# Biodiversity impacts of the 2019–2020 Australian megafires

https://doi.org/10.1038/s41586-024-08174-6

Received: 8 November 2023

Accepted: 8 October 2024

Published online: 13 November 2024

Open access

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With large wildfires becoming more frequent<sup>1,2</sup>, we must rapidly learn how megafires impact biodiversity to prioritize mitigation and improve policy. A key challenge is to discover how interactions among fire-regime components, drought and land tenure shape wildfire impacts. The globally unprecedented<sup>3,4</sup> 2019–2020 Australian megafires burnt more than 10 million hectares<sup>5</sup>, prompting major investment in biodiversity monitoring. Collated data include responses of more than 2,000 taxa, providing an unparalleled opportunity to quantify how megafires affect biodiversity. We reveal that the largest effects on plants and animals were in areas with frequent or recent past fires and within extensively burnt areas. Areas burnt at high severity, outside protected areas or under extreme drought also had larger effects. The effects included declines and increases after fire, with the largest responses in rainforests and by mammals. Our results implicate species interactions, dispersal and extent of in situ survival as mechanisms underlying fire responses. Building wildfire resilience into these ecosystems depends on reducing fire recurrence, including with rapid wildfire suppression in areas frequently burnt. Defending wet ecosystems, expanding protected areas and considering localized drought could also contribute. While these countermeasures can help mitigate the impacts of more frequent megafires, reversing anthropogenic climate change remains the urgent broad-scale solution.

Wildfires are increasing in many parts of the world owing to anthropogenic land-use and climate change, and fire weather is becoming more severe globally<sup>1,2,6</sup>. Extreme megafires have occurred recently in the Americas, Mediterranean, Russia and Australia<sup>1,2</sup>. Fire risk is predicted to grow, particularly in boreal and temperate zones<sup>7</sup>, with increasingly extreme fire activity in the Nearctic and Australasia<sup>8</sup>. The 2019-2020 megafires in Australia (hereafter, the '2019-20 fires') burnt 10.3 million ha (ref. 5), including the largest documented area burnt at high severity<sup>4</sup>. These fires generated a record number of pyro-convective storms and disrupted the planet's stratosphere<sup>3</sup>. What happened in Australia is being repeated around the world, with over 18 million ha burnt in Canada in 2023 (ref. 9) and the European Union experiencing its largest fires on record. The increasing frequency and extent of these megafires worsens the biodiversity extinction crisis<sup>2,10</sup>. At the same time, appropriate policy and management are hampered by limited ecological understanding of factors that mediate fire impacts<sup>11</sup>.

The 2019–20 fires were predicted to have catastrophic impacts on biodiversity. Rapid assessments estimated that almost 900 plant and animal species were severely impacted or placed at heightened risk from future fires<sup>12,13</sup>. Predicted declines triggered assessment of the conservation status of over 300 species under national environment legislation<sup>14</sup>. Responding to this crisis, government and non-government organizations allocated hundreds of millions of dollars for field-based monitoring and recovery actions<sup>14</sup>. This extraordinary monitoring effort provided an unparalleled opportunity to quantify how extreme fire events affect biodiversity.

Here, we collate site-level data from 62 datasets with over 810,000 abundance or occurrence records, covering over 2,200 taxa, including vertebrates, insects, molluscs and plants, from six broad ecosystem

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types. This comprises the largest known dataset of post-fire responses to a single fire season globally. The study area extends more than 1,000 km along the Australian east coast, with additional sites in South and Western Australia (Fig. 1). Our dataset enabled us to explore interactions among fire-regime components, drought and land tenure to an extent not previously possible, providing timely insight into what might be expected from recent and future megafires around the world.

Using meta-analytical methods, we evaluated the effect of fire severity and its interaction with fire frequency, inter-fire interval, fire extent, drought and protected area status (Extended Data Table 1), fitting project, species and taxonomic group as random effects (Extended Data Figs. 1-6, Extended Data Tables 2-4 and Supplementary Tables 1-8; Methods). We did this by selecting subsets of sites with specific levels of each covariate, then calculated effect sizes by comparing abundance or occurrence in unburnt sites with sites burnt at low or high severity (Extended Data Fig. 1). We also examined responses of taxonomic groups and ecosystems. We used standardized effect sizes to maximize generality but supplemented this with mean difference effect sizes for insights into absolute differences in the response. Meta-analysis conventionally reports the average effect of an intervention, but this can mask responses in opposing directions. We therefore also report mean effect sizes for positive and negative effects separately, given the expectation that some species will increase, and others decline after fire via different mechanisms.

We found that the 2019–20 fires had a negative overall effect on abundance or occurrence (effect size -0.08; 95% confidence interval (CI) -0.14, -0.02), although this effect was small, reflecting the similar negative (-0.34 (-0.39, -0.29)) and positive (0.29 (0.24, 0.35)) effect sizes (Supplementary Table 1). Across 1,648 effects, 44% were positive



**Fig. 1** | **Study regions relative to fire extent. a**-**c**, Maps of study regions within Australia, showing Stirling Ranges (Western Australia) (**a**), Kangaroo Island (South Australia) (**b**) and eastern Australian (**c**) sites, highlighting areas burnt in the 2019–2020 fire season and sites surveyed. Basemap copyright 2014 Esri. Data sources: Esri, Maxar, Earthstar Geographics and the GIS User Community. State boundaries: Australian Bureau of Statistics (July 2021–June 2026), Australian Statistical Geography Standard (ASGS) Edition 3, https://www.abs. gov.au/, accessed September 2024.

and 55% were negative (Extended Data Fig. 2a). Most importantly, the impacts of wildfire on plant and animal responses were moderated by covariates, with responses influenced by the interplay of land tenure, drought and recent fire history. More extreme disturbance generally led to larger positive and negative effects (Fig. 2; see also, video summary in ref. 15).

#### **Fire severity**

Severe fire, by definition, consumes more plant biomass than lowseverity fire (Extended Data Table 1) and is therefore expected to have larger effects across all taxonomic groups<sup>16,17</sup>. While not evident when considering the overall effect sizes, we found that negative and positive effects were 19% and 21% larger, respectively, for sites burnt at high compared with low severity (Fig. 3a and see Supplementary Table 1 for test statistics), with a mean absolute change in abundance or occurrence of only 1% (Extended Data Table 2). We next consider how fire severity interacted with additional covariates, revealing that high fire severity can have stronger effects in particular circumstances.

#### **Frequency and interval**

Fire that is too frequent can make plants vulnerable to decline by reducing survival and limiting the time available to set seed<sup>18</sup>. In forests, habitat features, such as logs, standing dead trees and tree hollows, decline when fires are frequent<sup>19</sup>, yet can be critical for animal<sup>20</sup> and plant<sup>21</sup> recovery. We found that sites with high fire frequency (three or more fires in the 40 years preceding 2019–2020) had negative effects that were 87–93% larger compared with sites not burnt or burnt once over the same period (Fig. 3b). Similarly, when the most recent inter-fire intervals were short (10 years or less), negative effects were 70% larger compared with sites burnt more than 20 years previously (Fig. 3c). These corresponded to an additional 10–11% decline in average absolute abundance or occurrence after fire (Extended Data Table 2). These effects were evident even for low-severity fires, which is of particular concern for fire management. It implies that, even where prescribed burning in Australian forest has reduced the severity of a wildfire, large declines are still likely if past fires were recent or frequent.

We also found that the positive effects were 46% larger at frequently burnt sites (Fig. 3b), representing an average absolute increase of 12% (Extended Data Table 2). This increase after fire could arise through three mechanisms. First, if fire is frequent with short intervals, early successional species will have large pre-fire populations, which could allow more individuals to persist through fire, leading to successively larger populations. Second, successively smaller populations of species that decline after fire could lead to reduced competition<sup>22</sup> or risk of predation<sup>23</sup>. Third, compounding growth of different resources, such as grass in the understorey<sup>24</sup>, may foster more rapid population growth or immigration of animal species favoured by fire (Table 1).

Habitat that is created and maintained through frequent and high-severity fires is vital for some species and is becoming more common owing to climate change<sup>10</sup>. Species that decline after fire are therefore of greatest conservation concern, especially in regions with increased fire activity. A key management objective will be to maintain areas with intermediate and long inter-fire intervals. We observed the smallest effect sizes at intermediate fire intervals (11–20 years; Fig. 3c), indicating that communities undergo the least disruption at these intervals. Long intervals are also needed to serve as refuges<sup>25</sup>, create time-dependent habitat attributes such as tree hollows<sup>19</sup>, and support source populations for species that might be lost from areas burnt too frequently<sup>26</sup>.

