

Fire ecology for the 21st century: Conserving biodiversity in the age of megafire

1 | BIODIVERSITY CONSERVATION IN THE AGE OF MEGAFIRE

Fire is one of Earth's most potent agents of ecological change. This Special Issue comes in the wake of a series of extreme wildfires across the world, from the Amazon, to Siberia, California, Portugal, South Africa and eastern Australia (Duane et al., 2021). These "megafires," variously defined according to their size, intensity, or impacts (Attiwill & Binkley, 2013), are perhaps the signature feature of Earth's fiery transition to what Pyne (2020) has termed the "Pyrocene." Projections of increased fire weather and extended fire seasons portend an increasingly flammable planet (Ellis et al.; Jain et al., 2021; Wu et al., 2021).

Recent megafires have alarmed conservation scientists and practitioners because their scale and intensity demands new ways of thinking about biodiversity conservation in fire-prone landscapes, and, potentially, new tools tailored to avoid or minimise fire-induced declines and extinctions (Wintle et al., 2020). Megafires have the potential to transform landscapes at a speed and scale unmatched by most abiotic disturbances. Urgent questions remain regarding how ecosystems are affected by, and recover from, megafires (Jolly et al., 2022); the effectiveness of interventions aimed at minimising decline and promoting recovery of species, communities, and ecosystems following megafire (Wintle et al., 2020); how to best monitor the ecological impacts of megafire, and how to prioritise conservation investment within increasingly massive fire footprints (Southwell et al., 2022). This Special Issue of *Diversity and Distributions* grapples with some of these complexities and challenges.

The 2019–20 Australian megafires feature prominently in this Special Issue. These fires were unprecedented in more ways than one: fanned by unprecedented climatic conditions (Abram et al., 2021), they burned an unprecedented percentage of a continental forest biome (Boer et al., 2020), including an unprecedented area of high severity fire (Collins et al., 2021). They burned habitat for >3 billion individuals of >800 species of vertebrates (Van Eeden et al., 2020; Ward et al., 2020), including some species with entire geographic ranges encompassed by the fires (Legge et al., 2022). Hundreds of species are having their conservation status reviewed because of this single "season in hell" (Wintle et al., 2020). This Special Issue provides an opportunity to reflect upon the potential

impacts of those fires, and the lessons learned that will be relevant to other regions grappling with megafires (Geary et al., 2022; Legge et al., 2022), while also contrasting Australia's experience with other record-breaking recent fire seasons (e.g., California).

2 | FIRE ECOLOGY: FROM TEMPORAL TO SPATIOTEMPORAL

Fire is an inherently spatiotemporal process, yet fire ecology has, for much of its history, been more concerned with the temporal than the spatial effects of fire—with a particular focus on local post-fire successional trajectories of species and communities (Keith, 2021). Studies in this Special Issue provide examples of the insights that temporal studies of fire can provide: Connell et al. (2022) showed that species' post-fire responses are contingent on prevailing climatic conditions; Miller et al. (2022) demonstrated the surprisingly long-term (100+ year) post-fire successional dynamics of lichen communities; Rainsford et al. (2022) revealed the variable successional trajectories of different functional groups of plants and birds, and how that information can be used to assess tolerable minimum and maximum fire intervals, and; Topp et al. (2022) showed that the response of butterflies to fire depends on species' mobility, mediated through the effects of fire on vegetation structure.

In the last decade, the impacts of spatiotemporal measures of fire, such as "pyrodiversity"—the diversity of fire histories across space—have become major foci (Furnas et al., 2022; Parr & Andersen, 2006; Taylor et al., 2012). Pyrodiversity has received particular attention because of the hypothesis that a diversity of fire histories would increase biodiversity (Martin & Sapsis, 1992). Yet, the multi-dimensional nature of the fire regime—encompassing fire frequency, interval, seasonality, intensity, severity and spatial aspects (size, extent, configuration)—gave rise to a proliferation of pyrodiversity concepts (Bowman, Perry, et al., 2016; Hempson et al., 2018; Kelly et al., 2016) and an equally diverse array of approaches to examine the relationships between pyrodiversity and biodiversity (Jones & Tingley, 2022).

