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Shifting fire regimes cause continent-wide transformation of threatened species habitat

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Human actions are causing widespread increases in fire size, frequency, and severity in diverse ecosystems globally. This alteration of fire regimes is considered a threat to numerous animal species, but empirical evidence of how fire regimes are shifting within both threatened species' ranges and protected areas is scarce, particularly at large spatial and temporal scales. We used a big data approach to quantify multidecadal changes in fire regimes in southern Australia from 1980 to 2021, spanning 415 reserves (21.5 million ha) and 129 threatened species' ranges including birds, mammals, reptiles, invertebrates, and frogs. Most reserves and threatened species' ranges within the region have experienced declines in unburnt vegetation (≥30 y without fire), increases in recently burnt vegetation (≤5 y since fire), and increases in fire frequency. The mean percentage of unburnt vegetation within reserves declined from 61 to 36% (1980 to 2021), whereas the mean percentage of recently burnt vegetation increased from 20 to 35%, and mean fire frequency increased by 32%, with the latter two trends primarily driven by the record-breaking 2019 to 2020 fire season. The strongest changes occurred for high-elevation threatened species, and reserves of high elevation, high productivity, and strong rainfall decline, particularly in the southeast of the continent. Our results provide evidence for the widely held but poorly tested assumption that threatened species are experiencing widespread declines in unburnt habitat and increases in fire frequency. This underscores the imperative for developing management strategies that conserve fire-threatened species in an increasingly fiery future.

climate change | long unburnt | megafire | old-growth forest | wildfire

Significance

Global fire regimes are being transformed via increased fire frequency, severity, and extent. Large, high-severity fires are now becoming commonplace across the globe. Our study reveals multidecadal shifts in fire regimes across southern Australia, leading to reductions in the amount of unburnt vegetation and increases in fire frequency. These widespread changes are affecting conservation reserves and fire-threatened species within the region, with areas at high elevation, high environmental productivity, and strong rainfall decline experiencing the most severe impacts. Our results paint a sobering picture for threatened species in fire-prone landscapes, particularly high-elevation species, and call for a renewed emphasis on the development of fire management approaches that protect vulnerable species in a changing climate.

Fire has been a feature of Earth's ecosystems for more than 400 My (1). Many organisms coevolved with fire and are adapted to particular combinations of fire frequency, severity, size, and other characteristics that make up a fire regime (2). However, fire regimes are being transformed globally by climate change, land-use change, the displacement of Indigenous people, the spread of exotic plants, and novel anthropogenic burning (3). For instance, fire frequency, area burnt, and the amount of high-severity fire in southwestern USA have increased since 1984 (4). The mean fire age of Australian forests has declined by 44% since the 1980s (5), and climate change is projected to increase the annual area burnt in the Brazilian Cerrado by 11 to 95% by 2100 (6). Large, high-severity fires–including megafires >10,000 ha (7)–are becoming commonplace in the Amazon, western USA, northern Canada, the Mediterranean, Siberia, Australia, and many other regions (8, 9).

Altered fire regimes are having widespread ecological impacts, including massive emissions of carbon dioxide (10), waterway pollution via sedimentation (11), extirpation of plants that have slow recruitment processes (12), and the destruction of habitat for threatened wildlife (13). "Long unburnt" vegetation—that which has remained unburned for a long period relative to an ecosystem's fire cycle—is increasingly recognized as crucial habitat for animal species in fire-prone landscapes (14, 15). These areas, some of which can be described as "old growth" vegetation, typically contain stable microclimates, tree hollows, fallen timber, and other complex habitat structures that are critical for animal shelter, breeding, movement, and feeding, but which take decades to centuries to accumulate in woody ecosystems (16, 17). The increased frequency and extent of wildfires are likely reducing the amount of long unburnt habitat across many regions, potentially endangering a suite of fire-sensitive animal species. Increased fire frequency can also impact animal populations through frequent mortality (18), initiation of ecosystem state shifts (8), and exacerbation other threats such as drought and invasive species (19). By contrast, increases in fire activity may benefit early successional species that thrive in more open habitat or benefit from the resources available postfire (20). Altered fire regimes are considered a threat to >1,000 animal species (21), yet evidence of how fire regimes are shifting

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within the ranges of fire-threatened species or conservation reserves is scarce, particularly at large spatial and temporal scales.

We quantified multidecadal changes (1980 to 2021) in i) the proportion of unburnt vegetation (≥30 y without fire), ii) the proportion of recently burnt vegetation (≤5 y since last fire), and iii) mean fire frequency within 415 state forests, national parks, and other protected areas in southern Australia (hereafter, "reserves"; see *Materials and Methods* and *SI Appendix*, Fig. S1). The analysis is based on a time-series of ~17,000 annual fire ages covering 21.5 million ha and is focused on woody vegetation, i.e., forests, woodlands, shrublands, and heathlands. We characterized temporal trends in the three fire metrics for each reserve using a change coefficient where positive values indicate increasing fire frequency or proportion of unburnt or recently burnt vegetation, and the opposite for negative values (*Materials and Methods*). We then fitted statistical models to test the relative effects of climatic and landscape factors in driving these temporal trends (*SI Appendix*, Tables S1 and S2). We consulted formal conservation assessments to identify 129 threatened animal species and subspecies threatened by fire, and similarly quantified multidecadal changes in the same three fire metrics within their ranges (both inside and outside reserves) to identify species experiencing the strongest changes in fire regimes. To assess the influence of the record-breaking 2019 to 2020 fire season (22) on both the reserve and threatened species results, we also conducted sensitivity analyses using a dataset truncated at the 2018 to 2019 fire season.