#### Unburnt area

High fire severity can cause severe population declines or extirpations, making re-establishment dependent on colonization from adjacent unburnt areas<sup>16</sup>. Recovery from high-severity fire could therefore be accelerated by proximity to large areas of unburnt vegetation<sup>27</sup>. We found that declines after high-severity fire were 114% larger when sites had less unburnt vegetation nearby-an effect not seen for low-severity fire (Fig. 3d) and representing an average 7% additional decline (Extended Data Table 2). The implication is that high-severity fire reduces abundance or occurrence of many species, but reductions can be offset by immigration from nearby unburnt areas. The importance of immigration from surrounding unburnt areas is also implied by the large positive effects associated with high levels of unburnt area (53% and 24% larger than mid and low sites, respectively; Fig. 3d). Our results suggest that many taxa either depend on colonization from unburnt areas or use those areas as temporary refuges before returning after the fire. When high-severity fires occur, our results suggest that reducing the spatial extent that is burnt can ameliorate bushfire impacts on species that would otherwise suffer large declines.

#### **Pre-fire drought**

Declines after fire were 27% and 40% greater (for low and high severity, respectively) in areas subjected to the strongest pre-fire drought compared with areas where drought was least severe (Fig. 4a), although the absolute average change was small (2%; Extended Data Table 2) and statistical support weak. Drought can increase post-fire tree mortality<sup>28</sup>, and reduce moisture and carbohydrate reserves, making plants more susceptible to fire damage<sup>29</sup>. Time-series studies show that fire can exacerbate drought impacts on animals or stall recovery from drought<sup>30</sup>. However, it has not been possible before now to examine how contrasting levels of pre-fire drought within a single season affect responses to fire. By bringing together data across a gradient of pre-fire



Fig. 2 | More extreme pre-fire disturbance led to larger increases and declines after fire. Conceptual diagram illustrating the main finding that more extreme pre-fire disturbance and more extensive or severe fires led to

both larger increases and larger declines after fire. Upper and lower rows indicate high and low disturbance relationships, respectively. Effect sizes are illustrative only.

drought conditions, our synthesis provides the first, to our knowledge, multi-taxon evidence of drought-fire interactions with a design that is not confounded by time.

For sites burnt at high severity, we found the largest increases when sites experienced moderate pre-fire drought (32–40% higher; 3% difference; Fig. 4a and Extended Data Table 2), requiring at least two mechanisms to explain. First, although high-severity fire produces large positive effects (Fig. 3a), extreme pre-fire drought could limit the capacity of taxa to increase. Second, under low drought conditions, the size of negative effects is reduced (Fig. 4a), so there are larger numbers of taxa that would otherwise decline still present after the fire. Those species could have negative ecological interactions with taxa that would increase after high-severity fire, limiting the magnitudes of positive responses. Interactions could include responses to more rapidly recovering vegetation, competition or predation. This suggested interaction has not been explored, although fires and drought can alter competitive or predator–prey interactions, leading to changes in community composition<sup>22,23</sup>.

#### **Protected** areas

Few studies have examined the relative impacts of fire on taxa across land tenures. Our results show that unprotected areas had 23% larger negative and 26% larger positive effect sizes than protected areas, although statistical support was weak (Fig. 4b) and absolute average changes were small (2%; Extended Data Table 2). A similar weak damping effect was evident for protected area coverage within 2.5 km (Fig. 4c). Protected areas might have more resources that buffer species' responses to fire (for example, logs, dead trees)<sup>31</sup>, fewer co-occurring threats (for example, invasive species)<sup>32</sup>, larger seed banks and more resilient resprouting capacity<sup>33</sup>. Further, productivity can alter the strength of species interactions after disturbance and protected areas are often on the least productive land<sup>34</sup>, but it is unclear how this would affect occurrence or abundance. The apparent buffering effect of protected areas could deliver overall conservation gains by minimizing declines. Although this will also lead to smaller increases after fire, taxa that increase are probably at least conservation risk because burnt area is becoming more common<sup>10</sup>. If the global goal to protect 30% of land area by 2030 can be met in our study area, there is potential to increase resistance to wildfires, albeit slightly, contributing towards adapting to climate change.

#### **Taxonomic group**

The impacts of fire severity varied by taxonomic group (Fig. 5a). We found larger positive and negative effects at high-severity sites for amphibians (25% larger negative effects, 95% larger positive effects), birds (46%, 36%) and mammals (46%, 38%). Negative effects were larger for reptiles (29%, -2%), and there were small differences for insects (7%, 18%) and plants (10%, 0%). With the exceptions of positive effects for amphibians, and negative effects for birds, confidence limits of high and low-severity effects overlapped the means, indicating substantial variation within taxonomic groups.

Amphibians had particularly small increases at low severity, but at high severity had larger increases, similar to plants, reptiles, insects and birds (Fig. 5a). Amphibians may be more resistant to low-severity fire than other taxa. They have lower metabolic demands, prefer wetter parts of the landscape, and use micro-refuges to survive dry summers, providing some protection from wildfire<sup>35</sup>. This resistance may restrict increases after low-severity fire. However, after high-severity fire, substantial increases may be related to reduced negative interactions with species that decline, including other amphibians, birds and mammals (Fig. 5a). There may also be reduced impacts of chytridiomycosis in warmer, sun-exposed post-fire environments<sup>36</sup>.

Birds had the second smallest negative effect size at low severity but not at high severity (Fig. 5a). High mobility probably explains the smaller effects of low-severity fire on birds than the less mobile plants, reptiles and most insects. However, this additional mobility may have been less effective at countering impacts of high-severity fire. A combination of higher metabolic demands and dependence on vegetation for nests, hollows, foraging substrates and protective cover probably make many birds as vulnerable as most other taxa to high-severity fire.

Mammals had larger positive and negative effect sizes than all other taxa, especially at sites burnt at high severity where negative effects were 94–155% larger and positive effects 66–96% larger than other taxa (Fig. 5a). This is consistent with a global meta-analysis showing that mammal abundance and richness had negative effects while other taxa had neutral effects<sup>37</sup>. Reduced survival shortly after fire and direct mortality are considered the most important causes of mammal declines due to fire<sup>38</sup>. Mammals may be more vulnerable to large declines than other taxa because some are too large to take refuge in small places, in contrast to reptiles, frogs and insects; most cannot fly to escape fire, in contrast with birds; they are severely impacted by close contact



Fig. 3 | Effects of wildfire on occurrence or abundance were modified by fire-regime components. a-d, Mean standardized effect sizes (±95% CIs) for fire severity (a), and main effects or interactions with fire severity for fire frequency (number of fires 1979-2019) (b); inter-fire interval (years) preceding 2019-20 fires (c); unburnt vegetation within 2.5 km (d) (see Table 1 and Extended Data Fig. 6 for high, mid and low category boundaries). Orange row labels, low-severity fire; red row labels, high-severity fire; black row labels, main effect without severity interaction. Main effects are plotted when interactions had no statistical support (P > 0.1). Left panels (black), negative mean effect size (average effect size for all effects less than 0); central panels (grey), overall mean effect sizes (mean of all negative, zero and positive effects); right panels (blue), positive mean effect sizes (average effect size for all effects greater than 0). Error bars are symmetrical but truncated at -1 and 1. Vertical dotted line at 0 is a guide to when effects differ from zero. Numbers in black within panels above each result are the number of effects contributing to each mean effect (n). Boxplots of raw data are in light grey, indicating median, 25th and 75th percentiles, with whiskers 1.5× interquartile range. Numbers in light grey below a result at panel margins indicate whisker values (left and right panels) or box margins (centre panel) that exceeded x axis limits. Predicted values consider random effects so may not align with raw data. P values for plotted results are the omnibus two-tailed test. Test F statistics (from left to right) for fire severity: *F*(1,41) = 7.74; *F*(1,41) = 0.42; *F*(1,26) = 10.18; fire frequency: *F*(3,39) = 11.3; F(3,33) = 11.78; F(3,30) = 6.41; inter-fire interval: F(2,42) = 10.28; F(2,37) = 5.44; F(2,31) = 13.35; unburnt area: F(2,22) = 19.93; F(2,29) = 1.02; F(2,21) = 9.2.

with fire, in contrast with many plants, and; being endothermic, have higher resource demands than reptiles, frogs, insects and plants. On the flip side, mammals may have the largest increases through an

## Table 1 | Key moderators of fire impacts and suggested mechanisms

State	Observed response	Suggested mechanism
More frequent fire and shorter pre-fire interval	Larger negative effects	Inadequate time for key resources to recover (seed, carbohydrate, habitat components)
	Larger positive effects	Successively larger pre-fire populations. Reduction of dominant competitors or predators. Creation of open habitat that favours early successional species
High-severity fire and proximity to high proportion of unburnt vegetation	Smaller negative effects	Recolonization of burnt areas depends on invasion from unburnt areas for many species after high-severity fire
High pre-fire drought	Larger negative effects	Drought-stressed plants with low reserves and low body condition in animals
Medium pre-fire drought with high-severity fire	Larger positive effects	(1) High drought limits the benefits of high-severity fire for a subset of species and (2) low drought allows stronger competitors or predators to survive fire, and allows faster plant recovery, reducing open post-fire habitat
High amount of surrounding protected area	Smaller mean positive and negative effects	Protected areas, by being less disturbed, contain legacies after fire that enable species to persist

influx of wide-ranging species, particularly herbivores that eat fresh regrowth<sup>39</sup>, and reduced competition associated with large declines of other mammals.