Jones and Tingley (2022) make a significant contribution by defining criteria for direct tests of the "pyrodiversity begets biodiversity" hypothesis. The most important feature is that measurements

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of pyrodiversity are captured *within* the observational unit of the study, not *among* them. While there remain many obstacles to resolving whether, where, and when pyrodiversity promotes biodiversity, clear criteria for what constitutes a test of the hypothesis represent a substantial move forward. The next steps will be clarifying and unifying metrics of pyrodiversity across studies, a greater consideration of the role of spatial scale in studies of the relationship between pyrodiversity and biodiversity (Jones & Tingley, 2022), and consideration of how contemporary pyrodiversity compares to pyrodiversity maintained under fire regimes to which biota have adapted, especially Indigenous fire regimes (Greenwood et al., 2021).

In the context of megafires, the importance of spatial aspects of fire become painfully obvious, but the mechanisms facilitating the recovery of biodiversity following megafires remain uncertain. Models of post-fire recovery of animals emphasise three potential pathways: *in situ* recovery, driven by fire survivors within the burned landscape; *ex situ* recovery, driven by colonisation from outside of the fire footprint; and nucleated recovery, driven by survivors in fire refuges (Banks et al., 2011, 2017). Megafires can create landscapes in which the potential sources of *ex situ* recovery—organisms outside of the fire footprint—are tens of kilometres removed from fire-affected points of the landscape (Collins et al., 2021), and in which few refuges remain within the fire boundary to allow nucleated recovery, potentially hampering or slowing post-fire recovery (Nimmo et al., 2019). Bradstock (2008) highlighted that, contrary to popular opinion, recovery of plant species from large fires can often be driven internally, by *in situ* survivors. Recent work from Australia's 2009 Black Saturday fires confirmed the surprising importance of *in situ* survivors for animal recovery too (Banks et al., 2011, 2017).

In this Special Issue, Hale et al. (2022) provide further evidence of within-fire survival being the impetus of recovery for small mammals following a series of large wildfires in south-eastern Australia. In the aftermath of the fires, there was no relationship between the occurrence of several mammal species and distance to potential sources of recovery. Instead, features that could provide an internal refuge—rocks and large trees—were related to species' occurrence within the fire footprint. In contrast to Hale—but encompassing a longer successional time-scale—Steel et al. (2022) identify a clear spatial gradient in richness and composition of Californian bird communities driven by distance to the edge of high severity patches: communities near the interior of high severity patches differed from those near the edge, with the former being comprised disproportionately of ground- and shrub-nesting species, and relatively fewer tree and cavity-nesting species. They also show that the richness of bird communities decreases with the size of patches that burned at high severity, due to the loss of tree and cavity-nesting species. Given the increasing regularity of large, severe fires in California (Keeley & Syphard, 2021), Steel et al. (2022) warn of the substantial changes in bird community composition that shifting fire regimes could deliver. In an important contribution, Calhoun et al. (2022) illustrate that such impacts have already spread well beyond the conifer forest ecosystems where the political and media focus of recent Californian fires has typically centred.

3 | MONITORING MEGAFIRES

While manipulative experiments will always be the gold standard in many areas of ecology, including fire ecology (Andersen, 2021), there are processes that operate at spatial scales that make manipulation unethical or impossible (Barley & Meeuwig, 2017). Megafire is one of these processes. Our understanding of megafire will necessarily be derived from opportunistic studies that draw on Control-Impact or Before-After-Control-Impact (BACI) designs. Megafires that occur across part of an existing monitoring program provide an opportunity to deploy BACI designs (e.g., Jones et al., 2016), but the unpredictable nature of megafire means that the number of sites that are burned and unburned will be highly variable across monitoring programs. Wood (2022) use simulations and empirical data to assess the power to detect species' responses to megafire that burn a subset of sites belonging to a longer-term monitoring program. They show that landscape-scale monitoring could detect crude changes in populations, but typically lack power to ascertain the form of the post-fire trajectory (Wood, 2022). Of course, power to detect such responses was enhanced by having many sites, underscoring the importance of large, long-term monitoring networks in fire-prone landscapes.

