Megafire-induced interval squeeze threatens vegetation at landscape scales

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Wildfires in 2019–2020 broke global records for extent and severity, affirming the arrival of the megafire era. Frequent megafires reflect changes to fire regimes that can negatively impact species and ecosystems. Here, we offer what we believe to be the first comprehensive analysis of megafire impacts on southeastern Australian vegetation communities, combining remote-sensing data, fire-history records, and plant trait-derived fire interval thresholds. In our study area, fires burned over 5.5 million ha. We found that one-third of all native vegetation in this region has burned too frequently following the megafires, particularly impacting fire-sensitive vegetation (for example, rainforests). This represents a single-year increase of 36% in the vegetation at risk of interval squeeze (vegetation transitions driven by altered fire regimes) compared to the previous 59 years combined. We demonstrate that megafires can overrun recently burned vegetation and infiltrate refugia, reducing fire intervals beyond the persistence thresholds of plant species and increasing the risk of ecosystem collapse. Averting this will require innovative approaches to fire management. However, if climate change is not addressed, ecosystem collapse may be unavoidable especially for ecosystems adapted to infrequent, high-severity fire.

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Megafires are increasingly common global phenomena (Stephens *et al*. 2014; Bowman *et al*. 2017). Since 2017, record-breaking megafires have occurred in Brazil (Fidelis *et al*. 2018), Siberia (McCarty *et al*. 2020), and Portugal (Turco *et al*. 2019), among numerous other places; in 2020 alone, California experienced five of the six largest fires in the state's recorded history (Higuera and Abatzoglou 2021). On the east coast of Australia, a series of megafires – including the largest ever recorded in the country – consumed 21% of the Australian temperate forest biome during the 2019–2020 fire season (Boer *et al*. 2020; Nolan *et al*. 2020), potentially pushing many ecosystems toward thresholds for "threatened" classification under International Union for Conservation of Nature (IUCN) Red List of Ecosystems criteria (Bland *et al*. 2017). Driven jointly by climate change, fire suppression/exclusion, and land-use changes (Stephens *et al*. 2014), this increase in Australian megafire occurrence is consistent with climate-change projections (Abram *et al*. 2021; van Oldenborgh *et al*. 2021) and is likely to continue.

In a nutshell:

- Megafires impact much larger areas than in most fire seasons
- We used historical data records and modern analytical methods to determine how multiple megafires that occurred across over 5.5 million ha in southeastern Australia can impact ecosystems
- Following the 2019–2020 bushfire season, one-third of the native vegetation has now been burned too frequently, putting it at risk of state shift or collapse
- With megafires expected to become more common, the risk of losing unique vegetation communities will increase unless urgent action on climate change and innovative approaches to fire management are adopted

Fire is a natural ecosystem process, particularly in fire-adapted communities (Stephens *et al*. 2014; Fidelis 2020), but changes to fire regimes can have negative consequences that are exacerbated by more frequent occurrence of large, intense megafires (Stephens *et al*. 2014). Such fires may increase the likelihood of burning of fire-sensitive vegetation (eg rainforests) and lead to high plant mortality, as reproductive strategies that drive regeneration either act independently of or are impaired by fire (Barlow *et al*. 2020). Fire-sensitive vegetation recovers more slowly from fire and in some cases may not recover at all, increasing the risk of a state transition (Tepley *et al*. 2018). Although fire-driven transitions between alternative stable states are a natural part of fire–vegetation dynamics in many fire-prone systems (Pausas 2015), interactions with climate change and other drivers (eg altered fire regimes) may lead to irreversible shifts or ecosystem collapse (Batllori *et al*. 2019; Kelly *et al*. 2020). Despite improved understanding of fire ecology in these communities, the impacts of extremely large, intense fires on persistence and the interactions with temporal elements of the fire regime require further research (Batllori *et al*. 2019).