Results and Discussion

Reserves. Most reserves had a declining trend of unburnt vegetation (66% of reserves), an increasing trend of recently burnt vegetation (56%), and an increasing trend of fire frequency (60%; *SI Appendix*, Table S3*A*) between 1980 and 2021. Excluding data from 2019 to 2020 onward resulted in slightly fewer reserves (2 to 5%) matching these trends (*SI Appendix*, Table S3*B*). The mean percentage of unburnt vegetation within reserves declined from 61 ± 38% (mean ± SD) in 1980 to 44 ± 35% in 2018 and 36 ± 36% in 2021, whereas the mean percentage of a reserve that was recently burnt changed from 20 ± 27% in 1980 to 16 ± 22% in 2018 and 35 ± 37% in 2021 (Fig. 1). Mean annual fire frequency per reserve, measured as the number of fires per 250 m grid cell in the previous 20 y, changed from 0.65 ± 0.96 in 1980 to 0.66 ± 0.56 in 2018 and 0.86 ± 0.66 in 2021. The fire frequency change coefficient was strongly correlated with that of both unburnt vegetation (r = −0.73) and recently burnt vegetation (0.84; *SI Appendix*, Fig. S2), thus indicating that changes in fire frequency are tightly linked with changes in age class proportions.

These analyses reveal both chronic and acute changes in age class proportions and fire frequency within reserves over multiple decades. The mean amount of unburnt vegetation has been declining across the study region since 1980 and this was exacerbated by the 2019 to 2020 fires. In contrast, the mean proportion of recently burnt vegetation and mean fire frequency were relatively stable, but the 2019 to 2020 fires caused large spikes in both metrics. At the individual state level, Victoria showed a pattern of persistent multidecadal change, whereas New South Wales initially displayed increasing fire frequency and declining unburnt vegetation since 1980 before stabilizing around the year 2000 (Figs. 1 and 2). The dramatic effects of the 2019 to 2020 fire season are evident in both of those states (Fig. 1). In contrast, South Australia shows very little change and Western Australia has experienced decreasing fire frequency and a slight decline in unburnt vegetation (Figs. 1 and 2). Increases in dangerous fire weather over the past 70 y have been stronger in the southeast than the southwest of the continent (23), which may explain the differing trajectories of these metrics (Fig. 2). Additionally, Western Australia generally had higher fire frequencies than other states at the start of the analysis period, primarily due to a widespread prescribed burning program that began in the 1960s (24). The negative trend in fire frequency observed in Western Australia since 1980 is likely due to both the effectiveness of the prescribed burning program in reducing wildfire occurrence (25) and a decline in the area treated by prescribed burns over time (24).

Bayesian mixed effects models show that declines in unburnt vegetation were stronger for larger reserves and those with higher normalized difference vegetation index (NDVI), elevation, rainfall decline, initial proportion unburnt, and annual proportion burnt, and lower Human Footprint Index (HFI; Fig. 3 and *SI Appendix*, Table S4). Increases of recently burnt vegetation were stronger when reserves were protected areas (cf. state forests primarily designated for timber extraction), had higher NDVI, elevation, rainfall decline, and initial proportion unburnt, and lower HFI (Fig. 3 and *SI Appendix*, Table S4). Mean fire frequency also increased most strongly in protected areas, where NDVI, elevation, rainfall

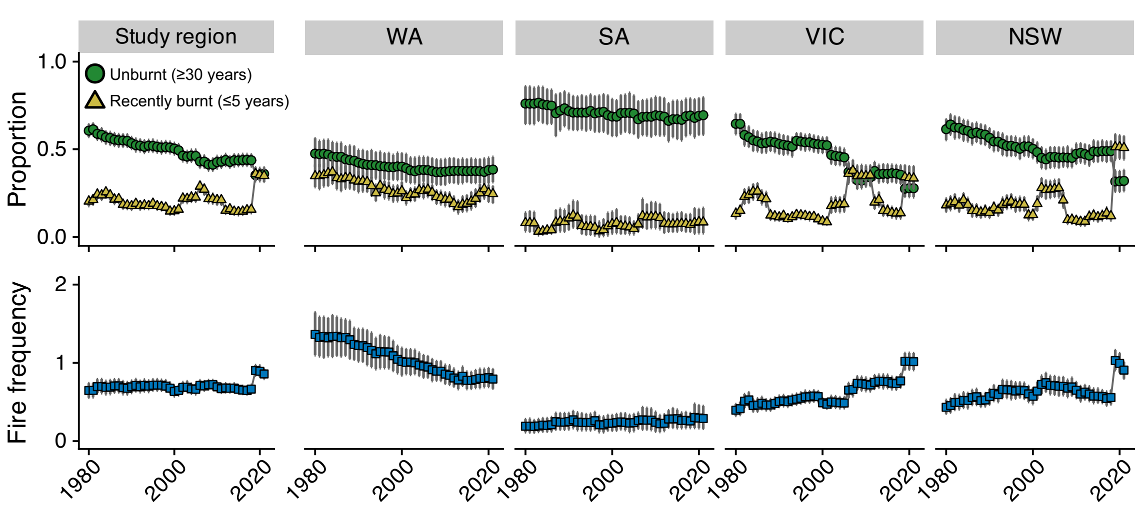

Fig. 1. Temporal changes (1980-2021) within reserves in the proportion of unburnt vegetation (≥30 y) and proportion of recently burnt vegetation (≤5 y) (*Top*), and mean fire frequency (*Bottom*) for the entire study region and each state (WA, Western Australia; SA, South Australia; VIC, Victoria; NSW, New South Wales). Points are means and vertical lines are 95% CIs. Fire frequency is measured as the number of fires per grid cell in the previous 20 y, averaged for each reserve.