Plants, insects and reptiles had moderate negative and positive effects within the study period, regardless of fire severity (absolute declines 5-10%; Fig. 5a and Extended Data Table 2). While high-severity fire has been associated with declines of many reptiles, the strength of evidence for this was weak because it was based on expert opinion and qualitative field evidence<sup>40</sup>. Very few studies have quantified the impacts of fire severity on insects, although a meta-analysis found that fire severity did not affect arthropod abundance<sup>41</sup>. Plants are expected to suffer increased impacts from high-severity fire; however, the mechanisms often relate to loss of stored seed<sup>29</sup>, which may not have affected a large proportion of plants that have other regenerative methods, such as resprouting<sup>42</sup>. A deeper understanding of these trends awaits detailed evaluation of the fire responses of individual taxa relative to their traits. Nevertheless, our study highlights that there may be fundamental differences in how the main taxonomic groups respond to high-severity fire.

#### Ecosystem

Increases after fire exhibited only small differences among ecosystems (Fig. 5b). By contrast, high-severity fires caused larger decreases in rainforest compared with dry sclerophyll and alpine ecosystems (44% and 60% larger, respectively; Fig. 5b), with moderate absolute differences (4%; Extended Data Table 2). On one hand, this is concerning given that rainforests experienced high-severity fire at an unprecedented rate during the 2019–20 fires<sup>4</sup>. On the other hand, the average absolute decline is relatively small, suggesting most rainforest taxa can rebound after fire. Taxa in wet sclerophyll forests also experienced larger declines compared with those in dry sclerophyll and alpine ecosystems (22% and 35% larger, respectively; Fig. 5b). Taxa within wet forest ecosystems may be most vulnerable to decline owing to limited exposure to fire over evolutionary timeframes<sup>43</sup>, and because they are highly exposed to a broader range of threats than other ecosystems<sup>17</sup>.



**Fig. 4** | **Pre-fire drought and tenure mediated the effects of wildfire.**  $\mathbf{a}-\mathbf{c}$ , Mean standardized effects (±95% CI) of wildfire were modified by fire severity and its interaction with pre-fire drought ( $\mathbf{a}$ ), being in a protected area or not ( $\mathbf{b}$ ) and the proportion of protected area within 2.5 km ( $\mathbf{c}$ ). Orange row labels, low-severity fire; red row labels, high-severity fire; black row labels, main effect without severity interaction. Numbers in black within panels (n) are the number of effects contributing to each mean effect, and P values are for the

Implications

The expansive taxonomic, ecological and geographic scope of this study enabled deeper exploration of how biodiversity responds to fire than has been possible previously. Our results show that negative responses to wildfire are ameliorated when areas have experienced fewer past fires at longer intervals, ecosystems are not in drought, are within protected areas or if a substantial part of the surrounding area is unburnt. Our findings have parallels to the recovery dynamics of other ecosystems, such as coral reefs, subject to severe disturbance. Here too, the importance of biological legacies and resilience conferred by mobile links, such as recolonizers from less disturbed refuges promote resilience<sup>44</sup>. Furthermore, as in our study, there is some evidence that the resilience of coral reefs is enhanced by protected areas<sup>45</sup>. Combined, these findings offer pathways to mitigate the impacts of disturbance under a rapidly changing climate. Our study of an unprecedented fire event provides lessons for many flammable regions around the world.

#### **Future management**

As extreme fire increases<sup>8</sup>, we encourage fire managers to consider three main responses as part of an overall strategy for conserving biodiversity. The most important aspect to consider is the influence of fire frequency and interval on the vulnerability of species to future wildfires. Frequent fires exacerbate declines following wildfire, whereas unburnt surroundings ameliorate them. With prescribed burning the primary tool aimed at reducing fire risk, there is a significant management dilemma. Prescribed burns must be frequent, at less than 8-year intervals, to reduce fire severity in forest and shrublands<sup>46</sup>. Further, to limit wildfire area, larger areas must be burnt by prescription than would have burnt in wildfire<sup>47</sup>. Given that under extreme weather, prescribed fires have limited capacity to prevent vulnerable areas from burning<sup>46</sup>, widespread and frequent prescribed fire is a poor choice for responding to the growing fire threat. With such a vast area of Australian forests in an early post-fire state, increasing rapid wildfire suppression is now an important alternative strategy for limiting short fire intervals<sup>48</sup>.

plotted result. Panel layout and graphic features as in Fig. 3. Although the

interaction of severity with drought for negative effects was weakly

supported (a), the main effect was strongly supported (F(1,37) = 14.82,

P < 0.001; Supplementary Table 1). Test F statistics (from left to right) for

pre-fire drought: F(2,37) = 2.53; F(2,46) = 4.58; F(2,28) = 4.05; protected/

unprotected area: F(1,44) = 3.33; F(1,46) = 0.62; F(1,31) = 8.54; extent of

protected area: F(2,36) = 2.47; F(2,45) = 17.14; F(2,31) = 2.65.



**Fig. 5** | **Wildfire impacts varied across taxa and ecosystems. a**, **b**, Mean standardized effects (±95% CI) of wildfire on occurrence or abundance was modified by the interaction of fire severity with taxon (**a**) and ecosystem (**b**). Orange row labels, low severity fire; red row labels, high severity fire; black row labels, main effect without severity interaction. Numbers in black within

panels are the number of effects contributing to each mean effect (*n*), and *P* values are for the plotted result. Panel layout and graphic features as in Fig. 3. Test *F* statistics (from left to right) for taxon: F(5,29) = 5.84; F(5,29) = 23.39; F(5,15) = 8.15; ecosystem: F(3,31) = 8.48; F(3,32) = 5.3; F(4,30) = 69.19.

Increasing use of rapid wildfire suppression is likely to apply to other regions of the world that experience vast fires, such as Canada in 2023 (ref. 9), and in ecosystems that are threatened by fire, such as rainforest<sup>1</sup>. Some forest types, like Australia's ash forest<sup>49</sup> or North America's coastal temperate forest<sup>50</sup>, could benefit from rapid wildfire suppression continued over many decades or centuries, consistent with historic fire regimes, but this will not be the case everywhere. Some dry forests of western United States can be restored by adding frequent, low-severity fire to maintain an early successional understorey<sup>50</sup>. Further, many US forests can benefit from allowing mixed severity wildfires to burn<sup>51</sup>. With increasingly severe fire weather, a range of counter measures are needed, tailored to specific ecosystems. Indigenous fire practices that place the right fire regimes into the right country<sup>52</sup>, are therefore increasingly important for improving fire management for biodiversity conservation<sup>53</sup>. Complementing these ecosystem-specific approaches, we expect rapid wildfire suppression will need to be used more often to limit the extent of land burnt at short intervals.

While fire management agencies already prepare for high-risk fire seasons during drought, localized climatic conditions are another aspect for managers to consider. Species in sites experiencing extreme drought face increased threat from fire. On the other hand, drought refuges—areas that experience lower drought than the surrounding landscape—are more resilient to fire so may be less important to protect, but also may be less degraded with higher biodiversity value. Therefore, fire management priorities should consider past fire interval and the location of threatened taxa, in addition to drought status. The average absolute effect of drought was small, implying managing for drought is less important than avoiding frequent fire, at least in the short term. With the expectation that pre-fire drought poses a major threat to certain ecosystems<sup>17</sup>, an important next step will be to identify any taxa with declines that substantially exceed the average for conservation attention.

Third, our study provides new evidence that protected areas ameliorate fire impacts. Expanding and managing the protected area estate could therefore help to buffer species from the effects of changing fire regimes. Research is urgently needed to understand how protected areas reduce positive and negative impacts of wildfires, with a focus on the availability and use of micro-refuges and the influence of productivity across tenures. Knowledge of these mechanisms could enable improved management, potentially increasing the benefits beyond the small absolute effect sizes that we observed.

#### **Future research**

In the past, our understanding of how species respond to fire has been beset with poorly understood context dependency. Research that spans several locations often report idiosyncratic responses to

fire<sup>54</sup> that challenge traditional concepts of a predictable post-fire succession but without a pathway towards generalization. We suggest that mechanisms linked to fire severity, history and extent, drought and land tenure modify outcomes for biodiversity after fire (Table 1).

The proposed mechanisms open pathways to advance our understanding of why wildfire impacts are spatially and temporally variable. Priority research should aim to discover which species survive fire in situ or must recolonize, assess how dispersal ability arbitrates re-establishment and identify important competitive, predatory and habitat relationships. These aims need to consider interactions with the pre-fire status of populations (drought impacts, population size) and the spatial resilience mediated by the condition of the surrounding landscape (burnt, protected areas). When combined with spatial data including drought, other disturbances, fire history and post-fire vegetation recovery, new modelling approaches<sup>55</sup> may allow for mechanistic prediction of plant and animal responses to fire. These challenging interactions must be addressed by researchers to move from the bafflement of spatially variable fire responses towards a predictive capacity that supports improved biodiversity conservation. To make such progress, ongoing funding is needed on the scale provided in the heat of the 2019-20 fires-a challenge that we urge society and governments to rise to.