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Globally, extreme drought events are becoming more frequent under climate change (Dai and Zhao 2017; Miralles *et al.* 2019); for example, the two most severe drought events in the historical record of eastern Australia occurred in 2000–2009 and in 2017–2019 (De Kauwe *et al.* 2020). Heat waves frequently coincide with drought due to reduced sensible heat in the atmosphere (Miralles *et al.* 2019). Drought and heat waves are associated with severe fire seasons in high biomass environments (such as mesic forests) because these environments are normally too wet to burn except during drought (Nolan *et al.* 2016). In addition to increasing the risk of megafires, severe droughts affect demography by triggering large-scale forest mortality and canopy die-off events, an outcome that has been increasing globally (eg Allen *et al.* 2015). In fire-prone systems, if drought persists following fire, recruitment and vegetative recovery may be delayed or impeded (Pratt *et al.* 2014), which may mean that vegetation communities effectively require longer fire-free periods.

The potential for fire, as a driver of demography, to impact plant species and communities through interactions with changing climatic conditions has been conceptualized as a model termed "interval squeeze" (Enright *et al.* 2015). Interval squeeze results from climate-change-induced conditions (such as prolonged drought, heat waves, and extreme fire weather) simultaneously increasing the time required for plants to recover post-fire and reducing the time between fire events (Enright *et al.* 2015). Species are consequently "squeezed" out through rapid shifts in demography, slowing recovery and lowering reproductive ability, altering species composition, and potentially leading to extinctions (Enright *et al.* 2015). Therefore, interval squeeze is also a mechanism that may drive state transitions (Fairman *et al.* 2016; Coop *et al.* 2020), an example of which has been recently observed in Australian forests (Bowman *et al.* 2014). Notably, the extreme conditions contributing to interval squeeze also produce high-severity megafires, suggesting that megafires have a profound influence on vegetation by increasing fire frequency or penetrating into fire-sensitive vegetation (Tolhurst and McCarthy 2016; Barlow *et al.* 2020). This idea is supported by a recent review of extreme fire seasons that highlighted the relationship between extent of area burned and increased fire frequency across landscapes (Fairman *et al.* 2016). The negative ecological effects of large fires will be compounded as megafires become more frequent (Bradstock 2008).

In 2019, Australia experienced its driest and hottest year on record (Abram *et al.* 2021), with eastern Australia experiencing a third consecutive year of drought (BoM 2019). This climate-change-driven confluence of conditions was partially responsible for Australia's record-breaking 2019–2020 fire season (Abram *et al.* 2021; van Oldenborgh *et al.* 2021). The extent and severity of these megafires are unprecedented in the modern fire record (Boer *et al.* 2020; Collins *et al.* 2021), as are the breadth of their impacts across terrestrial biomes and species (Ward *et al.* 2020; Gallagher *et al.* 2021). Much of the preliminary work on these impacts focused on prioritization of species requiring recovery actions, but how megafires might alter the underlying temporal characteristics of the fire regime at the ecosystem scale remains to be quantified.

Here we assessed the impact of the 2019–2020 megafires on fire intervals across southeast Australian vegetation types and classes in New South Wales (NSW), the Australian state with the largest area impacted. Originally defined as fires encompassing >10,000 ha (Stephens *et al.* 2014), megafires have more recently been defined as wildfires or wildfire complexes that encompass >100,000 ha (Collins *et al.* 2021). Depending on how they are defined, between 8 and 30 megafires occurred during the 2019–2020 fire season (DPC NSW 2020; Collins *et al.* 2021). Because our focus was on the fire season as a whole, we did not distinguish between individual megafires but considered and referred to them collectively. We identified vegetation types that were burned below their minimum recommended fire interval, defined as the shortest time between fires that allows regeneration and persistence of component species (Kenny *et al.* 2004). Intersecting the 2019–2020 megafires with historical fire maps to identify areas previously burned below the minimum fire interval during each of the past 60 fire-years, we calculated the frequency of these fires and identified areas experiencing fire interval shift (primarily an increase in frequency), subsequently increasing the risk of interval squeeze. Finally, we placed our results within the context of the IUCN Red List of Ecosystems criteria (Bland *et al.* 2017) to show how the scale of a single megafire event can push plant communities toward thresholds of collapse risk.

Methods

Our study region consisted of the state of NSW (excluding the Australian Capital Territory) on Australia's east coast, comprising 12 distinct vegetation types and 96 classes (Keith 2004) and covering 801,150 km^2. The state has a diverse array of vegetation, ranging from temperate dry sclerophyll forests and heaths to mesic forests (including wet sclerophyll forests and rainforests) to alpine and arid vegetation types. Historical fire regimes are equally diverse, with more frequent, low- to medium-severity fires occurring in drier vegetation, whereas mesic forests typically experience long fire-free periods punctuated by high-severity fires (Murphy *et al.* 2013).