A prime objective in the immediate aftermath of a megafire is to undertake rapid surveys that assess the immediate impacts on biodiversity (Southwell et al., 2022). Ultimately, these reconnaissance missions aim to search for signs of life in the firegrounds and to help deliver a rapid understanding of the potential impacts on species or communities, which can guide management interventions. Such surveys are typically undertaken at short notice, in reaction to a fire event with no "rule book" to follow. Southwell et al. (2022) provide guidelines for best practice reconnaissance surveys following megafire that maximise the chance of detecting focal species, minimise the costs of surveys, and draw upon—wherever possible—existing monitoring programmes. They highlight that species distribution models can be paired with fire severity maps to prioritise areas for rapid reconnaissance; the importance of considering detectability and the statistical power of surveys; and the capacity to value-add to on-ground surveys by concurrently measuring potential threats.

4 | IDENTIFYING POTENTIALLY IMPACTED SPECIES

A pressing need during and after megafires are to rapidly identify species most likely in need of conservation investment. Three approaches are described in this Special Issue, each relating to the Australian megafires (two at a continental scale, and one at a regional scale).

Legge et al. (2022) outlines a method for identifying potentially impacted animal species after megafires, which combines the overlap between a species' geographic range and the fire event, and the pre-fire imperilment of a species, indicated by its conservation status. The intersection of these two measures creates a matrix: critically endangered species with a high proportion (>80%) of their geographic range within the fire footprint receive the highest score,

while unlisted species with a small proportion of their habitat within the fire footprint (e.g., <10%) receive the lowest score. This approach provides a rapid means of identifying potentially imperilled species with just two inputs. However, species have different relationships with fire (Topp et al., 2022): some species may be minimally affected, others may be substantially affected. To account for this, Legge et al. (2022) consider traits of animals that could confer vulnerability to both fire and the post-fire landscape. They use these traits to decide on the inclusion or exclusion species with intermediate risk scores.

Gallagher et al. (2021) demonstrate another continental approach to prioritising species in need of urgent conservation interventions, focussing on plants. In addition to the amount of a species range that overlaps with the Australian megafires, Gallaher et al. (2021) consider the cumulative effects of past fires, and how they might interact with the megafires to further imperil species, depending on their traits (e.g., obligate seeding species vulnerability to repeated fires in short succession). In doing so, they identified nearly 600 species at risk of decline or extinction from the Australian megafires. Given that species' responses to fire depend not only on the most recent fire, but on the cumulative fire history of an area (i.e., the fire regime; Gill, 1975), some consideration of fire history is warranted for other taxa as well.

Finally, Geary et al. (2022) demonstrate prioritisation at the regional level (Victoria, Australia). Here, distribution models of ~4,200 plants and animals were used to rapidly assess fire overlap while the fires were still burning. Geary et al. (2022) provide a more nuanced measure of fire overlap, drawing on their models to weigh proportional fire overlap by habitat suitability. Geary et al. (2022) used 40% of fire overlap as their threshold for consideration as a priority species, which they then vetted further using expert advice and consideration of traits that could mediate a species response to fire. Geary et al. (2022) also highlight the utility of spatial conservation action planning (Thomson et al., 2020) to help guide decisions on where and when to act to derive the most cost-effective conservation benefit (i.e., minimising species decline). If the goal of prioritisation following a megafire is to meet an objective (e.g., minimising the probability of extinction) within a given budget, then a move towards prioritising actions will be needed at all levels (see Game et al., 2013).

