group. Selected groups include those globally assessed for the IUCN Red List, either comprehensively (amphibians, birds, gymnosperms, mammals) or through a sampled approach (dragonflies, freshwater fishes, legumes, monocots, reptiles). The percentage of species in each group that has been assessed include: gymnosperms, 91%; legumes, 18%; birds, 100%; monocots, 12%; amphibians, 84%; dragonflies, 63%; mammals, 90%; reptiles, 71%; and freshwater fishes, 54%. **(B)** The percentage of threatened species for which modification of fire regimes is a threat, for seven selected habitat types, in seven biogeographic realms. n is the total number of threatened species, of the nine taxonomic groups, within each habitat type (as defined in the IUCN Red List). [Source: *(24)*].

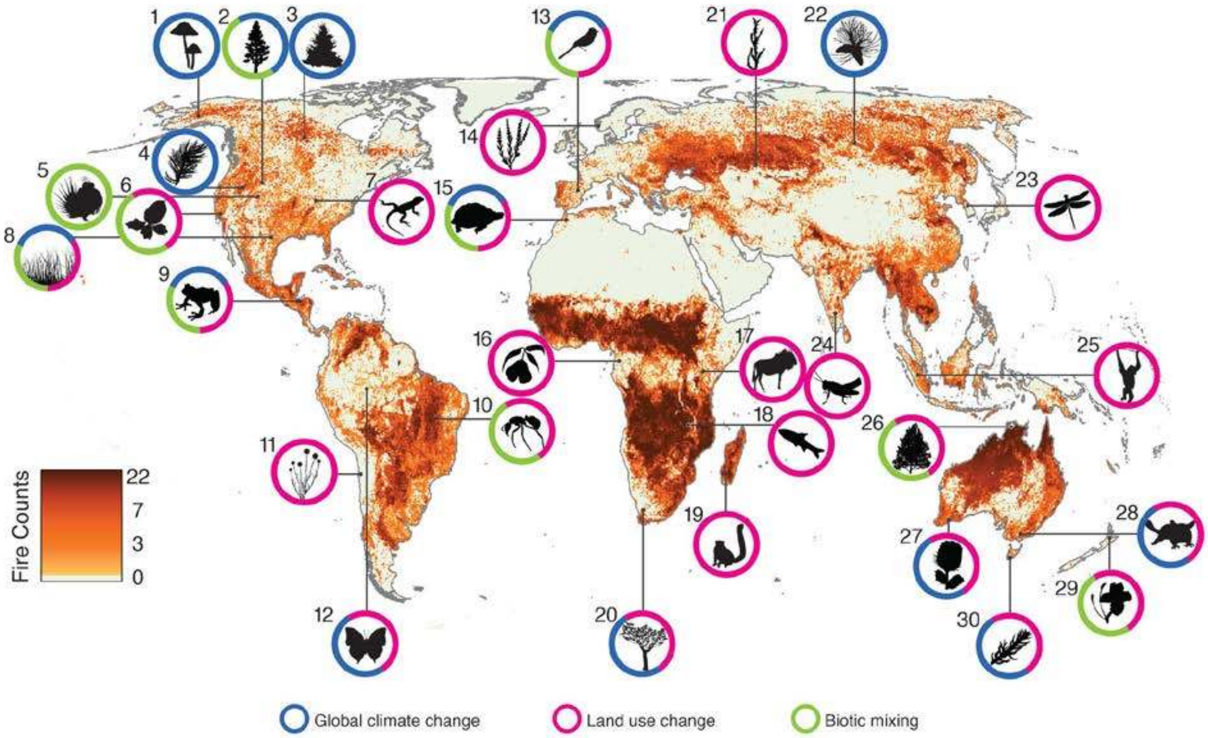

Fig. 2. A global portrait of linked changes in fire and biodiversity. Examples of documented and predicted fire-driven changes in biodiversity are shown. Details of the anthropogenic drivers associated with each of these changes are provided in the main text or Table S1, following the numbered key. Examples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