Vegetation mapping was obtained from the NSW Department of Planning, Industry and Environment (DPIE); the NSW State Vegetation Type Map was derived from aerial photography, satellite imagery, and extensive ground-truthing, and classified with an accuracy of 60–75% and a resolution of 15 m (NSW OEH 2017). The map was divided into 14 vegetation types, including one, a "candidate native grasslands" type, that for the purposes of this analysis was conservatively assumed to be true native grasslands and was consequently re-categorized accordingly. Nonnative vegetation was excluded. Vegetation types and classes are state-level, hierarchical categorizations (Keith 2004) broadly equivalent to "ecosystem functional groups" and "biogeographic ecotypes", respectively, within the IUCN Global Ecosystem Typology (Keith *et al.* 2020).

Minimum fire intervals for each vegetation type were taken from the *Guidelines for ecologically sustainable fire management* (Kenny *et al.* 2004), which have informed fire management activities across NSW for the past 16 years. A range of fire intervals, meant to allow sufficient time for population replacement and persistence, were initially derived from reproductive traits (primarily primary juvenile period; Kenny 2013) of plant species within each vegetation type, but were later amended, and 3 years added to allow for replenishment of the seed bank (Kenny 2013). Fire intervals below the minimum thresholds lead to species declines or loss from these vegetation types. Each vegetation type has a corresponding minimum fire interval (WebTable 1), with the exception of rainforests, alpine complex, and saline wetlands, all of which are considered so fire-sensitive that their recovery to a pre-fire state after even a single burn would be unlikely or substantially prolonged. To allow their incorporation into the same mathematical framework as the other vegetation types, we assigned these three types a minimum interval of 100 years, which, in a management context, is effectively equivalent to "never" and consistent with the current understanding of fire-sensitive systems (eg rainforests), being restricted to rarely burned fire refugia (Bowman 2000).

Fire-history raster layers for each fire-year (the year centered on the austral fire season: in this case, July 2019–June 2020) were compiled and rasterized from digital, land tenure-blind fire-history maps maintained by the NSW Rural Fire Service.

Analysis

Although the complete fire-history dataset spanned a century, accuracy and comprehensiveness declined markedly with age, and therefore data prior to 1950 were excluded. To allow comparison with the vegetation mapping, we reprojected fire-year rasters to the same projection (Albers equal area, SR-ORG:7689/EPSG:3857) and resolution, based on nearest neighbor resampling, using the *gdalUtils* package (Greenberg and Mattiuzzi 2020) in R (v4.0.2; R Core Team 2020).

A continuous raster layer was created to represent the fire intervals experienced by each individual pixel across the study area. This layer was created by summing the fire-year rasters in a way that calculated "time since last fire" for each individual pixel across the study area. Intervals only commenced once a burned pixel was identified that followed a confirmed unburned status, and the interval ended once the pixel was burned again. The "time since last fire" values were summarized to create a raster in which any pixel across the study area could be tested for the number of times it was burned below a given fire interval.

The resulting rasters were then compared against the NSW State Vegetation Type Map to identify which pixels had been burned below the minimum interval specific to each vegetation type. These data from 1960 onward were then cross-tabulated to identify how many pixels in each vegetation type and class had been burned below minimum interval and how many times this had occurred. Because there were no data prior to 1950, the first 10 years of the dataset (1950–1959) could not have pixels recorded as "burned below minimum interval", and were used as our baseline decade. Analysis of times burned below threshold was therefore from 1960 onward.