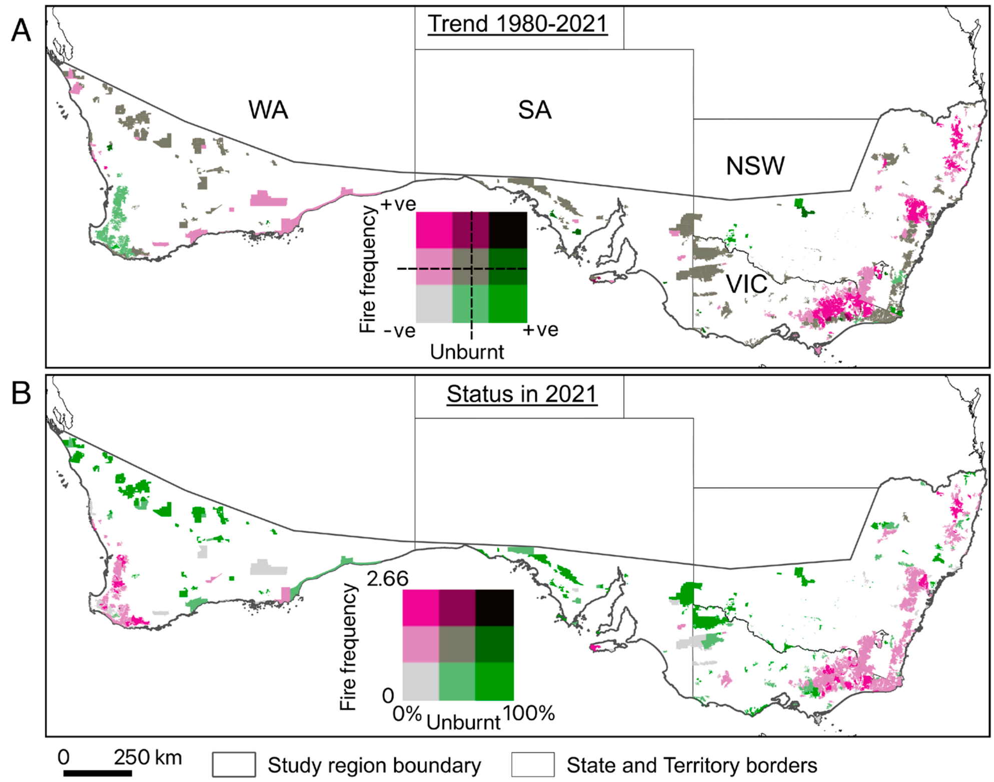

Fig. 2. (*A*) Bivariate map representing the trends of proportion unburnt (≥30 y) and mean fire frequency for each reserve from 1980 to 2021. Dark pink represents reserves where unburnt vegetation has declined most strongly and fire frequency has increased most strongly, whereas dark green represents reserves where unburnt vegetation has increased most strongly and fire frequency has declined most strongly. States are indicated as WA, Western Australia; SA, South Australia; VIC, Victoria; NSW, New South Wales). +ve and −ve represent positive and negative change coefficients, respectively. (*B*) Bivariate map displaying values of proportion unburnt vegetation and mean fire frequency for each reserve in 2021. Dark pink represents the highest fire frequencies combined with the lowest proportions of unburnt vegetation, whereas dark green represents the highest proportions of unburnt vegetation combined with the lowest fire frequencies. Fire frequency is measured as the number of fires per grid cell in the previous 20 y, averaged for each reserve.

decline, initial proportion unburnt, and mean annual proportion burnt were higher, and HFI was lower (Fig. 3 and *SI Appendix*, Table S4). Excluding 2019 to 2020 onward had minimal impact on the effects of covariates (*SI Appendix*, Fig. S3 and Table S5). Four effects were no longer statistically influential: HFI for unburnt vegetation, annual proportion burnt and NDVI for fire