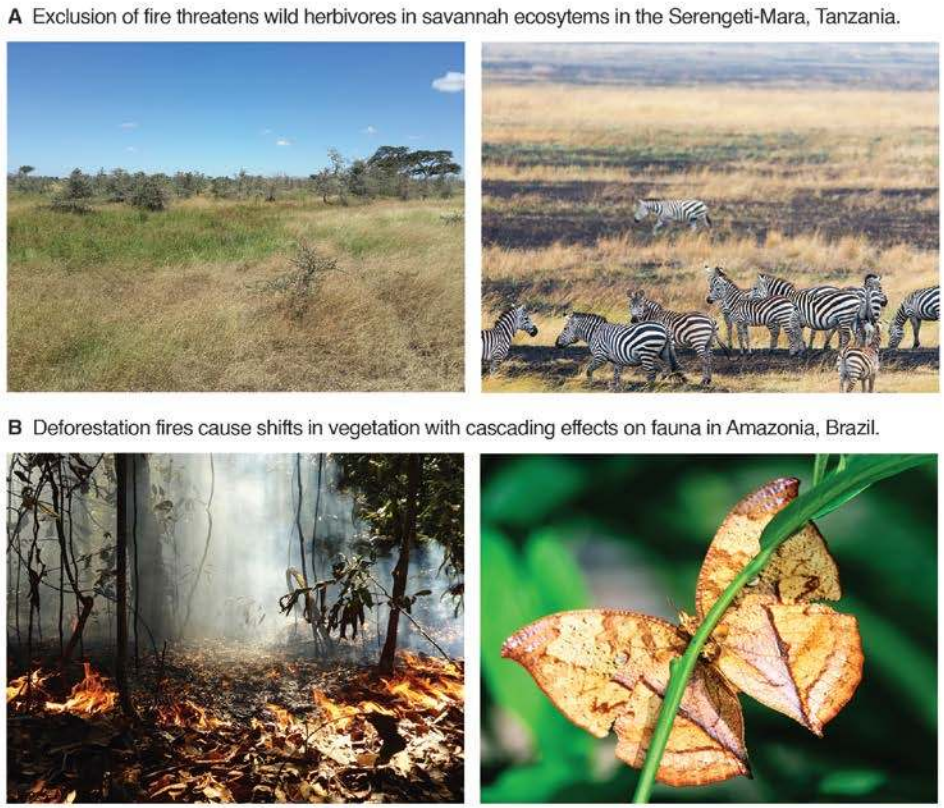

Fig. 3. Some tropical ecosystems are experiencing too much fire and others not enough. (**A**) Frequent fires are a key aspect of African savanna ecosystems that support a large portion of the world's remaining wild large mammals. However, fire activity in the Serengeti-Mara of Tanzania has been reduced, and some areas no longer experience fire. This could increase shrub encroachment (top left) and the displacement of wild herbivores that prefer open areas (top right) *(18, 42)*. (**B**) The Amazon basin is home to about 10-15% of the world's terrestrial biodiversity. In southeast Amazonia (bottom left), 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 Leaf Wing Butterfly (*Zaretis itys*) (bottom right) *(40)*. [Additional image credits: Paulo M. Brando (Amazon rainforest), agefotostock (butterfly) and Daniel D'Auria (zebras).]