Results and discussion

We found that ~5.5 million ha burned in NSW in 2019–2020. The fire footprint was primarily located in the eastern third of the state (Figure 1a), and severely impacted five of nine burned vegetation types (ie burned 20–51% of the total distribution; Figure 1b). Approximately 1.88 million ha (34%) of the total burned area burned below minimum recommended fire intervals. Of this area, more than half (1 million ha, 18.5% of total area burned) had experienced multiple burns below minimum intervals over the past 60 years (Figure 1a). We interpret this as evidence of a fire interval shift at a landscape scale. The three most impacted vegetation types were wet sclerophyll forests (27.9%), rainforests (19.2%), and alpine complex (18.8%), which together accounted for two-thirds of the total area burned below minimum interval (Figure 1b). They are also among the most fire-sensitive vegetation types, with recommended minimum fire intervals of 25 to >100 years (WebTable 1). Dry sclerophyll forests and heathlands, which are more fire-prone and have much shorter minimum fire intervals (10 years), still had 7–12% of their area burned below minimum intervals in 2019–2020 (Figure 1b). The same pattern held for vegetation types burned multiple times below minimum intervals, with wet sclerophyll forests, rainforests, and alpine complex again the worst affected, having 8–17% of their extent burned (Figure 1b).

Of particular concern are vegetation types that are most sensitive to fire and that require long minimum fire intervals to fully recover between fire events. The sheer size of the megafires means vast areas are now at risk of high fire frequency should they be burned again before the minimum interval has passed, and subsequently face increased risk from interval squeeze. Consequently, for wet sclerophyll forests, the area burned in 2019–2020 needs to remain free of fire until 2048, whereas for alpine complex and rainforest vegetation types, the fire-free period required extends to at least 2119. Combined factors of climate change and state transition toward more flammable vegetation types increases the likelihood of higher fire frequency (Pausas 2015). In addition to climate-change-induced pressures, such as

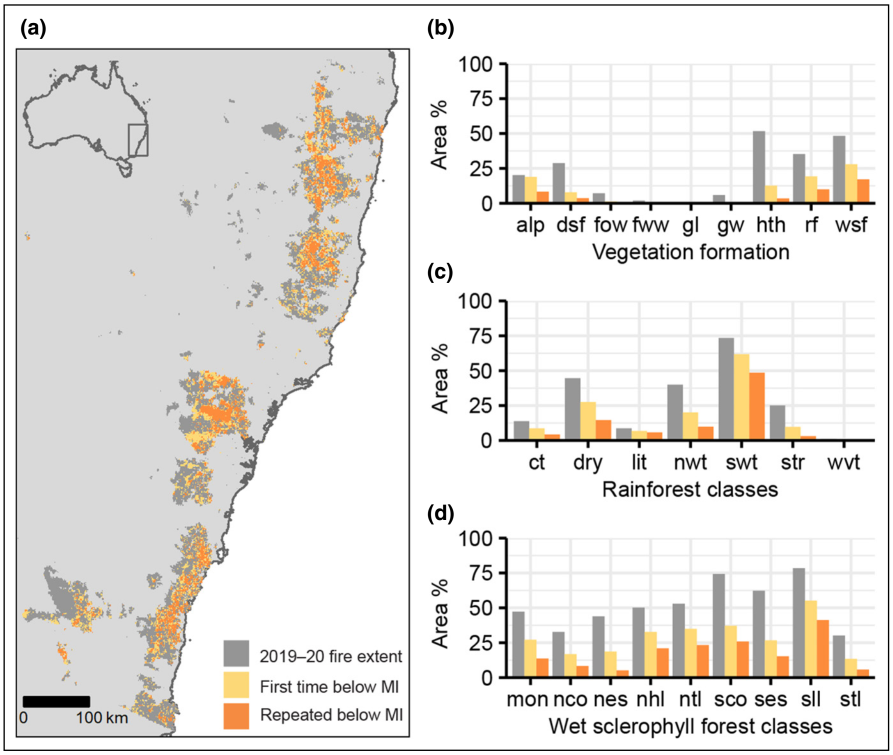

Figure 1. Fire frequency impacts of 2019–2020 fires on vegetation types in New South Wales (NSW), Australia. (a) Extent of 2019–2020 fires across eastern NSW, which includes three areas: namely, the total extent of the 2019–2020 fires, areas burned below the minimum interval (MI), and areas burned below the MI in 2019–2020 and at least once previously since 1960 (colored categories in [a] correspond to those in [b], [c], and [d]). Vegetation types: alp: alpine complex; dsf: dry sclerophyll forests; fow: forested wetlands; fww: freshwater wetlands; gl: grasslands; gw: grassy woodlands; hth: heathlands; rf: rainforests; wsf: wet sclerophyll forests. (b) Proportion of vegetation types impacted by 2019–2020 fires. (c and d) Proportion of rainforest classes and wet sclerophyll forest classes impacted by 2019–2020 fires, respectively. See WebTable 1 for rainforest and wet sclerophyll class abbreviations.