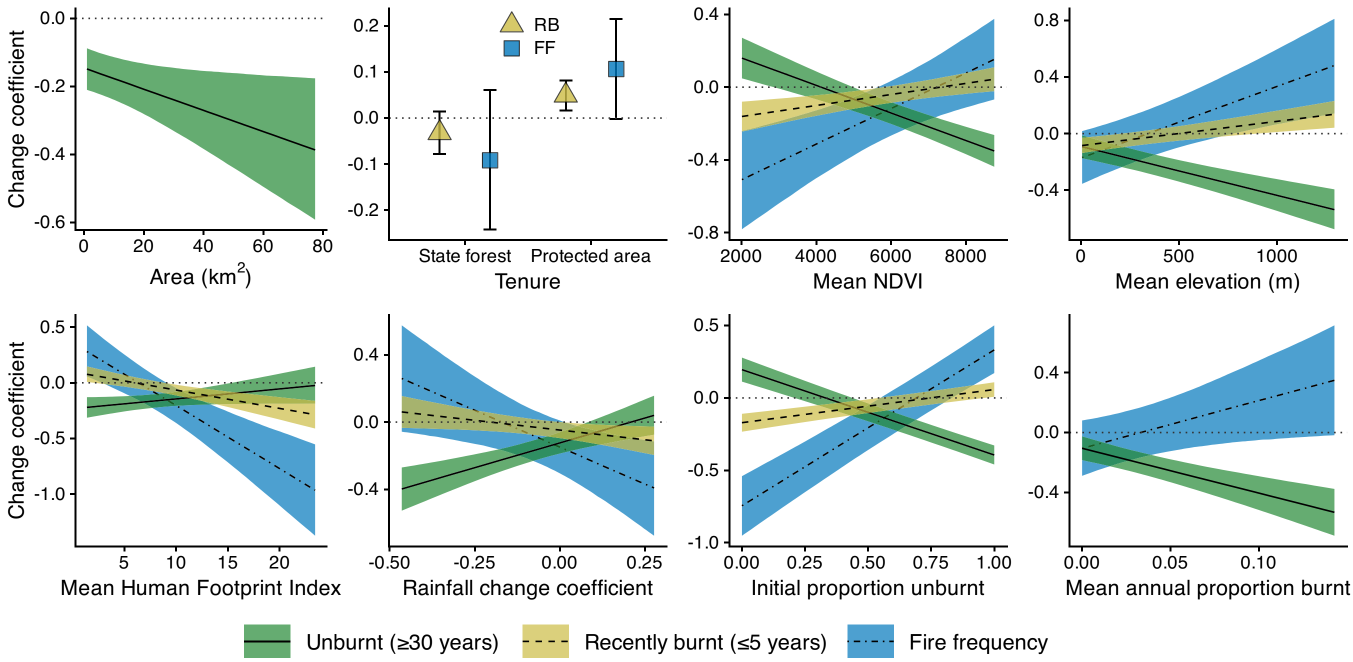

Fig. 3. Model estimated effects of influential predictor variables on the change coefficients for proportion unburnt, proportion recently burnt, and mean fire frequency of reserves. A negative change coefficient (*y*-axes) indicates a declining trend in unburnt vegetation, recently burnt vegetation, or fire frequency, whereas positive values indicate positive trends. Lines and points represent posterior means and error bands represent 95% credible intervals. The dotted horizontal line represents a change coefficient of zero. RB, recently burnt; FF, fire frequency.

frequency, and rainfall decline for one unburnt vegetation model (*SI Appendix*, Table S5). There was also a new negative effect of annual proportion burnt on the amount of recently burnt vegetation (*SI Appendix*, Table S5).

We have revealed that multiple biogeographic factors are driving the observed trends, with areas that either have high elevation, high productivity (NDVI), or strong rainfall decline experiencing the biggest changes. Our results build on previous work documenting climate-driven increases in the annual area burnt in southeast Australian forests (26). Eastern Victoria and northern New South Wales are hotspots for declining unburnt vegetation and increased fire frequency (Fig. 2). Within eastern Victoria, a series of large and severe wildfires burnt the Australian Alps in 2002 to 2003, 2006 to 2007, 2009, 2013 and 2019 to 2020, including repeated burning of large areas of early-successional vegetation (*SI Appendix*, Fig. S4). This may be indicative of a positive feedback between climate, fire, and flammability, given that high severity fire can increase the chances that areas reburn at short intervals (27). Climatic changes at high elevations may be driving stronger increases in dangerous fire weather compared to lower elevations (28). Our findings paint a similar picture to that playing out in the western USA, where high-elevation areas are experiencing increased fire danger (28), increased occurrence of stand-replacing fire (29), increased area burnt, and decreased inter-fire interval (30). The short fire return interval in Australia's alpine region has caused ecosystem transformation in some areas from eucalypt forest to acacia shrubland due to the failure of obligate seeder eucalypts to regenerate, which may drive further change in fire regimes (31).

The fact that all three fire metrics were influenced by both vegetation productivity and rainfall decline suggests that both the spatial distribution of fuel load and fuel moisture play a pivotal role in driving these trends. Two of the four "switches" that are necessary for forest fires to burn are fuel load and fuel dryness (32). Many forests of southern Australia are climate- rather than fuel-limited (33). Our study suggests that productive forests with higher natural fuel loads that are prone to drying may be burning more frequently because of increased fuel dryness due to climate change (33). The decline of rainfall in productive forests and woodlands sets the scene for large and intense fires by extending the window for when large fuel loads are dry enough to burn, as observed in the 2019 to 2020 fire season. Abnormal drying may explain why many Australian ecosystems typically regarded as "fire free" have experienced intense fires in recent years (34).

We expected smaller reserves and those with a high HFI would show the largest declines in unburnt vegetation and increases in fire frequency (*SI Appendix*, Table S2). By contrast, larger reserves and those with a lower HFI were more likely to experience declines in unburnt vegetation, and HFI was negatively associated with increased fire frequency and recently burnt vegetation. Of the 50 reserves >1,000 km^2, 80% experienced a decline in unburnt vegetation. The greater spatial coverage of large reserves likely increases their exposure to stochastic ignition sources such as lighting (35), while also allowing fires to burn across larger areas due to greater fuel connectivity. Additionally, many of the largest reserves are remote and have a low HFI. Their size and remoteness may diminish or hamper firefighting efforts (e.g., due to restricted access), and control efforts may be deprioritized over other locations where fires pose a greater risk to life and property. Both fire frequency and proportion recently burnt increased more strongly in protected areas relative to state forests, although we do not deem these results to be ecologically meaningful. Inspection of the data revealed that these results are driven by the lack of state forests in Western Australia in low rainfall areas (see *SI Appendix*, Fig. S5 for further discussion).

An important caveat of our results is that we were unable to account for differing fire severities over space and time because such information is not available at the scale of our analyses. Prescribed burns generally burn vegetation at a lower severity than wildfires (although not always) and can retain larger areas of unburnt vegetation within fire boundaries. As such, landscapes with similar fire metrics, but dominated by either wildfires or prescribed burns, are likely to be quite different ecologically (e.g., volume of coarse woody debris, 36). We did not assess the role of fire severity or fire type largely because of data limitations. Analytical approaches taking advantage of fire severity metrics that can be applied at large spatial and temporal scales (e.g., normalized burn ratio) are a promising approach for future studies. We suggest that examination of fire type and severity should be a priority for future research, especially given concern regarding the efficacy and impacts of prescribed burning programs against the backdrop of climate change (37, 38). A second important caveat is that the trends for the fire metrics may be inflated if there are large numbers of early fires (e.g., 1950 to 1970) that have not been mapped. We excluded the states of Queensland and Tasmania due to deficiencies in the available data. While it is unlikely that any regional fire history dataset is entirely comprehensive, we do not think there is systematic underreporting of fires for the other states that would bias our results. Nonetheless, this potential issue should be kept in mind for both this study and other studies adopting similar approaches (e.g., ref. 5).