Although our data capture short-term responses, they are by no means trivial. Time-since-fire response curves<sup>54</sup> show responses to fire are most acute in the months and years immediately following fire. Our data capture these abrupt changes and show how the magnitude of change can be moderated by covariates, particularly fire history. While post-fire succession continues for decades or centuries, for many species the abrupt short-term changes<sup>56</sup>, or their absence<sup>57</sup>, have a strong influence on subsequent successional pathways. Further, our dataset includes over 2,200 taxa, probably including species with diverse long-term responses. Some species are expected to return to pre-fire numbers within a few years, with no long-lasting conservation implications. Others that declined may struggle to recover<sup>58</sup> or may never return<sup>59</sup>. Our results therefore offer a useful guide for conservation action. However, investment in widespread long-term monitoring is needed to identify species that may not have time to recover before the next fires.

The response of Australia's biodiversity to the 2019–20 fires must also be contextualized in terms of the post-fire conditions. The pre-fire drought that contributed to such volatile conditions in 2019 broke in eastern Australia in March 2020 soon after the fires, potentially hastening post-fire recovery and reducing impacts<sup>57</sup>. Larger effects might be expected under drier post-fire conditions<sup>28,30</sup>.

Countries around the world face increasing extreme and extensive wildfires caused by anthropogenic climate and land-use change<sup>1,2,8</sup>. Our empirical insights highlight underappreciated response pathways that emphasize critical research directions for understanding wildfire impact. Our results can also be used to improve environmental policy and management for a fire-resilient, biodiverse future. We stress, however, that extreme fires have doubled over the past 20 years<sup>8</sup>, coinciding with a 0.43° rise in the global temperature anomaly. Current global commitments to limit fossil-fuel use will probably see a further 0.8° rise<sup>60</sup>, with catastrophic worsening of extreme and extensive wildfires the predictable outcome. Urgent and massive reduction of fossil-fuel use remains an absolute priority.

#### **Online content**

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-024-08174-6.

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## Article Methods

We refer to megafires as those more than 100,000 ha, with 12 megafires recognized throughout the 2019-20 fire area<sup>5</sup>, although proposed terminology would classify these as giga- and tera-fires<sup>61</sup>. We gathered site-level data for 62 projects (Supplementary Table 2) by inviting contributors to join our collaboration. We emailed leaders of projects studying post-fire biodiversity impacts that were funded by the Australian Government's Wildlife and Habitat Bushfire Recovery Program. We promoted our proposal on social media in summer 2021-2022, ran a workshop at the Ecological Society of Australia conference in November 2021 and held a 2-day online symposium in February 2022. Projects were collated throughout 2022 after potential contributors contacted us. Projects had to include site-level data from sites burnt in 2019–2020 within the megafire region<sup>62</sup>. To ensure a minimum level of treatment replication, enabling means and s.d. to be estimated, datasets needed at least three burnt and unburnt sites (for example, survey points, plots or transects), or three sites with before-after data and at least three non-zero records across all sites (at the species/taxon level). Projects also needed to report either an estimate or index of abundance (44 projects), occurrence (17 projects) or probability of occurrence after accounting for detection (1 project). Although we canvassed researchers for a full range of response variables, the datasets provided included almost exclusively presence-absence or abundance data. Abundance and occurrence effect sizes were similar, justifying using both together (Extended Data Fig. 2c). Only one project met all other criteria but reported responses that were not related to abundance or occurrence (effects of grazing on reproduction in one orchid species), and thus was omitted from analysis. Five other projects were excluded because they did not have at least three unburnt sites.

Most projects were from eastern Australia ranging from southeast Queensland to eastern Victoria, with an additional four projects from Kangaroo Island, South Australia, and one from southwest Western Australia. Effect sizes showed some regional variation (Extended Data Fig. 2d). Individual projects had several sites spanning an average of 192 km (s.d. 284 km) with the most extensive study spanning 1,631 km. While there were many fires in Australia's northern savannas, these were not anomalous and so are not part of the 2019–20 fire footprint (Fig. 1).

#### **Effect sizes**

Effect size calculations differed based on project design. Projects used one of three general designs and effect size calculations differed to accommodate the expected non-independence in some designs (for example, repeated sampling of the same sites). Before–after studies (n = 14) had data from the same sites 1–5 years before the fires and one period post-fire. Effect sizes for these datasets were calculated as the standardized mean change (mean-after minus mean-before) using change score standardization (SMCC, using SMCC option in escalc function of R package metafor)<sup>63–65</sup>, which accommodates the expected non-independence of repeated measures of the same sites<sup>65</sup>.

Control-impact was the second design. These surveyed independent unburnt and burnt sites after the fires (n = 46). Standardized mean differences (SMD, using SMD option of escalc) were calculated as mean-burnt minus mean-unburnt divided by a function of the s.d.<sup>63,64,66</sup>.

The third design included before–after-control-impact projects (n = 3). These were converted to control (unburnt) and impact (burnt) designs by subtracting the before-fire response from the after-fire response for each site<sup>67</sup>. Subsequently, the SMD was calculated using the same method as the second design.

We used standardized mean change and SMD because these effect sizes are more generalizable than unstandardized effect sizes; they are more likely to reflect the true values of a larger pool of samples<sup>68</sup>. SMCC and SMD return NA values when the s.d. is zero. A very small percentage of effect sizes (0.9%) had no variation, such as when a taxon was present on all sites before and after the fire. Omitting such values has minimal impact on our results because there are so few of them and because we focus on the size of negative and positive effects separately, rather than pooling all effect sizes including zeros (see 'Meta-analysis' below). However, standardized effects can be difficult to interpret, and Takeshima et al.<sup>68</sup> recommend providing supplementary analyses using mean differences. We therefore also calculate effect sizes using the MC option of escalc to calculate the raw mean change in before–after designs, and the MD option to calculate the raw mean difference for control-impact and before–after-control-impact designs<sup>63,64</sup>. These gave very similar results to the standardized effect sizes (Extended Data Fig. 3 and Supplementary Table 3), but provide additional insight into the scale of changes observed. Mean differences are the most appropriate effect size to use with our dataset where 21.6% of effect sizes included zero values for either the burnt or unburnt response.

Before using the MC and MD functions, data for species within projects were standardized by dividing all values by the maximum value for that species within that project, so that the data for calculating each effect size ranged from zero to one. While this makes data with different ranges of values comparable, it also risks biasing down effect sizes when there are large outliers. We therefore also calculate MC and MD after removing outliers. We assumed our count data (x) approximate a Poisson distribution, and by transforming our data as  $y = 2\sqrt{x}$ , outliers can be identified as those greater than (median(y) + 3), based on the approximation that y is normally distributed with a s.d. of 1 (ref. 69). This approach is conservative, such that if the Poisson lambda value is less than three, it will identify fewer outliers. When applied to binomial data, it does not identify any outliers. This produced results similar to when outliers were included, but effect sizes were slightly larger (Extended Data Fig. 4 and Supplementary Table 4).

Some variances for mean change and mean difference effects were zero. These prevented meta-analysis models from converging. To enable models to converge, and to use a dataset similar to the SMCC and SMD, we removed effects with zero variance before analysis (mean removed = 2.4% s.d. = 2.3%; Supplementary Table 1).

Effect sizes were calculated for a taxon within a project when there were at least three unburnt and burnt sites, or at least three sites surveyed before and after fire. In addition, there had to be at least three sites with non-zero values across treatments per taxon. A taxon may be absent from a site, regardless of whether the site was burnt, if the site was in an ecosystem never used by that taxon. Sites excluded for taxa within projects due to absence from that ecosystem across all projects are detailed in Supplementary Table 5. A taxon may also be absent if the site was beyond its geographic range. To identify unoccupied sites that were probably beyond the natural range of the taxon, we took the occupied latitudinal and longitudinal range from our database, added 20% in each cardinal direction to include the nearest unoccupied sites, then excluded remaining unoccupied sites beyond that buffer (Supplementary Table 6). For taxa with small ranges, this method could leave fewer than six sites-our minimum criterion for inclusion. We therefore added the nearest sites to bring the total up to six sites, based on site coordinates using sf1.0-16 (ref. 70). Projects with a single target species or where data providers indicated they surveyed sites where species were expected were not subjected to ecosystem or range filtering.

To evaluate differences in effect sizes between years, datasets were categorized by 'Year' and, if possible, further divided into two periods: Year 1 and Year 2. We used time gaps between survey periods in each multi-year study to define surveys that measured responses up to approximately 1.5 years after fire (to June 2021), and those that examined responses between approximately 1.5 and 2.5 years after fire (June 2021 to June 2022). We used the time gaps in survey dates to maximize the data that could be included for each project, with the compromise that this led to minor temporal overlap of our year 1 and year 2 effects (one Year 2 project started in February 2021; two Year 1 projects ended in June 2022). Ten datasets had 1–5 months of data excluded (Extended Data Table 3).