prolonged drought and megafires increasing fire frequency, socioecological impacts may also contribute to interval squeeze (Alencar *et al*. 2015). Where sensitive vegetation types occur near populated areas or key infrastructure, calls for more frequent fire management activities (such as hazard reduction burns) may contribute to the amount of fire experienced in the landscape, in efforts to protect human lives and assets (Whittaker *et al*. 2020). When ecological assets need to be considered, a clear framework identifying when such activities actually reduce risk to life and property must be incorporated into decision making.

The impacts of the 2019–2020 fire season on vegetation classes, a higher resolution of vegetation type classification, were both more variable and in some cases more severe. Seventy-three vegetation classes were burned, 30 (41%) of which had more than 10% of their area burned below minimum intervals, and seven of these had 30–60% of their extent burned below minimum intervals. Southern wet temperate rainforests had the highest proportion of their extent burned below the minimum interval (61%) and experienced multiple fires below the minimum interval (48%), with other rainforest classes having up to 45% of their distribution burned below minimum intervals (Figure 1c). Wet sclerophyll forest classes were the most consistently impacted, with >25% of all classes burned during the 2019–2020 fire season. Two-thirds of wet sclerophyll classes also had >25% of their area burned below minimum intervals, and four of the nine classes with >20% burned experienced multiple fires below minimum intervals (Figure 1d). Southern lowland wet sclerophyll forest was the second-most impacted class overall, with 78% burned during the fires, 50% burned below the minimum interval, and 41% experiencing multiple fires below the minimum interval (Figure 1d).

To put these impacts into context, the IUCN Red List Criteria for Ecosystems (www.iucn.org/resources/conservation-tools/iucn-red-list-ecosystems) considers ecosystems to be "vulnerable" to threat of collapse if 30% of their area experiences environmental degradation, with thresholds for "endangered" and "critically endangered" at 50% and 80%, respectively. In our study, for the vegetation classes analyzed (that is, the unit most analogous to ecosystems), 16 had 30% of their area impacted by this single megafire event, 13 were close to or above 50% impacted, and two were over 80% impacted. Although the impact of a single fire is not enough to push these vegetation types to collapse, interactions between this event and broader changes to the fire regime, the large areas now subject to fire interval squeeze, and the presence of other ongoing threatening processes suggest that many vegetation types in this region likely meet the IUCN criteria and are at greater risk in the future.

Fire interval shift toward higher fire frequency is an increasingly prevalent threat in fire-prone systems (Enright *et al*. 2015). By studying its occurrence at landscape scales, we have shown that one season of megafires can markedly increase the number of ecosystems experiencing this shift, threatening them with interval squeeze. From 1960 to 2018, approximately 2.35 million ha of vegetation in NSW burned below minimum intervals at least once. Following the 2019–2020 fire season, this increased by 36%, to 3.2 million ha (Figure 2a), an order of magnitude greater than the annual average of ~40,000 ha. Although a large extent of impacted vegetation had only been burned below minimum intervals once (53%), there were distinct hotspots that burned below minimum intervals up to nine times over the study period (Figure 2a). Moreover, areas that burned below minimum intervals at least twice increased by 50%, from 1 million ha to 1.5 million ha. Within vegetation types, areas that burned below minimum intervals at least once increased by 32.5%, with the largest increase occurring in rainforests (64%; Figure 2b, i), followed by alpine complex (56%; Figure 2b, iv), wet sclerophyll forests (38%; Figure 2b, iii) and heathlands (37%; Figure 2b, ii).