Threatened Species. We consulted formal conservation assessments of listed threatened species to identify 62 animal taxa within the region threatened by declining unburnt vegetation and 129 taxa threatened by increasing fire frequency, spanning birds, reptiles, frogs, invertebrates, and mammals (*Materials and Methods*). Most species have experienced declines in unburnt habitat within the region (65% of species threatened by declining unburnt vegetation), increases in recently burnt habitat (58%), and increases in fire frequency (70% of species threatened by increasing fire frequency; *SI Appendix*, Table S3*A*). Excluding 2019 to 2020 onward and 23 taxa that were listed as threatened thereafter (*Materials and Methods*) caused these percentages to decrease by 4 to 9% each (*SI Appendix*, Table S3*B*).

Within taxonomic groups, most vertebrate species experienced declining unburnt habitat within the region (from 62% of birds and mammals to 100% of reptiles) and increasing fire frequency (66% of mammals to 83% of reptiles), whereas increases in recently burnt habitat were more variable (46% of birds to 100% of reptiles; *SI Appendix*, Fig. S6). Most invertebrate species also experienced increasing fire frequency (70%) and amount of recently burnt habitat (63%), but only 38% experienced declining unburnt habitat (*SI Appendix*, Fig. S6). Excluding 2019 to 2020 onward and 23 taxa classified as threatened thereafter caused the percentages of birds with declining unburnt habitat to decrease from 62 to 48%, and those with increasing fire frequency to decrease from 66 to 48% (*SI Appendix*, Fig. S6). Additionally, the percentages for reptiles and invertebrates with increasing recently burnt habitat decreased from 63 to 33% and 100 to 33%, respectively, and the percentage of invertebrates with declining unburnt habitat increased from 38 to 50%. All other combinations of taxonomic group and fire metric changed by 0 to 10% each (*SI Appendix*, Fig. S6).

The mean percentage of unburnt vegetation (≥30 y) within species' ranges in the region declined from 69 ± 25% in 1980 to 57 ± 25% in 2018 and 51 ± 26% in 2021, whereas the mean percentage of recently burnt vegetation (≤5 y) changed from 15 ± 15% in 1980 to 13 ± 15% in 2018 and 26 ± 24% in 2021.

For species threatened by increasing fire frequency, mean fire frequency increased from 0.42 ± 0.55 in 1980 to 0.48 ± 0.35 in 2018 and 0.66 ± 0.44 in 2021. Note that values for 1980 and 2018 exclude 23 taxa listed as threatened after 2019 (*Materials and Methods*).

Similar to reserves, fire-threatened species that occur at higher elevations, such as the spotted tree frog *Litoria spenceri*, mountain skink *Liopholis montana,* and mountain pygmy possum *Burramys parvus* (Fig. 4), experienced the strongest declines in unburnt vegetation, strongest increases in recently burnt vegetation, and strongest increases in fire frequency (Fig. 5 and *SI Appendix*, Table S6). Unburnt habitat also declined more where the initial proportion of unburnt vegetation and mean annual proportion burnt were higher, whereas increases in recently burnt habitat were stronger with higher NDVI, and increases in fire frequency were higher when the initial proportion unburnt was higher (Fig. 5). Reptiles and frogs experienced the strongest declines in amount of unburnt habitat (Fig. 5 and *SI Appendix*, Table S6). Excluding 2019 to 2020 onward caused minor changes in the results, namely that there was no effect of NDVI on recently burnt vegetation, the effects of initial proportion unburnt and mean annual proportion burnt on recently burnt vegetation became stronger, there was a new negative effect of mean annual proportion burnt on fire frequency but no longer an effect on proportion unburnt, and the relationships between unburnt vegetation and both frogs and reptiles weakened (CIs crossing zero; *SI Appendix*, Table S7).

Montane and alpine species are at high risk of extinction from repeated disturbance due to their typically smaller range sizes (39, 40). Although range size was not an influential predictor in the modeling, the mean range size of species with mean range elevation >600 m (7,875 km^2) was much smaller than that of lower elevation species (39,254 km^2). A single fire can burn the majority, or sometimes the entirety, of habitat for species with restricted distributions, placing them at high risk of extinction (22). Indeed, one of our study species, the *Banksia montana* mealybug *Pseudococcus markharveyi* (Fig. 4), may now be extinct after all of its remaining host plants were burnt by fires in 2018 and 2019 (41).

Some species showed improvements in the fire metrics, such as the numbat *Myrmecobius fasciatus* and ngwayir *Pseudocheirus occidentalis* (western ringtail possum), that have experienced decreased fire frequency and increased amount of unburnt habitat since 1980, respectively (Fig. 4). Similar to reserves, we attribute these results to the generally lower amounts of unburnt vegetation and higher fire frequencies in Western Australia at the start of the analysis period, potentially combined with the previously mentioned prescribed burning program (24, 42).