When we fitted the meta-analytical models (described below) to evaluate the year effect, there were only very small changes in mean effect sizes between years (Extended Data Fig. 2b), suggesting positive and negative impacts of the fires had not substantively changed 2 years after the fires. Consequently, in all other analyses, we averaged response values across time periods for sites within projects when there were several survey times after fire.

In another initial step, we fitted a two-level factor delimiting beforeafter survey designs from those that sampled burnt and unburnt sites after the fires. Before–after designs were confounded by the breaking of a multi-year drought shortly after the bushfires. This meant that measured effects of the bushfires could be smaller owing to compensating effects of higher rainfall. We found some evidence for this expectation, with mean effects shifted to the right for before–after compared with burnt–unburnt designs (Extended Data Fig. 2a). We therefore omitted before–after designs from all other analyses. This removed 14 before–after projects representing 6.4% of effect sizes and made no substantive difference to the outcomes of the analysis (Extended Data Fig. 5 and Supplementary Table 7). Rejecting before– after designs in meta-analysis has been recommended owing to the risk of confounding<sup>71</sup>.

We classified sites based on six covariates (Extended Data Table 1): three covariates for fire-regime characteristics (fire frequency, inter-fire interval, area unburnt in the 2019–20 fires within 2.5 km); a drought index and two covariates for protected areas (protected area or not, area protected within 2.5 km). The number of past fires was weakly related to the ecosystem group, with all ecosystems represented within each category of number of past fires (Extended Data Table 4). Four other covariates (broad taxon, ecosystem type, design (before–after, unburnt-burnt) and response (occurrence, abundance); Extended Data Table 1) varied at the taxon-within-project level or higher (a single value across sites within projects) so no further sub-selection of sites was needed before calculating effects (Extended Data Fig. 1).

We calculated effects sizes for species/taxa within projects using an appropriate subset of sites. Effect sizes were calculated for unburnt versus burnt sites, and two fire severity contrasts where there were enough sites burnt at that severity within the project: unburnt versus high/extreme severity, and unburnt versus low/medium severity (Extended Data Table 1). We did this using all sites within the project, and then using each subset of sites based on covariate values (Extended Data Fig. 6). For example, with sites experiencing one of three levels of pre-fire drought within a project, we calculated three effect sizes for species X, using unburnt sites compared with (1) all burnt sites, (2) just the low-severity sites and (3) just the high-severity sites (Extended Data Fig. 1). This was repeated for each level of drought.

#### **Meta-analysis**

We fitted meta-analytic linear mixed-effects models with the rma.mv function of the metafor v.1.4.1 (ref. 63)  $R^{72}$  package. We used restricted maximum likelihood<sup>73</sup>, with the Nelder–Mean method of model optimization, which enabled most models to converge. We used a *t*-test with denominator degrees of freedom adjusted for random effects using the 'contain' option<sup>63,73</sup>.

Models included the interaction of fire severity (high, low severity) with each covariate, and we included three random effects to account for structure in the data, namely project identity, taxon (species most commonly) and broad taxon (amphibian, bird, insect, mammal, mollusc, plant and reptile; Extended Data Table 1). Broad taxon was omitted as a random effect when it was fitted as the covariate. Unburnt sites were the baseline for calculating high and low-severity effect sizes. To account for using the unburnt sites twice in each analysis, we used the vcalc function to obtain the appropriate variance–covariance matrix. To better account for non-independence associated with separate projects leading to better control of type 1 errors, we subsequently

used robust variance estimation<sup>74</sup> with project as the cluster, using the robust function in metafor.

Where there was no evidence for an interaction between a covariate and fire severity (P > 0.1) we applied a univariate model with the covariate as the only moderator. In these cases, we used the effects calculated using unburnt versus burnt sites rather than unburnt versus sites burnt at either high or low severity. Analyses were otherwise the same as for the interaction but without the need for the variance–covariance matrix because unburnt sites were used only once.

Species are expected to have varying responses to wildfire, with some declining and others increasing shortly after fire. Meta-analytic models fitted to plant and animal responses to fire are therefore not modelling a homogeneous process. We applied our meta-analysis to all effects, giving the overall mean effect sizes. However, to better understand the effect sizes of taxa that increased or decreased in response to fire, we used a new approach that also applied our analysis to just those effects that were less than zero (negative effects), and, separately, to those effects greater than zero (positive effects). We calculated P values for the omnibus test of differences among levels of the covariate using an F-distribution<sup>63</sup> for the overall mean effect sizes, for the negative effects and the positive effects. P values for comparisons for the increasing or decreasing taxa must be treated with caution because the distribution of data is not symmetrical, with decreasing numbers of responses with larger effect sizes<sup>75</sup>. We agree with Muff et al.'s<sup>76</sup> recommended approach for interpreting P values as a continuum and regard results with P > 0.1 as having no support. We plot interactions when they had *P* values < 0.1, or main effects otherwise.

#### **Reporting summary**

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

#### **Data availability**

The effect size datasets that led to Figs. 3–5 and Extended Data Figs. 2–5 are available on Figshare, with dataset header rows explained at https://doi.org/10.26187/deakin.26264369.v1. Effect size dataset SMD and SMCC are available at https://doi.org/10.26187/deakin.26264366.v1. Effect sizes using MD and MC are available at https://doi.org/10.26187/deakin.26264360.v1. Effect sizes using MD excluding outliers are available at https://doi.org/10.26187/deakin.26264360.v1. Effect sizes using MD excluding outliers are available at https://doi.org/10.26187/deakin.26264351.v1. The site-level dataset was provided to referees for peer review. A condition enabling participation of project leaders was that these data remain private.

#### **Code availability**

R code used for analysis is available at https://doi.org/10.26187/ deakin.26264372.v1. Code for final figures is available at https://doi. org/10.26187/deakin.26968267.v1.

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Acknowledgements D.A.D. and R.K.G. designed Fig. 2 with P. Sherratt at Litoria Design. R. Gallagher contributed to initial discussions. B. Geary standardized some species names. Funding and contributions of volunteers and casual staff are listed for each project in Supplementary Table 2. The New South Wales government's Applied Bushfire Science programme provided funding to help collate the data and upgrade Fig. 2.

Author contributions K.J.M. and R.K.G. are joint second authors. T.S.D. and D.G.N. are joint third authors. All other authors are in order of contribution. The executive team (D.A.D., K.J.M., R.K.G., T.S.D., D.G.N., R.H.N. and E.G.R.) all contributed to planning, writing and provided data. In addition, D.A.D. led the project, planning, analysis, writing, video and contributed to data collation; K.J.M. led data collation; R.K.G. led spatial data collection; and T.S.D. contributed to analysis and Extended Data Fig. 1. All other authors commented on the final draft before submission and/or provided data (Supplementary Table 8).

**Competing interests** The authors declare that some of them work for government agencies involved in forestry and implementing planned burns (Supplementary Table 8). The lead author declares that, despite the potential for government agencies to impose policy positions on staff communications (see ref. 51), scientific independence and integrity has been maintained throughout this project.

#### Additional information

 $\label{eq:supplementary} Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-024-08174-6.$ 

**Correspondence and requests for materials** should be addressed to Don A. Driscoll. **Peer review information** *Nature* thanks Adam Mahood, David Makowski and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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**Extended Data Fig. 1** | **Data extraction for calculating effect sizes.** Flow diagram illustrating how the full dataset (1) was subdivided so that effect sizes could be calculated for each taxon within each project. Each row represents a record of taxon occurrence or abundance at an individual survey site within

a project. (2) represents data treatment for covariates that varied at the taxonwithin-project level (broad taxon, ecosystem type). (3) represents data treatment for covariates that differed between sites within projects (e.g. drought, inter-fire interval).