The most frequently burned vegetation types were those considered most fire-prone (eg dry sclerophyll). Of the 36 vegetation classes that burned six or more times below minimum intervals, only six had minimum thresholds longer than 28 years. That some vegetation types burned below minimum intervals as many as nine times over the study period, yet still retain their respective vegetation classes, raises some interesting questions. Aside from limitations in mapping accuracy, perhaps the most likely explanation is that vegetation types burned this frequently have already undergone or are undergoing state shifts. These areas are therefore a priority for floristic survey and field verification of such extreme frequency impacts. Some vegetation types (eg dry sclerophyll forests) that are adapted to more frequent fire can also possibly tolerate a higher level of frequency than represented by the current minimum intervals. However, such outcomes may also be a consequence of interactions between fire frequency and fire severity, particularly in fire-prone vegetation; greater frequency of higher severity fires (as compared with lower severity fires) may result in increased mortality of dominant species (Bennett *et al*. 2016). Although frequent but low-severity fires may remove fire-sensitive species from the shrub and ground layer (eg Le Breton *et al*. 2020), the fire-severity gradient may play a role when a state shift is triggered by interval squeeze. This effect will vary depending on the sensitivity of the vegetation community and component species. Recommended fire intervals for vegetation types in NSW only include limited consideration of fire severity (Kenny *et al*. 2004). Further research is required to understand how interactions between fire frequency and other fire regime elements, including fire severity and season (Miller *et al*. 2019), impact vegetation persistence.

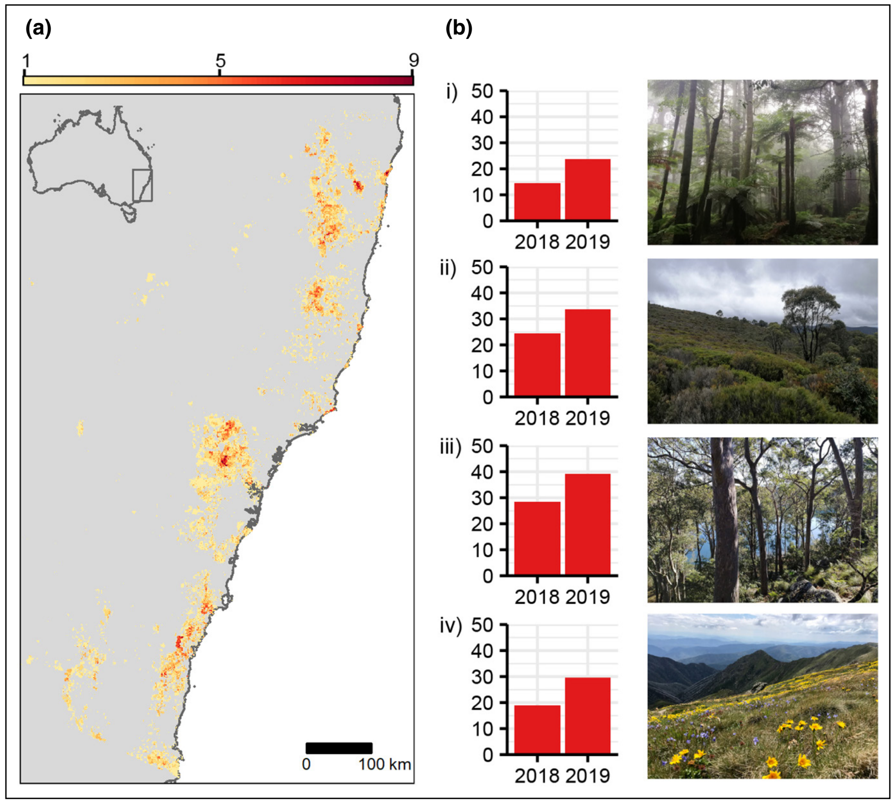

Figure 2. Frequency of fires below minimum intervals from 1960 to 2020 across NSW. (a) Mapped frequency of fires (1 to 9) below minimum intervals from 1960 to 2020. (b) Percentage of total area (y-axis) that burned below minimum intervals at least once from 1960 to 2018/19 ("2018") and from 1960 to 2019/20 ("2019") (x-axis) for (i) rainforests, (ii) heathlands, (iii) wet sclerophyll forests, and (iv) alpine complex vegetation types. Image credit for the alpine photo: C Kirchhoff.