Our analysis shows that shifting fire regimes are transforming the habitat of a wide range of fire-sensitive threatened species (*SI Appendix*, Figs. S7 and S8), likely constituting a significant reduction in habitat availability and, in some cases, increased extinction risk, which is consistent with fire being listed as a threat to these species. The 2019 to 2020 fires are thought to have increased extinction risk for at least 91 terrestrial and aquatic taxa (43) and we show that, for many of these species, declines in unburnt habitat and increases in fire frequency are a chronic issue that was exacerbated by the 2019 to 2020 fire season

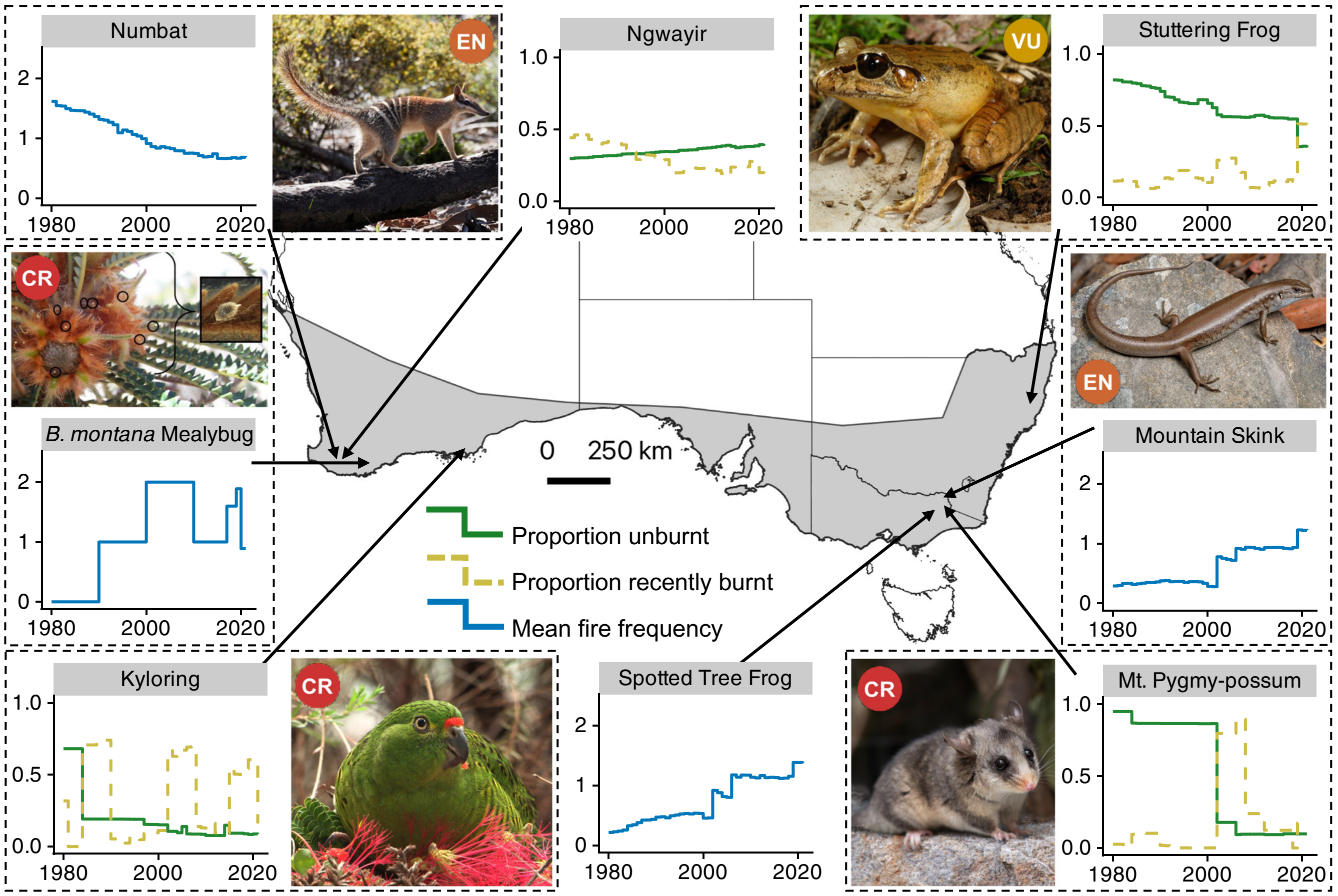

Fig. 4. Examples of threatened species mentioned in the text experiencing large increases or decreases in unburnt habitat (green solid lines), recently burnt habitat (yellow dashed lines), or fire frequency (blue solid lines) within their ranges. Only fire frequency or the two age class proportions are shown for each species. Fire frequency is measured as the number of fires per grid cell in the previous 20 y, averaged for each species' range. Conservation status is labeled as either CR (Critically Endangered), EN (Endangered), or VU (Vulnerable). Arrows indicate species' approximate range centers. Photo credits (clockwise from *Top-Left*): Judy Dunlop, Jules Farquhar, Jules Farquhar, Zoos Victoria, Jenenne Riggs, Melinda Moir.