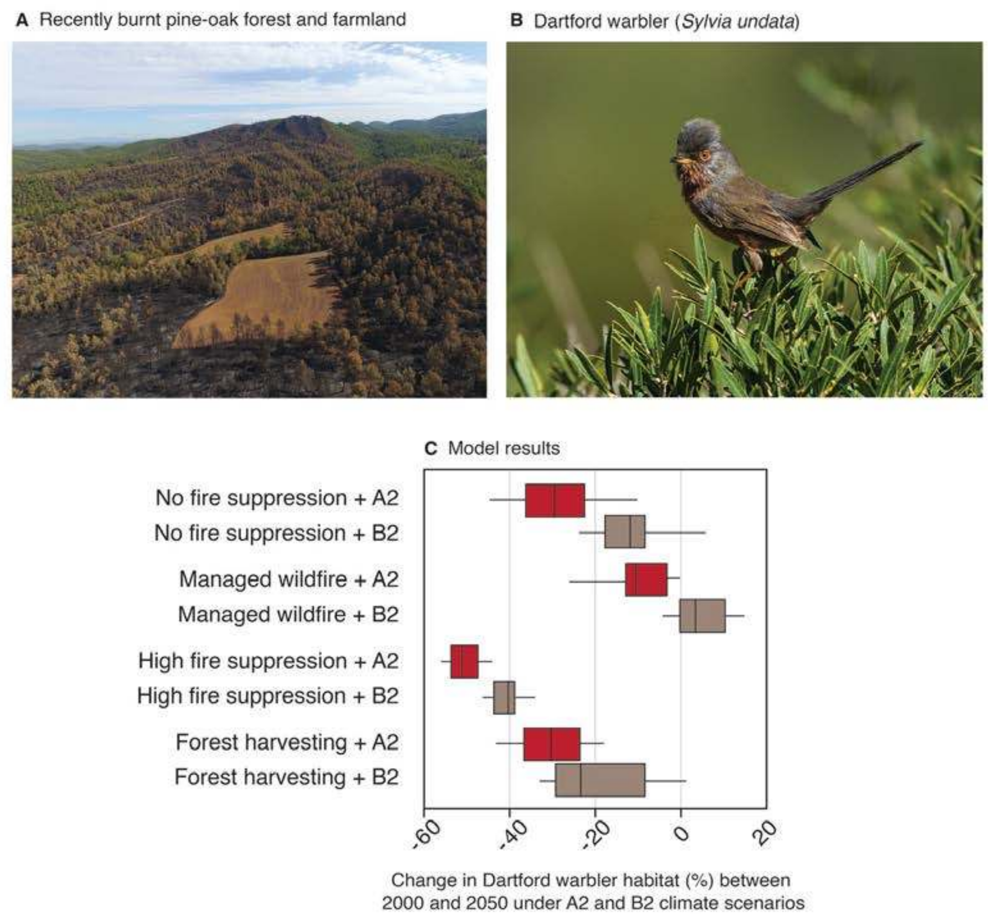

Fig. 4. Modelling ecosystems in transition in the Mediterranean basin. (**A**) Integrating data on land-use, climate change and fire dynamics with (**B**) empirical bird occurrence data is helping to predict the impact of social and ecological changes on species distributions. (**C**) A comparison of management actions showed the Dartford warbler, an open-country species, will benefit from managed wildfire that creates new open spaces *(47)*. A2 climate scenarios were associated with a lower number of large wildfires than B2 climate scenarios. [Additional image credits: Francesco Veronesi from Italy / CC BY-SA (https://creativecommons.org/licenses/by-sa/2.0) (Dartford warbler).]

Fig. 5. Pyrodiversity with purpose in temperate forests of western USA. (**A**) The Klamath-Siskiyou region is home to Indigenous peoples with different languages and histories. After more than a century of policy which 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. (**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)*.

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

Emerging approach	**Refs**
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' which can be used to reduce woody plant encroachments in savannas and grasslands.	*(87)*
Build evolutionary resilience through 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 modify 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)*

Supplementary Materials for

Fire and biodiversity in the Anthropocene

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Tables S1

Table S1.

Details of linked changes in fire regimes and biodiversity documented in Figure 2.