In addition to the 3.2 million ha of NSW native vegetation now at risk of fire interval shift, there are two additional dimensions of interval squeeze: demographic shift and post-fire recruitment shift (Enright *et al*. 2015). Demographic shift refers to altered rates of plant growth, survival, and reproduction in response to shifts in climate (Enright *et al*. 2015). Preliminary observations following the 2019–2020 fire season suggest that both shifts in demography and post-fire recruitment are widespread across the fire grounds. Preceding the 2019–2020 fire season, the most severe drought in the historical record triggered large-scale canopy die-back across eastern Australia (Nolan *et al*. 2021) and most likely a substantial increase in tree mortality (De Kauwe *et al*. 2020), consistent with predictions of climate-change-driven demographic shifts. At the same time, post-fire recruitment and regeneration has been inconsistent (Kirchhoff *et al*. 2021), and in some areas has likely been delayed (Bowman *et al*. 2021). The co-occurrence of these shifts, alongside the evidence of fire interval shift documented here, indicates that interval squeeze is occurring over large scales and will lead to declines in many species if the current trajectory continues.

Climate change is driving fire regimes toward a state where megafires are more common (Stephens *et al*. 2014), and consequently the nature of fire as a threat will change, as too must management approaches for addressing that threat. The immense scale of megafires amplifying fire interval shift and increasing the threat of interval squeeze presents a potentially intractable issue for land managers seeking to balance conservation with preservation of life and infrastructure. Fuel reduction burns are typically used to reduce the spread and severity of wildfires, but their efficacy varies by vegetation type (Prichard *et al*. 2020) and may be reduced by extreme fire seasons (Clarke *et al*. 2020). Any increase in the application of prescribed burns will necessarily also increase the frequency of fire in the landscape. With over 5.5 million ha of NSW now vulnerable to being burned below minimum intervals for the next 10–100 years, the options for implementing hazard reduction burns that do not contribute to fire interval shift are limited. Furthermore, although prescribed fire can help manage fire behavior in vegetation types adapted to high-frequency fire (Lydersen *et al.* 2017; Prichard *et al.* 2020), there are fewer management options for mesic forests adapted to longer fire intervals and higher severity fire, and these forests may face unavoidable declines due to climate change and altered fire regimes (Westerling *et al.* 2011).

Fortunately, there are novel and innovative approaches to management that can protect biodiversity from megafires while reducing the frequency of fire in the landscape (Kelly *et al.* 2020). For example, reducing land clearing and restoring cleared landscapes around fire-sensitive vegetation types may lower flammability and increase target vegetation resilience. Land clearing is a major driver of increased flammability of fire-sensitive vegetation (Cardil *et al.* 2020; Lindenmayer *et al.* 2020) and is occurring at concerning rates across many of the countries experiencing megafires (Moutinho *et al.* 2016; Calderón-Loor *et al.* 2021). Clearing for firebreaks could occasionally be replaced with green firebreaks consisting of low-flammability species, which can both reduce fire spread and provide refugia for biota (Cui *et al.* 2019). At smaller scales, targeted control of fires around species or communities with high conservation value is a viable, albeit expensive, option. For example, this strategy proved effective for the Wollemi pine (*Wollemia nobilis*) (Mackenzie *et al.* 2021), a highly endangered species threatened by the 2019–2020 fires. However, this would require clear identification of ecological assets within the landscape, based both on their current threat status, and the potential for threat under emerging changes to climate and the fire regime. Ultimately, climate change remains a fundamental driver that will inhibit fire management strategies, and thus must be confronted. No fuel or restoration treatment will impede the advance of a megafire during severe fire weather, but strategic and appropriately scaled deployment of these strategies can modify fire behavior and reduce spread.

Fire and conservation managers have little or no control over global climatic change. With climate change unlikely to be mitigated or reversed in the foreseeable future, conservation and fire management must adopt strategies that are responsive to the ongoing and nonlinear changes expected from climate-change impacts on fire and ecological communities. In the absence of such strategies, vegetation types and ecosystems adapted to longer fire intervals (eg mesic forests) will likely undergo state transition and be lost from the landscape, along with the species that define them.

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Data availability statement

Data are archived on Figshare (doi.org/10.6084/m9.figshare.15111333). The novel code that was used to prepare and analyze the data and produce the figures is archived on Zenodo (doi.org/10.5281/zenodo.4495837).

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2482/suppinfo