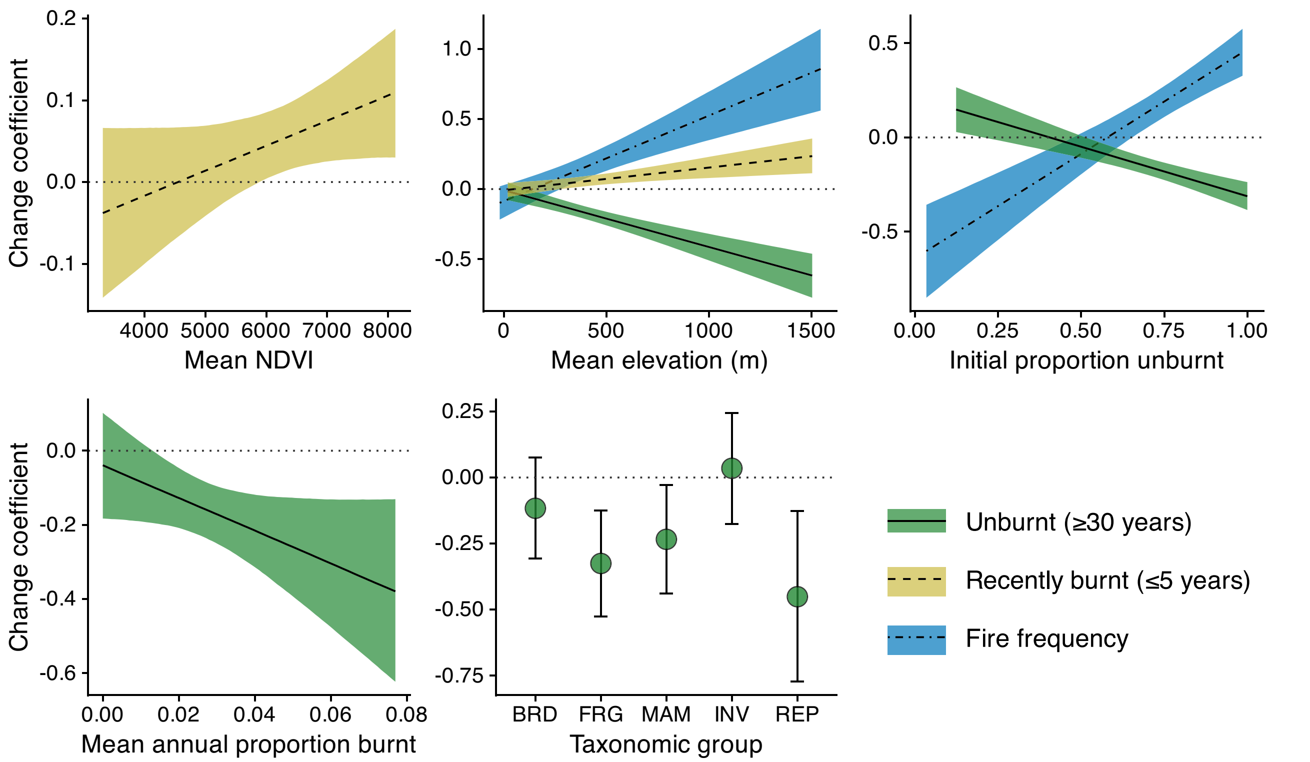

Fig. 5. Model estimated effects of influential predictor variables on proportion unburnt, proportion recently burnt, and mean fire frequency within fire-threatened species' ranges within the region. Lines and points represent posterior means and error bands represent 95% credible intervals. The dotted horizontal line represents a change coefficient of zero. Taxonomic groups are birds (BRD), frogs (FRG), mammals (MAM), invertebrates (INV), and reptiles (REP).

(*SI Appendix*, Figs. S7 and S8). Reductions in suitable habitat become protracted when large fires reburn areas before vegetation can reach maturity. For instance, the critically endangered kyloring *Pezoporus flaviventris* (western ground parrot), which reaches its highest densities in long unburnt vegetation (44), experienced a decline in unburnt habitat from 68 to 19% in 1984, followed by several further large fires that have since prevented the reestablishment of unburnt habitat (Fig. 4). Similarly, fires in 2002 reduced the amount of unburnt habitat of the mountain pygmy possum from 87 to 18%, and the 2019 to 2020 fires more than quadrupled the amount of recently burnt habitat of the stuttering frog *Mixophyes balbus* (Fig. 4). A major concern is that future fires will continue to prevent the recruitment of new unburnt habitat across these species' ranges, a scenario already playing out in Australia's alpine region (*SI Appendix*, Fig. S4).

It is important to acknowledge that threatened species have varying habitat requirements, thus analyses focused on an individual species may define the fire metrics differently to how we have here. For instance, many hollow-dependent species require trees that are >100 y old, but unfortunately it is not yet feasible to robustly map century old forests across very large spatial scales. Further, it should be noted that while our focus is on species threatened by increasing fire frequency or loss of unburnt habitat, the fire regime changes documented in this study may favor other species that benefit from the resources and habitat available in recently burnt areas. An advantage of our approach is that it is standardized across the region, thus allowing direct comparisons for a wide range of species and reserves. Our findings can act as a springboard for more targeted work at smaller spatial scales, including forecasting the impacts of future fire regimes on vulnerable threatened species (45, 46), and identifying species that might need targeted conservation action to mitigate the effects of fire (47). For example, our results could help identify where fire suppression resources or additional fuel treatments may be needed to improve the likelihood that sufficient unburnt habitat is maintained for fire sensitive species. Historically, long unburnt vegetation in southern Australia may have been preserved by frequent, low-intensity burning by Indigenous people that limited the occurrence of large, intense fires (48, 49). Research from arid Australia has shown that frequent, low-intensity burning by Indigenous people creates pyrodiverse landscapes that limit the incidence of large fires (50), even when climatic conditions are favorable (51), potentially leading to the retention of more unburnt vegetation. We recommend that further research is conducted into the role that Indigenous fire practices can play in biodiversity conservation in southern Australia.

Conclusions

It is well established that fire regimes will change globally due to climate change and other human actions. Our findings illustrate that this change is well underway across southern Australia, typified by declines in unburnt vegetation and increases in fire frequency. These changes are a major threat to fire-sensitive threatened species and the reserves they inhabit. Some reserves in our study contain ecosystem types undergoing considerable transformation, and many of the threatened species assessed here persist in small, relictual populations that are at extreme risk of fire-induced extinction. While some of the trends in our study are primarily driven by the 2019 to 2020 fire season, the conditions that precipitated that fire season are expected to reoccur (52). Our results serve as a warning sign for biodiversity conservation worldwide, especially as megafires are increasingly burning large areas of threatened species habitat on almost every continent (53, 54). Similar analyses of this spatial and temporal scale have not been conducted for other continents, but we suggest this should be a priority so that high risk species and ecosystems can be prioritized for management. This could include identifying locations where unburnt habitat is a higher priority for protection than human property because of the number of species that rely on it (55) or in extreme circumstances, identification of species for which translocation may be required due to insufficient suitable habitat in their current range (56). Agencies and organizations around the world will increasingly grapple with these challenges as fire regimes undergo continued transformation in the decades ahead.