 **1. Saprotrophic fungi** A hotter, drier climate is projected to cause larger and more severe fires in the boreal forests of Alaska, USA. Within burned stands of Black Spruce forest and spruce-aspen forest, saprotrophic fungi decline in areas that are severely burnt *(37)*.	 **2. Whitebark Pine** Whitebark Pine populations in subalpine forests of western North America are declining through mortality caused by the Mountain Pine Beetle and White Pine Blister Rust. Yet, some individual White Pine trees are putatively pest-resistant and provide the foundation for future restoration efforts. Loss of pest-resistant trees from wildfire could reduce Whitebark Pine regeneration. Wildfires are predicted to increase in subalpine forests because of global climate change and this may place Whitebark Pine populations at further risk of decline *(84)*.	 **3. White Spruce** Extreme fire weather is increasing fire frequency in Canadian boreal forests. Short intervals between fires negatively affect recruitment of obligate seeders such as White Spruce. Global climate change is likely to increase fire activity in these forests and amplify the negative impact of drought-fire interactions on White Spruce *(11)*.
 **4. Lodgepole Pine** Subalpine forests of Greater Yellowstone, USA, have been resilient to stand-replacing fires that historically burned	 **5. Greater Sage-grouse** Invasive Cheatgrass increases fuel loads and continuity in deserts and shrublands of western USA, which alters	 **6. Chaparral** In southern California, native shrublands known as chaparral support exceptionally high plant

at intervals of 100-300 years. However, fire intervals are projected to decrease as the climate warms. Short-interval stand-replacing fires in Lodgepole Pine forests reduce tree generation and biological legacies. There will likely be marked changes in forest structure and function if short-interval fires become more common in Lodgepole Pine forests *(36)*.	regional fire regimes. In turn, an increase in fire occurrence reduces habitat for Greater Sage-grouse that prefers to forage in dense sagebrush *(53)*.	diversity. Short intervals between fires, associated with proximity to trails and roads in recreation areas, are converting chaparral into vegetation dominated largely by exotic herbaceous cover. Landscape disturbances such as trail construction and fuel breaks also provide the means for exotic herbaceous species to colonize open vegetation *(45)*.
 **7. Eastern Collared Lizard** Prior to European settlement, fires were common in the woodlands and savannas of midwestern USA. Fire suppression throughout much of the 20th century shifted open woodlands and savanna to a woodland with a dense woody understory. This regime shift fragmented habitats of exposed bedrock used by the Eastern Collared Lizard, followed by local extinction of the species *(101)*.	 **8. Great Plains grasslands** The Great Plains of North America comprise extensive fire-prone grasslands. Exclusion of anthropogenic fire, including active fire suppression, has reduced the frequency of fire and led to the transition of species-rich grassland to areas dominated by woody plants such as Juniper species. Overgrazing by domestic livestock has also removed herbaceous species that contribute to grassland fires. Under global climate change, fire regimes in the Great Plains are expected to exhibit ranges of variability that have no historical analogue over millennia *(16)*.	 **9. Hylid frog** The Endangered frog *Bromeliohyla melacaena* occurs in mountain pine forests and broadleaf cloud forests of Honduras. Fire is naturally rare in these forests but intentional use of fire for agriculture is reducing habitat for this species. Government incentivization for the cultivation of coffee in protected areas is one reason for increasing alteration of primary forest habitat. In addition, a woodboring pine beetle has recently caused high tree mortality, which encourages harvesting of timber and, in turn, use of intentional fires to convert areas harvested for timber into cropland. Climate change is expected to further reduce

		suitable habitat for this hylid frog, and make populations more vulnerable to fire *(24)*.
 **10. Ant communities** In the cerrado ecosystems of Brazil, fire suppression is practiced in most nature reserves and protected areas because of the perception that fire is damaging to biodiversity. Reduction in fire occurrence is exacerbated by crops, pasture and forest plantations that fragment savanna landscapes. Fire suppression has transformed some savanna vegetation into forests, through woody encroachment, causing biodiversity losses and marked changes in ecological processes. Ant communities are less diverse when fire is excluded *(43)*.	 **11. ‘Pineapples’** Natural fire ignitions are rare in the shrubland ecosystem of central Chile called matorral. Since the 19th century, human-driven ignitions associated with agriculture and transportation have significantly increased fire frequency in matorral and are driving evolutionary changes in seed traits of the native herbaceous plant ‘pineapples’ *(76)*.	 **12. Forest butterflies** Until recent decades, tropical broadleaf forests of the Amazon rarely experienced large fires. Extensive fires in the Amazon rainforest are a result of deforestation, habitat fragmentation and climate change, underpinned by social, political and economic changes. Forest specialists such as Leaf Wing Butterfly decline in areas burnt recurrently *(41)*.
 **13. Dartford Warbler** In northern Spain, land abandonment continues to shift mosaics of farmland and	 **14. Common Heather** Common heather occurs across Europe in a variety of temperate, boreal and	 **15. Spur-thighed Tortoise** Fire frequency and extent is expected to increase in the Mediterranean woodlands