Extended Data Fig. 2 How wildfire impacted occurrence or abundance was modified by study design, year, response, and region. Mean standardised effect sizes (±95% CI) for study design (a), year (b), and main effects or interactions with fire severity for response (c), and region (d). Graphic features as for Fig. 1. P values are for the plotted result and are the omnibus two-tailed test based on an F distribution. Test statistics (from left to right) for Study design: F(1,55) = 1.09, P = 0.302; F(1,61) = 1.26, P = 0.266; F(1,40) = 0.01, P = 0.917; Year: F(1,44) = 7.83, P = 0.008; F(1,47) = 15.57, P < 0.001; F(1,33) = 0.43, P = 0.519;Response: F(1,44) = 0.13, P = 0.724; F(1,47) = 0.7, P = 0.408; F(1,24) = 20.87, P < 0.001; Region: F(2,43) = 46.66, P < 0.001; F(2,46) = 25.96, P < 0.001; F(2,26) = 5.11, P = 0.013. Unburnt-burnt designs (Unb-burn, (a)) were used for all other analyses, so represent the overall effects of the 2019-20 fires without additional covariates. Before-after (Bef-after) survey designs produced a distribution of effect sizes that was shifted to the right with smaller negative and larger positive effects compared with unburnt-burnt designs, suggesting bias associated with the drought-breaking rains after the fires (a). In the second year after the fires there was a subtle reduction in mean negative effect sizes,

hinting that recovery was beginning for some taxa that declined (b). Abundance (Abund) and occurrence (Occur) responses showed very similar effect sizes, with the only exception of higher positive effect sizes for occurrence data at high severity. The small number of effects in this group precludes further separate consideration of occurrence responses (c). The most striking regional effect was for weaker positive effects in the south, particularly at high severity (d). Fire conditions differed across regions. Our data suggest a weak trend towards stronger pre-fire drought in the south (Pearson's correlation with latitude = -0.03, t = -2.5343, df = 6239, P = 0.01). Fires that drove the world's most extreme pyrocumulonimbus event were all in our mid and southern regions, corresponding with larger contiguous areas of high severity fire<sup>3</sup>. Remote sensing data indicate that the southern parts of the study region had slower rates of vegetation recovery than in the north<sup>77</sup>. These differences in pre-fire conditions, fire behaviour, and recovery rates suggest that the level of disturbance and other stressors can constrain the response of taxa which would otherwise benefit from bushfires.





Reduced by fire Overall Increased by fire (a) Study design P=0.669 P=0.117 P=0.569 142 63 n = 72 Bef-after Be Be 870 1564 672 Unb-burn Un Un + (b) Year P=0.026 P=0.048 P=0.199 737 1285 + Year-1 Year-2 204 116 614 . Y1 122 Y2 -1091 153 648 91 Year-1 Year-2 • Y1 Y2 (c) Response P<0.001 P=0.594 P<0.001 502 689 Abund .... -84 1395 71 Ab 169 Oc 602 425 Abund + Ab -78 36 Occur Oc (d) Region P<0.001 P=0.001 P<0.001 259 473 208 -North + -No No 363 643 280 Mid Mi . -++ 243 441 195 South --157 274 117 North No No 550 187 358 Mid Mi Mi 300 551 248 South So -So -0.3 -0.1 ò -0.2 ό 0.1 ò 0.1 0.2 0.3 Mean difference



-0.1 0 -0.2

49

118

-0.3

DS

RF

WS

DS

RF

WS

17

131

0.1 0.2 0.3

66

250

0 0.1 0

Mean difference

Dry scler.

Rainforest

Wet scler.

**Extended Data Fig. 3** | **Mean difference effect sizes** (±**95% CI**). See previous figures for details. Panels match: top left; Fig. 3, top right; Fig. 4; bottom left; Fig. 5, bottom right Extended Data Fig. 2. Mean change effect size shown for Study design with before-after data, bottom right panel. P values are for the plotted result and are the omnibus two-tailed test based on an F distribution. Top left panel test statistics (from left to right): Fire severity: F(1,41) = 4.77, P = 0.035; F(1,41) = 0.7, P = 0.407; F(1,26) = 40.63, P < 0.001; Fire frequency: F(3,39) = 11.08, P < 0.001; F(3,33) = 2.68, P = 0.063; F(3,26) = 5.6, P = 0.004; Inter-fire interval: F(2,42) = 21.74, P < 0.001; F(2,37) = 13.77, P < 0.001; F(2,25) =54.2, P < 0.001; Unburnt area: F(2,22) = 15.7, P < 0.001; F(2,29) = 43.89, P < 0.001; F(2,21) = 1.4, P = 0.268. Top right panel test statistics (from left to right): Pre-fire drought: F(2,37) = 4.06, P = 0.025; F(2,46) = 21.77, P < 0.001; F(2,28) = 13.48, 
$$\begin{split} \mathsf{P} < 0.001; \mathsf{P.A. or Not: F}(1,39) = 2.85, \mathsf{P} = 0.1; \mathsf{F}(1,46) = 2.01, \mathsf{P} = 0.163; \mathsf{F}(1,31) = \\ 17.26, \mathsf{P} < 0.001; \mathsf{P.A. area: F}(2,36) = 12.09, \mathsf{P} < 0.001; \mathsf{F}(2,45) = 1.35, \mathsf{P} = 0.271; \\ \mathsf{F}(2,25) = 5.32, \mathsf{P} = 0.012. Bottom left panel test statistics (from left to right): \\ Taxon: \mathsf{F}(5,29) = 88.71, \mathsf{P} < 0.001; \mathsf{F}(5,29) = 22.98, \mathsf{P} < 0.001; \mathsf{F}(5,15) = 19.43, \\ \mathsf{P} < 0.001; \mathsf{E}cosystem: \mathsf{F}(3,31) = 7.6, \mathsf{P} = 0.001; \mathsf{F}(3,32) = 69.68, \mathsf{P} < 0.001; \\ \mathsf{F}(3,21) = 2.58, \mathsf{P} = 0.081. Bottom right panel test statistics (from left to right): \\ Study design: \mathsf{F}(1,55) = 0.18, \mathsf{P} = 0.669; \mathsf{F}(1,61) = 0.33, \mathsf{P} = 0.569; \mathsf{F}(1,40) = 2.56, \\ \mathsf{P} = 0.117; \mathsf{Year: F}(1,39) = 5.35, \mathsf{P} = 0.026; \mathsf{F}(1,39) = 4.17, \mathsf{P} = 0.048; \mathsf{F}(1,33) = 1.72, \\ \mathsf{P} = 0.199; \mathsf{Response: F}(1,39) = 14.86, \mathsf{P} < 0.001; \mathsf{F}(1,47) = 0.29, \mathsf{P} = 0.594; \mathsf{F}(1,24) = \\ 21.87, \mathsf{P} < 0.001; \mathsf{Region: F}(2,37) = 16.53, \mathsf{P} < 0.001; \mathsf{F}(2,37) = 8.62, \mathsf{P} = 0.001; \\ \mathsf{F}(2,26) = 19.61, \mathsf{P} < 0.001. \end{split}$$







Extended Data Fig. 4 | See next page for caption.

Extended Data Fig. 4 | Mean difference or mean change effect sizes (±95% CI) calculated after outliers were removed. See previous figures for details. Panels match: top left; Fig. 3, top right; Fig. 4; bottom left; Fig. 5, bottom right Extended Data Fig. 2. P values are for the plotted result and are the omnibus two-tailed test based on an F distribution. Top left panel test statistics (from left to right): Fire severity: F(1,38) = 6.16, P = 0.018; F(1,38) = 1.8, P = 0.188; F(1,28) = 17.69, P < 0.001; Fire frequency: F(3,36) = 9.83, P < 0.001; F(3,37) = 2.58, P = 0.068; F(3,29) = 30.56, P < 0.001; Inter-fire interval: F(2,38) = 31.14, P < 0.001; F(2,34) = 11.31, P < 0.001; F(2,26) = 4.53, P = 0.021; Unburnt area: F(2,19) = 7.32, P = 0.004; F(2,26) = 54.6, P < 0.001; F(2,21) = 2.57, P = 0.101. Top right panel test statistics (from left to right): Pre-fire drought: F(2,34) = 2.77, P = 0.077; 
$$\begin{split} F(2,44) = &17.99, P < 0.001; F(2,27) = 5.05, P = 0.014; P.A. or Not: F(1,42) = 1.37, \\ P = &0.248; F(1,43) = &2.2, P = &0.145; F(1,31) = &13.3, P = &0.001; P.A. area: F(2,31) = &12.15, \\ P < &0.001; F(2,40) = &1.25, P = &0.299; F(2,27) = &5.44, P = &0.01. Bottom left panel test statistics (from left to right): Taxon: F(5,27) = &131.46, P < &0.001; F(5,27) = &19.34, \\ P < &0.001; F(5,17) = &17.82, P < &0.001; Ecosystem: F(3,29) = &6.41, P = &0.002; F(3,30) = \\ 9.74, P < &0.001; F(3,24) = &3.99, P = &0.019. Bottom right panel test statistics (from left to right): Study design: F(1,44) = &3.37, P = &0.073; F(1,56) = &0.51, P = &0.478; \\ F(1,38) = &0.76, P = &0.389; Year: F(1,36) = &12.88, P = &0.001; F(1,36) = &9.9, P = &0.003; \\ F(1,33) = &0.07, P = &0.796; Response: F(1,36) = &4.97, P = &0.032; F(1,45) = &0.25, \\ P = &0.619; F(1,26) = &28.11, P < &0.001; Region: F(2,34) = &20.51, P < &0.001; F(2,34) = \\ 5.26, P = &0.01; F(2,27) = &4.42, P = &0.022. \end{split}$$



Extended Data Fig. 5 | See next page for caption.