While the attention and emotions of the world are captured in the moment by stories of the plights of animals at risk from mega-fires, there is a risk of losing public support if our data do not hold true. It is therefore imperative that these rapid assessment tools are accurate enough to provide a realistic picture of the risks. The three means of identifying vulnerable species each focus on the proportion of a species' range that occurs within the fire footprint. While measuring fire overlap might appear straightforward, Crates et al. (2022) show the importance of high-quality distributional data for assessing the overlap between megafire and species' ranges. Here, simple measures such as Extent of Occurrence or Area of Occupancy tended to underestimate the extent of overlap compared with more detailed measures such as overlap with known, recent breeding locations. These issues are magnified for less well-studied taxa, such as reptiles and invertebrates, due to poor monitoring data for most species, a lack of conservation assessments for described species, and the abundance of undescribed

or cryptic species (Legge et al., 2022). Uncertainty about species' traits and how they mediate responses to fire of varying severities is another area that requires attention if traits continue to be used in such frameworks. As monitoring data accrues, it will be vital to compare the actual impacts of the fires on species with those predicted by these rapid desktop assessments, and to adapt methods, where necessary, to bring on-ground and desktop assessments into closer alignment.

5 | STATE SHIFTS

Among the most concerning impacts of megafire—and of altered fire regimes more generally—is the capacity for fire to induce shifts in ecosystem states across vast areas (Harris et al., 2018; Rammer et al., 2021). Larger, more frequent fires result in shortened fire intervals, leading in some instances to ecological state shifts (Enright et al., 2015). For instance, forests dominated by obligate seeding species face “immaturity risk” when fire intervals are too short for them to reach reproductive maturity between successive fires (Keeley et al., 1999), potentially resulting in their replacement by resprouting species (Nolan et al., 2021). The conversion of dominant canopy species set in motion changes that flow throughout the ecosystem, likely compounded by further changes in fire regimes owing to altered fuel biomass and dryness (Coop et al., 2020; Enright et al., 2015). Via widespread state-shifts—reinforced by positive feedbacks that promote flammability—megafire could be a primary mechanism hastening widespread conversion of vegetation types under climate change.

McColl-Gausden et al. (2022) provide a case study of immaturity risk for the obligate seeding Alpine Ash (*Eucalyptus delegatensis*) in south-eastern Australia, a region that has undergone a substantial increase in fire activity in recent decades (Bowman et al., 2016; Fairman et al., 2015). Alpine ash requires 15–20 years to reach reproductive maturity, so if multiple fires occur within a 20-year window, alpine ash forests can be converted into shrublands (Bassett et al., 2015). Similar state shifts have been described in North America following the loss of obligate-seeding conifers (Coop et al., 2020). McColl-Gausden et al. (2022) use projections of future fire regimes to examine the extent and drivers of immaturity risk across 283,000 hectares of alpine ash forest. They show that over two-thirds of the forest was exposed to immaturity risk, with forests on the margins of the species' geographic range and in drier regions being most at risk. While obligate seeding species were the focus of this study, it is important to recognise that resprouting species are also considered vulnerable to fire-induced state shifts (Nolan et al., 2021).

6 | MEGAFIRE INTERVENTIONS

Although large and intense fires are not new (Bradstock, 2008), the unprecedented size, severity, and frequency of recent megafires have created a perceived need for a suite of conservation interventions aimed specifically at minimising post-fire impacts and promoting recovery of species and communities. Legge et al. (2022) and Geary

et al. (2022) highlight a number of these, including pre-fire extraction of populations with a low likelihood of post-fire survival, provision of artificial refuges (e.g., artificial hollows) or supplementary food to replace resources incinerated by fire, and the control of invasive species that could compound the impacts of fire. Virtually all these interventions have a piecemeal evidence base underpinning their implementation in a post-fire context, and so research is needed to help document their effectiveness. In some instances, action may not be needed, and unnecessary interventions could squander scarce conservation resources. In terms of reversing fire-induced state shifts, some ambitious projects have already been attempted. Bassett et al. (2015) aeriually sowed ~2,000 ha of alpine ash forests that had failed to regenerate after frequent fires in southern Australia, demonstrating that such an intervention could create a cohort of seedlings where interval squeeze has obliterated natural seed stores. The capacity to scale up such efforts from thousands to tens or hundreds of thousands of hectares, and the wisdom of doing so—of attempting to retain an ecological system in an artificial state while the niche of its dominant species disappears—requires careful consideration.