open forest to dense, fire-prone forests. A hotter and drier climate exacerbates the risk of very large fires. Higher tree cover has increased populations of some forest bird species, while causing declines in open-country species. Threatened bird species that prefer open habitat, such as Dartford Warbler, will benefit from open spaces created by wildfires *(47)*.	montane ecosystems. In Norway, coastal populations of this shrub species have experienced higher fire frequency than other ecosystems, under millenia of traditional burning for agriculture. Smoke-induced germination, which helps plants exploit frequent fire, is found in populations from traditionally burnt shrublands but is lacking in ecosystems where fire is rare. Thus, anthropogenic fire has likely shaped the evolution of this species and conservation management will be enhanced by considering these adaptations *(102)*.	and shrublands of northwest Africa because of global climate change, rural land abandonment and dense plantations of trees for timber production. Spur-thighed Tortoise can be killed by fires and areas recently burnt by wildfires do not provide suitable food and shelter resources. Short intervals between fires are expected to cause regional population crashes *(103)*.
 **16. Savanna trees** Humans are the main source of fires in the savannas of west and central Africa. In the savannas of Gabon's Bateke Plateaux there has been a change from annual to semi-annual fires over the past 40 years as governance has become less centralized. Fire are now lit several times a year by individual hunters to create pasture. Semi-annual fire regimes in the savannas of Gabon are increasing the survival and density of the dominant tree	 **17. Wild herbivores** Reduction in fuel loads through increased livestock grazing has virtually excluded fire in savannah ecosystems of the Serengeti-Mara, Tanzania. Fire plays an important role in the function of this region and its exclusion could lead to an increase in bush encroachment and the displacement of wild herbivores such as wildebeest *(18)*.	 **18. Cyprinid fish** The fish *Enteromius seymouri* occurs in river systems in Malawi. The freshwater habitat of *E. seymouri* is declining due to sedimentation caused by agriculture. Fires used to clear land, or as part of agriculture, threaten wetlands in the northern tributaries of the species geographic range, through siltation from soil erosion (*23*).

Hymenocardia acida. With less fuel to burn, semi-annual fires are patchier and cooler than the previous annual fires *(104)*.		
 **19. Red-fronted Brown Lemur** The lemur *Eulemur rufifrons* occurs in moist lowland forests, montane forests and dry tropical forests in Madagascar. Populations of this species have declined due to habitat loss and fragmentation caused by deforestation fires, land clearing, and illegal logging. Hunting is also a threat. Uncontrolled fires are an ongoing threat, particularly in dry tropical forests in the western part of the species geographic range (*24*).	 **20. Clanwilliam Cypress** Conifers are disproportionately threatened by changes in fire regimes. In South Africa, Clanwilliam Cypress has declined in shrubland ecosystems called fynbos that, in some areas, are subject to high fire frequency. Increases in temperature and more frequent anthropogenic fires are projected to cause further declines of this species and highlight the need for conservation interventions *(105)*.	 **21. Eurasian steppe** After the collapse of the Soviet Union, 12 million ha of cropland were abandoned in the steppe zone of Kazakhstan and livestock grazing ceased across large areas of fields and grasslands. In the absence of grazing, tall grasses dominate the recovering steppe grassland and increase fire frequency and severity. Dwarf shrubs, such as *Artemisia*, are tolerant of grazing but decline when fires are too frequent or intense *(62)*.
 **22. Scots Pine** Fire is expected to become more frequent and more severe under a hotter and drier climate in the boreal	 **23. Dragonfly** *Asiagomphus coreanus* is a dragonfly known from a single geographic location on the Korean Peninsula. The	 **24. Grasshopper communities** In high-altitude grasslands of the Western Ghats, India, planned burning is used to