Materials and Methods

Study Region and Focus. Our study region broadly aligns with the following biomes in southern and eastern Australia: temperate broadleaf and mixed forests; Mediterranean forests, woodlands and shrublands; and montane grasslands and shrublands (*SI Appendix*, Fig. S1) (57). We excluded areas with vastly different fire regimes to our target area, specifically arid and tropical areas (58). We focused on the states and territories of Western Australia, South Australia, Victoria, New South Wales and the Australian Capital Territory, and excluded Tasmania and Queensland because fire mapping for those states was incomplete prior to 1980 and 2000, respectively. Within the study region, we focused on woody native vegetation represented by the forest, woodland, shrubland, and heathland categories of the National Vegetation Information System (*SI Appendix*, Fig. S1 and Table S1).

The first stage of analysis focused on 415 state forests, national parks, nature reserves, and other protected areas, hereafter "reserves" (Dataset S1). We focused on reserves dominated by woody vegetation (≥80%) and ≥10,000 ha in size (*SI Appendix*). We excluded one very large reserve (Ngadju Indigenous Protected Area; 4.3 m ha) because it was an outlier relative to other reserves (10,001 to 772,905 ha). The second stage of analysis focused on the ranges of threatened animal species at risk from increased fire frequency (n = 129) or decline in unburnt vegetation (≥30 y without fire; n = 62) and which primarily inhabit woody vegetation. This comprised 20 amphibian, 41 bird, 20 invertebrate, 36 mammal, and 12 reptile species or subspecies from a total of 87 genera and 43 families (Dataset S2). Range maps were sourced from a federal government database (59) and we only included range areas representing known/likely habitat and excluded "possible habitat." We excluded species with <30% of their range within the study region. For species with <100% of their range within the region (n = 35), we excluded from analysis any areas falling outside the region. Full details regarding treatment of reserves and threatened species are provided in *SI Appendix*.

Fire Age Quantification. We used fire history maps from State Government databases to derive annualized spatial representations of the number of years since the last fire for each fire season (July–June) from 1980 to 2021, which included both wildfires and prescribed burns. For each season, we calculated the proportional area of each reserve and threatened species range that consisted of each of unburnt and recently burnt woody vegetation. We defined unburnt vegetation as not having been burnt for 30 y or more (≥30 y) and recently burnt vegetation as having been burnt within the previous 5 y (≤5 y). We chose these intervals based on relevant literature from the study region (*SI Appendix*). We do not refer to the proportion unburnt variable as "long unburnt" because the age at which vegetation is considered long unburnt varies between species and ecosystems within our study region. Grid cell size for analysis was 250 m.

We also calculated annual mean fire frequency for each reserve and threatened species range. For each year, we counted the number of times each cell was burnt in the previous 20 y, inclusive of the focal year (e.g., fires occurring 1961 to 1980 were counted when 1980 was the focal year). See *SI Appendix* for further details regarding treatment of fire maps.

Statistical Analyses. To quantify temporal changes in the three fire metrics for each reserve and threatened species' range, we calculated range standardized Pearson correlation coefficients (hereafter, "change coefficients") between year and each response variable (Datasets S1 and S2). Negative values of the change coefficient indicate a decreasing trend over time and positive values represent an increasing trend (*SI Appendix*). We then fitted Bayesian mixed effects models using the brms package (60) in program R (61) to determine whether the change coefficients of each fire metric for reserves could be predicted by reserve area (AREA), protected area status (PA), HFI, NDVI, annual rainfall change coefficient (RAIN_CHANGE), elevation (ELEV), initial proportion unburnt (INIT), and mean annual proportion of reserve burnt (APB). See *SI Appendix*, Table S2 for further detail about each variable, including the expected directions of effect.

The variable APB was moderately autocorrelated with INIT (−0.59) and NDVI (0.54) for reserves, while other pairs of covariates were not autocorrelated (<±0.50). To avoid autocorrelated variables appearing together, we fitted two models:

response ~ AREA + PA + HFI + RAIN_CHANGE + ELEV + APB

response ~ AREA + PA + HFI + NDVI + RAIN_CHANGE + ELEV + INIT

Full details of model fitting are provided in *SI Appendix*.

We fitted similar models for threatened species ranges, but the predictor variables we used were taxonomic group (TAXO: invertebrate, amphibian, reptile, bird, mammal), conservation status (CS: Vulnerable, Endangered, Critically Endangered), ELEV, NDVI, RAIN_CHANGE, INIT, APB, and range area (AREA). The models for proportion unburnt and proportion recently burnt included the 62 species considered threatened by loss of unburnt vegetation, and the models for mean fire frequency included the 129 species considered threatened by increasing fire frequency.

We included APB and INIT in separate models because they were moderately autocorrelated for fire frequency (−0.56). Due to the smaller sample size for threatened species relative to reserves, we also modeled RAIN_CHANGE and ELEV separately and fitted a third model containing only TAXO and CS. The set of models was

response ~ AREA + NDVI + RAIN_CHANGE + APB

response ~ AREA + NDVI + ELEV + INIT

response ~ TAXO + CS

All other aspects of model formulation and fitting were the same as for the reserve models. For the conservation status and taxonomic group covariates, the reference levels used in the models were Critically Endangered and Birds, respectively. Datasets are provided as Datasets S1 and S2 (also see *SI Appendix*, Table S8).

Data, Materials, and Software Availability. Previously published spatial data were used for this work, which are cited as (59, 62–75). All other data are included in the manuscript and/or supporting information.

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