Extended Data Fig. 5 | Standardised effect sizes (±95% Cl), with beforeafter designs retained in all analyses. See previous figures for details. Panels match: top left; Fig. 3, top right; Fig. 4; bottom left; Fig. 5, bottom right Extended Data Fig. 2. P values are for the plotted result and are the omnibus two-tailed test based on an F distribution. Top left panel test statistics (from left to right): Fire severity: F(1,50) = 8.49, P = 0.005; F(1,54) = 0.39, P = 0.533; F(1,35) = 11.54, P = 0.002; Fire frequency: F(3,49) = 12.21, P < 0.001; F(3,46) =4.49, P = 0.008; F(3,39) = 8.58, P < 0.001; Inter-fire interval: F(2,53) = 9.36, P < 0.001; F(2,59) = 14.16, P < 0.001; F(2,40) = 13.97, P < 0.001; Unburnt area: F(2,31) = 18.01, P < 0.001; F(2,43) = 1.06, P = 0.356; F(2,30) = 5.98, P = 0.007. Top right panel test statistics (from left to right): Pre-fire drought: F(2,46) = 2.96, 
$$\begin{split} \mathsf{P} &= 0.062; \ \mathsf{F}(2,60) = 4.07, \ \mathsf{P} = 0.022; \ \mathsf{F}(2,37) = 3.92, \ \mathsf{P} = 0.029; \ \mathsf{P}.A. \ or \ \mathsf{Not}: \\ \mathsf{F}(1,55) &= 2.02, \ \mathsf{P} = 0.161; \ \mathsf{F}(1,60) = 0.95, \ \mathsf{P} = 0.334; \ \mathsf{F}(1,40) = 3.82, \ \mathsf{P} = 0.058; \ \mathsf{P}.A. \\ area: \ \mathsf{F}(2,54) &= 0.62, \ \mathsf{P} = 0.54; \ \mathsf{F}(2,59) = 18.08, \ \mathsf{P} < 0.001; \ \mathsf{F}(2,40) = 2.19, \ \mathsf{P} = 0.126. \\ \mathsf{Bottom left panel test statistics} (from left to right): \ \mathsf{Taxon}: \ \mathsf{F}(5,38) = 6.85, \\ \mathsf{P} < 0.001; \ \mathsf{F}(5,42) = 23.4, \ \mathsf{P} < 0.001; \ \mathsf{F}(5,24) = 10.32, \ \mathsf{P} < 0.001; \ \mathsf{E}(5,38) = 6.85, \\ \mathsf{P} < 0.001; \ \mathsf{F}(5,42) = 23.4, \ \mathsf{P} < 0.001; \ \mathsf{F}(5,24) = 10.32, \ \mathsf{P} < 0.001; \ \mathsf{E}(50) = 0.001. \\ \mathsf{Bottom right panel test statistics} (from left to right): \ \mathsf{Study design}: \ \mathsf{F}(1,55) = 1.09, \ \mathsf{P} = 0.302; \ \mathsf{F}(1,61) = 1.26, \ \mathsf{P} = 0.266; \ \mathsf{F}(1,40) = 0.01, \ \mathsf{P} = 0.917; \ \mathsf{Year}: \ \mathsf{F}(1,55) = 5.82, \ \mathsf{P} = 0.019; \ \mathsf{F}(1,61) = 1.26, \ \mathsf{P} < 0.001; \ \mathsf{F}(1,42) = 0.17, \ \mathsf{P} = 0.682; \ \mathsf{Response:} \\ \mathsf{F}(1,55) = 0.32, \ \mathsf{P} = 0.576; \ \mathsf{F}(1,61) = 2.09, \ \mathsf{P} = 0.154; \ \mathsf{F}(1,33) = 5.98, \ \mathsf{P} = 0.02; \ \mathsf{Region:} \\ \mathsf{F}(2,54) = 28.4, \ \mathsf{P} < 0.001; \ \mathsf{F}(2,60) = 27.24, \ \mathsf{P} < 0.001; \ \mathsf{F}(2,35) = 5.26, \ \mathsf{P} = 0.01. \\ \end{split}$$





Extended Data Table I   Oovanates used in the analysis
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Covariate	Levels	Category definitions
Fire severity	Unburnt	Unburnt = unburnt surface with green canopy;
	Low	Low severity (combines low and medium severity) = burnt understory, unburnt canopy or, partial
	High	canopy scorch;
		High severity (combines high and extreme severity) = burnt understory and full canopy scorch or consumption. Data provided by project leads or if missing, extracted from agency mapping <sup>78,79</sup>
Fire frequency	0	A count of the number of fires based on state agency fire history records between 1979 and 2019.
	1	Few sites were burnt many times, so categories reflect data availability (see Extended Data Fig. 6)
	2	
	3+	
Inter-fire	<11 years	For burnt sites, the number of years between the 2019–20 fires and the previous fire. For unburnt
interval	11-20 years	sites, the number of years since the most recent fire (time since fire). Due to high numbers of
	>20 years	records in mid age classes, we divided data into the first 10 years, 11-20 years, and older than 20
		years as an approximate compromise between amount of data and the number of years between the high and low categories (see Extended Data Fig. 6).
Unburnt area	High unburnt	Fire extent mapping was used to delineate the proportion of unburnt area compared to total area
	Mid unburnt	(burnt and unburnt) within a 2.5 km radius from a given survey site. Buffer radii from 250 m to 2.5
	Low unburnt	km were highly correlated (Pearson correlation coefficient > 0.86) so we use 2.5 km for
		consistency with the protected area buffer size. 1/3 and 2/3 percentiles delimited categories; Low
		< 11.91%, High > 68.07%.
Drought	High drought	Pre-fire drought was assessed as the accumulated severity of drought in the 12 months prior to
	Wid drought	December 2019, using the Standardised Precipitation Index (SPI) dataset of Gallagher et al. <sup>80</sup> SPI is
	Low drought	the number of standard deviations that observed cumulative precipitation deviates from the
		average <sup>81</sup> . Values ranged 0 to -56.37, with lowest values (largest negative values) classed as high-
		drought, and values closer to zero classed as low drought. 1/3 and 2/3 percentiles delimited
		categories; High < -28.31, Low > -3.0.
P.A. or not	Protected	P.A. = protected area. Using ACLUMv8 Landuse <sup>82</sup> for % natural environments (undisturbed) within
	onprotected	1.2.0 'other minimal use' (11.6%) 1.2.0 'Managed recourse protection' (<1%) 0.20% of taxa x site
		affects had 50 or 70% cover, which we excluded from analysis because they could not be classified
		as P.A. or not.
P.A. area	High protected area	ACLUMv8 Landuse for % natural environments (undisturbed) within a 2.5 km radius around survey
	Mid protected area	site. Buffers of increasing radii difference exhibited decreasing correlation, so we use our largest
	Low protected area	radius, 2.5 km, to minimise correlation with P.A or not (Pearson correlation 0.6). 2.5 km was an
		arbitrary choice, likely with little consequence given high correlations with other radii (e.g. 1 km, r $$
		= 0.94). 1/3 and 2/3 percentiles delimited categories; Low < 47.08% , High >92.88%.
Ecosystem	Alpine_subalpine	Some contributors indicated ecosystem type and for others we used available spatial layers <sup>83</sup> . The
	Dry sclerophyll	detailed vegetation types were grouped into broadly similar ecosystems (except for grass-
	Grass_heathland	heathlands, which were less common in the dataset and could not be separately analysed).
	Rainforest	
	wetland Wet sclerophyll	
Taxon	Amphibian: Bird: Fish:	Taxa were grouped into broad taxonomic groups to evaluate differences among vastly different
	Insect: Mammal: Mollusc:	taxa, and to take these into account in analysis.
	Reptile; Plant	
Study design	Befor e-after	We compare before–after with burnt-unburnt designs. Our analysis converted the small number
	Burnt-Unburnt	of BACI designs to burnt-unburnt designs (methods).
Year	Year 1	Year 1: from end of fires in early 2020 up to June 2021.
	Year 2	Year 2: June 2021 – June 2022.
Response	Occurrence	All responses were either counts of plants or animals (abundance), or records of presence or
	Abundance	absence (occurrence).
Region	North	Three regions were defined based on 1/3 and 2/3 percentiles of site latitudes, with cut points of -
	Mid	35.858 and -33.470 (~240 km S and ~50 km N of Sydney).
	South	

For covariates with levels High, Medium, and Low, the focal dataset was divided into three categories using the 0.333 and 0.666 percentile values of the covariate. Extended Data Fig. 6 illustrates the distributions of continuous covariates and break points. For the ecosystem covariate, level grass\_heathland had five or fewer effect sizes in each analysis, precluding reliable estimates of mean effects, and causing models to fail to converge, so this ecosystem group was excluded when ecosystem was fitted as a fixed effect. Similarly, there were five or fewer wetland sites burnt at high severity, so these were also excluded from analysis when ecosystem was fitted as a fixed effect. Data sources<sup>78-83</sup>.