forests of Siberia, which will alter species composition, forest area and carbon storage. In particular, shifts from boreal forest, dominated by Scots pine, to grass-dominated vegetation are expected *(12)*.	population occurs in a freshwater stream inside the demilitarized zone (DMZ) between South Korea and North Korea. Military forces of both countries use fire to reduce vegetation for increased visibility. Forest fires negatively impact the preferred stream habitat of *A. coreanus*, but fires cannot be extinguished due to administrative restrictions. Forest reduction is ongoing and is particularly severe around this species' habitat (*24*).	create habitat for an endangered ungulate. But uniform burning has negative effects on grasshopper communities, which prefer patchier fires that facilitate rapid population recovery. 'Patchy' burning could be used to promote both the flagship ungulate species as well as species-rich grasshopper communities *(106)*.
 **25. Orangutan** Large fires in tropical forest of Indonesia are primarily associated with land clearing for agriculture, particularly oil-palm and paper-pulp plantations, and threaten one of the world's most biodiverse ecosystems and endangered species including orangutan *(8)*.	 **26. Obligate seeding conifer** The invasive grass, Gamba *Andropogon gayanus*, was introduced to the savannas of northern Australia as food for cattle. The high biomass of this invasive grass led to a switch from low-intensity surface fires to more intense fires that burn midstorey vegetation. Successive fires of high intensity have led to the decline of the obligate seeder *Callitris intratropica* through tree mortality. In turn, the reduction in canopy cover facilitates further invasion by grass. (*107*).	 **27. Banksias** Up to 90% of native vegetation has been cleared for cereal cropping and sheep grazing in a southwest Australian biodiversity hotspot. Consequently, shrubland ecosystems comprised of *Banksia* species occur in fragmented landscapes dominated by small patches. Interactions between fragmentation, fire and a drying climate are projected to increase local extinctions of *Banksia* species, especially in small, isolated patches that cannot be colonized post-fire through dispersal. Intervals between

		fires that are either too short or too long can place *Banksia* species at risk of local extinction *(73)*.
 **28. Leadbeater's possum** Temperate Mountain Ash forests of southeastern Australia provide habitat for species-rich animal and plant assemblages. The cumulative impacts of logging and extensive wildfires have removed large trees, placing populations of arboreal mammals that nest in old trees with hollows, such as Leadbeater's Possum (*Gymnobelideus leadbeateri*), at increased risk of extinction. In addition, high temperatures and droughts associated with climate change can directly increase mortality of large, hollow-bearing Mountain Ash trees and amplify the size and frequency of wildfires *(48)*.	 **29. Southern temperate forests** Invasive plant and animal species interact with fire to slow forest regeneration and cause shifts in vegetation types in New Zealand. Humans introduced fire to temperate forests that previously experienced low fire frequency, while seed predation by invasive mammals and the reduction of avian pollination and seed dispersal halted post-fire vegetation succession. Highly-flammable invasive plants can also contribute to regime shifts via higher fire frequency and by altering plant-soil feedbacks. Temperate forest is gradually replaced by more fire-prone shrubland *(55)*.	 **30. Endemic Tasmanian pine** Populations of the pine *Athrotaxis selaginoides* collapsed following the transition from Indigenous to European fire management in temperate forests of Tasmania, Australia. The species is now restricted to topographic refugia that offer protection from more severe fires *(64)*. More recently, large fires associated with global climate change are impacting these refugia and targeted fire management is required to protect the species. (*64*)