7 | MEGAFIRE ECOLOGY

Megafires have raised new questions for fire ecologists that might require a different way of thinking about fire and biodiversity (Kelly et al., 2020; Nimmo et al., 2021): a new “megafire ecology”. Megafire ecology is focussed on the specific drivers and outcomes of exceptionally large fires on species, communities, and ecosystems. Such large fires, although relatively rare, usually make up the majority of burned area and are ecologically extreme events (Attiwill & Binkley, 2013). One of their defining attributes—their size—means that megafires likely have distinct ecological impacts and may require distinct modes of ecological recovery, for instance, a greater reliance on *in situ* recovery than smaller fires. This could mean that the pace of recovery from megafire is slower for some ecosystem components, relative to smaller fires. The incidence of megafires over time comprises a megafire regime: the interval between megafires, their intensity and severity, are not divorced from the overall fire regime, but might leave a clear ecological signature, comprising a distinctive force shaping species and ecosystems.

Five core areas of research in megafire ecology are summarised below:

1. Identifying the drivers of megafire in search of options for managing fire size, intensity, and severity, including the relative and interacting roles of climate and land use (Khorshidi et al., 2020; Stephens et al., 2014). Of increasing interest is the potential for cultural fire to play a role in diminishing the threat of megafire amidst a warming climate (Dickson-Hoyle et al., 2021; Fletcher et al., 2021).
2. Understanding the effects (both short and long-term) of megafire on populations, species, communities, and ecosystems, including the impact on species' extinction risk and the mechanisms governing recovery, how these are mediated by species' traits (habitat specificity, mobility, fire-avoidance strategies), and how they are influenced by underlying fire regimes.
3. Developing tools to rapidly and accurately identify at-risk species, and to prioritise monitoring and actions that ensure interventions are undertaken when and where they are most effective.
4. Examining the efficacy of actions aimed at limiting decline and hastening recovery following megafire, from species-specific to ecosystem-level interventions.
5. Assessing how megafire reconfigures species interaction networks by transforming the ecological setting in which species interactions and ecological processes take place (Newsome & Spencer, 2022).

There is accruing evidence that the impacts of megafires are far-reaching (Peters et al., 2021; Tang et al., 2021). Very large fires change land surface properties (e.g., albedo, evapotranspiration, roughness) over large areas with the potential to affect regional weather conditions for the post-fire period (Saha et al., 2016). Hence, a holistic understanding of the ecological effects of megafires will require researchers to look far beyond the fire footprint. While political, public, and even scientific interest in megafires is most intense during and immediately after the fire event, the impacts of fires can persist for decades and centuries (Haslem et al., 2011; Nimmo et al., 2012). The 1988 Yellowstone fires provide a case study of lessons that can be learned by tracking an ecosystem's long-term post-fire trajectory (Romme et al., 2016). The megafires that motivated this Special Issue will continue to have their presence felt throughout landscapes in the coming decades and beyond. It is vital that ecologists and land managers continue to monitor how, or if, these ecosystems recover, and the factors that mediate post-fire dynamics. When doing so, it will be important to keep in mind that megafires will not act in isolation, but with indirect effects of climate change, land uses, and invasive species, opening a potentially whole new field in global change biology.

8 | BIO SKETCH

The authors of this manuscript acted as guest editors for the “Fire ecology for the 21st century: conserving biodiversity in the age of megafire” Special Issue and encompass expertise in fire ecology and behaviour from a range of ecosystems across the globe.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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