Extended Data Table 2 | Mean and maximum declines or increases based on mean difference effect sizes (Extended Data Fig. 3)

Covariate	Mean decline	Max diff decline	Mean increase	Max diff increase
Fire severity	-0.09	0.01	0.07	0.01
Fire frequency	-0.16	0.11	0.15	0.12
Inter-fire interval	-0.13	0.10	0.12	0.04
Unburnt area	-0.11	0.07	0.08	0.01
Pre-fire drought	-0.13	0.02	0.08	0.03
P.A. or Not	-0.12	0.02	0.08	0.02
P.A. area	-0.13	0.03	0.11	0.02
Taxon	-0.09	0.10	0.07	0.10
Ecosystem	-0.10	0.04	0.09	0.04
Study design	-0.09	0.01	0.11	0.08
Year	-0.09	0.01	0.06	0.00
Response	-0.10	0.04	0.08	0.04
Region	-0.10	0.03	0.07	0.03

Values indicate the proportional change in abundance/occurrence. Mean declines or increases are averaged across all levels of the covariate. The maximum difference (Max diff) in decline or increase across levels of the covariate are constrained to within fire severity levels when a fire severity interaction was significant. For example, positive responses to fire frequency depended on fire severity (Extended Data Fig. 3). The mean increase (15%) was averaged across the eight values (four levels of fire frequency x two levels of fire severity), while the maximum difference for positive responses (12%) was the difference at low severity (effect at 3+ fires minus effect at 0 fires).

xtended Data Table 3   Datasets with months excluded and reason for exclusion		
Project	Month/year excluded	Reason
018	Feb-20	Most data Aug 2020 – Jan 21; leave out data from immediately after fires.
045	Feb-Apr-20	Three post fire surveys; kept most recent two that align with most other data
071	Mar-21	One species with most data from Nov-20, before-after design and only two cases of this design with >1 survey time
065	Sep-21	The second of the before-after design with two post-fire surveys. Only used the first post- fire survey.
006	Dec-2021	one site surveyed at that time, rest of data from before 2021
051	Apr-20	Limits first year of data to spanning one year; Jul-20 to Apr-21
052	May-20, Jul-20	Excludes early surveys to make first and second year comparable Oct-Feb for each.
067	May-20	To limit first year to 12 months up to May-21, second year up to Jun-22.
076	Jan-May-20, Jun-22, Sep-22	To limit first and second year to 12 months each.
030	Mar-May-20, Apr-May 2021	Matched months sampled in both years, with most recent date available March 2022 and target start of year 2 June 2021.

Extended Data Table 4 | Proportion of sites burnt by 0 to 3+ fires since 1979 by ecosystem

Ecosystem Group	0	1	2	3+
Alpine-subalpine	0.12	0.41	0.4	0.07
Dry sclerophyll	0.38	0.32	0.15	0.15
Grass-heathland	0.22	0.37	0.21	0.19
Rainforest	0.51	0.28	0.13	0.08
Wet sclerophyll	0.4	0.3	0.18	0.12
Wetland	0.6	0.26	0.07	0.07

# nature portfolio

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Last updated by author(s): Sep 8, 2024

# **Reporting Summary**

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#### **Statistics**

For	all st	atistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.
n/a	Cor	ifirmed
	$\boxtimes$	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
	$\square$	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
		The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.
	$\square$	A description of all covariates tested
	$\square$	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
		A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
		For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted Give P values as exact values whenever suitable.
$\ge$		For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
	$\boxtimes$	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
	$\boxtimes$	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
		Our web collection on statistics for biologists contains articles on many of the points above.

## Software and code

 Policy information about availability of computer code

 Data collection
 Data were collected into csv files using Microsoft\* Excel\* for Microsoft 365 MSO (Version 2407 Build 16.0.17830.20166) 64-bit.

 Data analysis
 Analyses were completed in R 4.3.2 (R Core Team 2023) using packages metafor 1.4.1 (Viechtbauer 2010; Viechtbauer 2024), sf 1.0-16 (Pebesma & Bivand 2023) and dplyr 1.1.4 (Wickham et al. 2023).

 References
 Pebesma, E. & Bivand, R. (2023) Spatial Data Science: With Applications in R. . Chapman and Hall/CRC, New York, https://doi.org/10.1201/9780429459016.

 R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available from http://www.R-project.org.

 Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. Journal of Statistical Software, 36, 1-48.

 Viechtbauer, W. (2024) Metafor 4.7-11 Calculate Effect Sizes and Outcome Measures.

 Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023) dplyr: A Grammar of Data Manipulation. R package version 1.1.3. https://CRAN.R-project.org/package=dplyr.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

#### Data

Policy information about <u>availability of data</u>

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets

- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

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The data availability statement reads:
```

The effect size datasets that led to Figures 3 – 5 and Extended Data Figures 2 – 5 are available on Figshare.

Dataset header rows explained. https://doi.org/10.26187/deakin.26264369.v1

Effect size dataset SMD and SMCC. https://doi.org/10.26187/deakin.26264366.v1

Effect sizes using MD and MC. https://doi.org/10.26187/deakin.26264360.v1

Effect sizes using MD excluding outliers. https://doi.org/10.26187/deakin.26264351.v1

The site-level dataset was provided to referees for peer review. A condition enabling participation of project leaders was that these data remain private.

## Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

# Ecological, evolutionary & environmental sciences study design

in studies must disclose of	These points even when the disclosure is negative.
Study description	A meta-analysis of 62 projects examining interactions of fire severity with other covariates
Research sample	Occurrence or abundance of species, morphospecies, or higher taxa before/after fire or in burnt/unburnt areas after the fire. These provide matched contrasts from which effect sizes can be derived. Further details about individual projects are provided in Supplementary Information Table 2.
Sampling strategy	Project-specific sampling including plots, cameras and other methods. Details about individual projects are available in Supplementary Information Table 2. Sample sizes were those that could be achieved with the available resources.
Data collection	From the methods section: We gathered site-level data for 62 projects (Supplementary information Table 2) by inviting contributors to join our collaboration. We emailed leaders of projects studying post-fire biodiversity impacts that were funded by the Australian Government's Wildlife and Habitat Bushfire Recovery Program. We promoted our proposal on social media in summer 2021-2, ran a workshop at the Ecological Society of Australia conference in November 2021 and held a two-day on-line symposium in February 2022. Projects were collated throughout 2022 after potential contributors contacted us. Projects had to include site level data from sites burnt in 2019–20 within the megafire region 14. To ensure a minimum level of treatment replication, enabling means and standard deviations to be estimated, datasets needed at least three burnt and unburnt sites (e.g., survey points, plots, or transects), or three sites with before-after data and at least three non-zero records across all sites (at the species/taxon level). Projects also

	needed to report either an estimate or index of abundance (44 projects), occurrence (17 projects), or probability of occurrence after accounting for detection (1 project). Although we canvassed researchers for a full range of response variables, the datasets provided included almost exclusively presence-absence or abundance data. Abundance and occurrence effect sizes were similar, justifying using both together (Extended Data Fig. 2c). Only one project met all other criteria but reported responses that were not related to abundance or occurrence (effects of grazing on reproduction in one orchid species), and thus was omitted from analysis. Five other projects were excluded because they did not have at least three unburnt sites.
	Project details in Supplementary information Table 2, and ST Table 8 indicate who collected data in each project.
Timing and spatial scale	Before data were from surveys from 2015-2019. Burnt/unburnt designs included data from 2020-2022. Most projects were from eastern Australia ranging from south-east Queensland to eastern Victoria, with an additional four projects from Kangaroo Island, South Australia, and one from south-west Western Australia (see Fig. 1).
Data exclusions	Data exclusions are documented in Extended Data Table 3.
Reproducibility	NA. Requires independent gigantic dataset after future extensive megafires.
Randomization	There was no randomisation in before-after designs, and these were confounded with high rainfall after the fires. They were excluded from our main analysis. Projects with burnt/unburnt designs were stratified random designs, with sites randomly selected, within areas burnt or unburnt by the wildfires. Sites were constrained by practical considerations associated with accessibility, placing spatial limits on randomisation.
Blinding	Blinding is not relevant because researchers had to visit sites of known treatment (burnt or unburnt).
Did the study involve field	d work? Xes No

## Field work, collection and transport

Field conditions	This meta-analysis collated data from separate field projects (Supplementary Information Table 2)
Location	Most projects were from eastern Australia ranging from south-east Queensland to eastern Victoria, with an additional four projects from Kangaroo Island, South Australia, and one from south-west Western Australia (see Fig. 1). Supplementary Information Table 2 provides further details.
Access & import/export	Permits are detailed in Supplementary Information Table 2.
Disturbance	Typically field workers drive to sites using existing tracks then walk to the field data collection point, minimising site disturbance.

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Ma	terials & experimental systems
n/a	Involved in the study
$\boxtimes$	Antibodies
$\boxtimes$	Eukaryotic cell lines
$\boxtimes$	Palaeontology and archaeology
$\boxtimes$	Animals and other organisms
$\boxtimes$	Clinical data
$\boxtimes$	Dual use research of concern
$\boxtimes$	Plants

~

#### Methods

n/a Involved in the study

 ChIP-seq

 Flow cytometry

 MRI-based neuroimaging

## Plants

Seed stocks	NA
Novel plant genotypes	NA
Authentication	NA