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Biological responses to the press and pulse of climate trends and extreme events

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The interaction of gradual climate trends and extreme weather events since the turn of the century has triggered complex and, in some cases, catastrophic ecological responses around the world. We illustrate this using Australian examples within a press–pulse framework. Despite the Australian biota being adapted to high natural climate variability, recent combinations of climatic presses and pulses have led to population collapses, loss of relictual communities and shifts into novel ecosystems. These changes have been sudden and unpredictable, and may represent permanent transitions to new ecosystem states without adaptive management interventions. The press–pulse framework helps illuminate biological responses to climate change, grounds debate about suitable management interventions and highlights possible consequences of (non-) intervention.

Globally, the beginning of the twenty-first century has seen an unprecedented number of catastrophic biological events[1]. Although some events have received extensive attention (such as the 2016 Great Barrier Reef coral bleaching[2]), many others have gone largely unreported. Descriptions of the impacts of the changing climate on populations, species and communities have, until recently, typically focused on gradual responses to incremental change[3–6], but there is mounting evidence that suggests that major biodiversity impacts may be driven by extreme events[7–13].

Climatological extreme events are — by definition — rare, low-frequency, intense events[14]. Their biological impacts vary both taxonomically and geographically, according to the timing, severity and duration of each event relative to the life cycle and resilience of the affected organisms[8,15,16]. Extreme events can alter growth and reproduction in marked ways, because the development of many organisms is triggered by environmental signals (phenology). Examples of this include temperature-dependent sex determination[17]; embryonic development and earlier hatching of birds[18]; vernalization events[19] and flowering dates[20]. Consequently, biological responses to extreme events are difficult to both reliably predict and generalize across taxa. Nevertheless, a deeper understanding of biological responses to extreme events is essential to inform management interventions.

Scientific attribution of individual extreme weather events to anthropogenic climate change is increasing[21], but a similar attribution of biological events is lacking[22]. This reflects our poor understanding of the underlying biological mechanisms driving change, but also the fact that ecosystem responses generally do not occur immediately after a single weather event. Rather, the constellation of catastrophic events now occurring suggests cumulative responses to the long-term stress of the changing climate, in combination with extreme weather events.

The 'press and pulse' framework has been used to describe disturbances in ecological systems for many years[23], and demographic and physiological models of organisms based on both daily variability and long-term trends implicitly incorporate the concept. Here, we apply it to explain potential ecosystem responses to long-term changes in climate trajectories (presses) and extreme events (pulses). The impacts of an extreme event depend not only on the magnitude, duration, frequency and timing of the pulse, but also the state of the press. Although often considered separately in both climate models and biological experiments, in reality presses and pulses, exerted simultaneously, may be more likely to push systems to tipping points[24].

Ongoing climate change represents a press on (or long-term perturbation of) biological systems, which respond to increased temperatures, sea-level rise, ocean acidification or changes to

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water availability through behavioural and physiological adaptation, range shifts, phenological adjustments or local extinction. Extreme events can be seen as discrete pulses, which, when superimposed on the underlying press of climate change, have even greater potential to amplify impacts on the distribution of populations and species, leading to community-level responses such as changes in species richness, composition and/or dominance[25,26]. These changes may be long lasting or irreversible especially if interspecific interactions and stabilizing ecological feedbacks (such as predation, competition, facilitation) are altered, or repeated extreme events occur[2,12,27].

Many organisms have adapted to cope with long-term and short-term climate variability, but as climate change accelerates, both the magnitude and frequency of extreme events is expected to increase (Fig. 1). The threshold between survivable extreme weather events and extinction extremes is therefore crossed more frequently. This can prevent recovery to previous population sizes[28] and may have long-term consequences for population size and persistence.

The biological impact of pulse events depends on their spatial scale. Localized events may lead to regional extinction (or outbreaks) of populations, or major declines in productivity from which the system can only recover through immigration from surrounding populations. Other events, if spread over a wider area relative to species' ranges, will result in long-lasting or irreversible effects. Even if these pulses primarily affect a single species or population in a community, they may instigate knock-on effects on a community[9] or ecosystem level[29].

We use Australia as a model system of the press–pulse framework. Australia is one of the most climatically variable places in the world[30,31], so the detection of biological impacts indicates a strong linkage with historically anomalous climate extremes. First, we outline observed changes to climate (the press) and changes in extreme events with climate change (the pulses) from 1961–2015 for Australia in general, and specifically for six contemporary case studies (see Table 1, Fig. 2 and Supplementary Information). We then illustrate, using empirical evidence for each of the case studies, the impacts of climatic presses and pulses and demonstrate potential mechanisms underlying changes of state. These include a shift in ecosystem state from kelp forests to seaweed turfs following a single marine heatwave event (2011); the destruction of Gondwanan refugia by wildfire ignited by lightning storms (2016); dieback of floodplain forests across Australia's largest river system during the millennium drought (2003–2009); the large-scale conversion of obligate seeder forest to shrubland following repeated fires (2003–2014); community-level boom and bust in the arid zone following extreme rainfall (2011–2012); and extensive mangrove dieback in the Gulf of Carpentaria after a weak monsoon (2015–2016). Finally, we consider future projections of extremes and discuss the changes in conservation management required to anticipate and mitigate these drivers of ecosystem change.

Climate drivers of extreme events

With its vast area and latitudinal span, Australia encompasses many climate zones, including equatorial, tropical, subtropical, temperate, desert and grasslands[32]. These climate zones are influenced on interdecadal to intraseasonal timescales by large-scale ocean–atmospheric processes stemming from the surrounding Pacific, Indian and Southern oceans. These processes — which include the El Niño/Southern Oscillation (ENSO), the Indian Ocean Dipole (IOD) and Southern Annular Mode (SAM) — affect weather and climate in different regions of Australia[33,34], influencing flooding, drought, storms and bushfire activity[30,35–38], and making Australia's climate more variable than similar climate zones elsewhere in the world[30,31,39].

The baseline. For the next few decades (to 2050), natural variability across much of Australia is expected to exceed the effects of climate change[40,41]. Understanding the interaction of natural climate variability (the baseline) and the resultant shifts stemming from

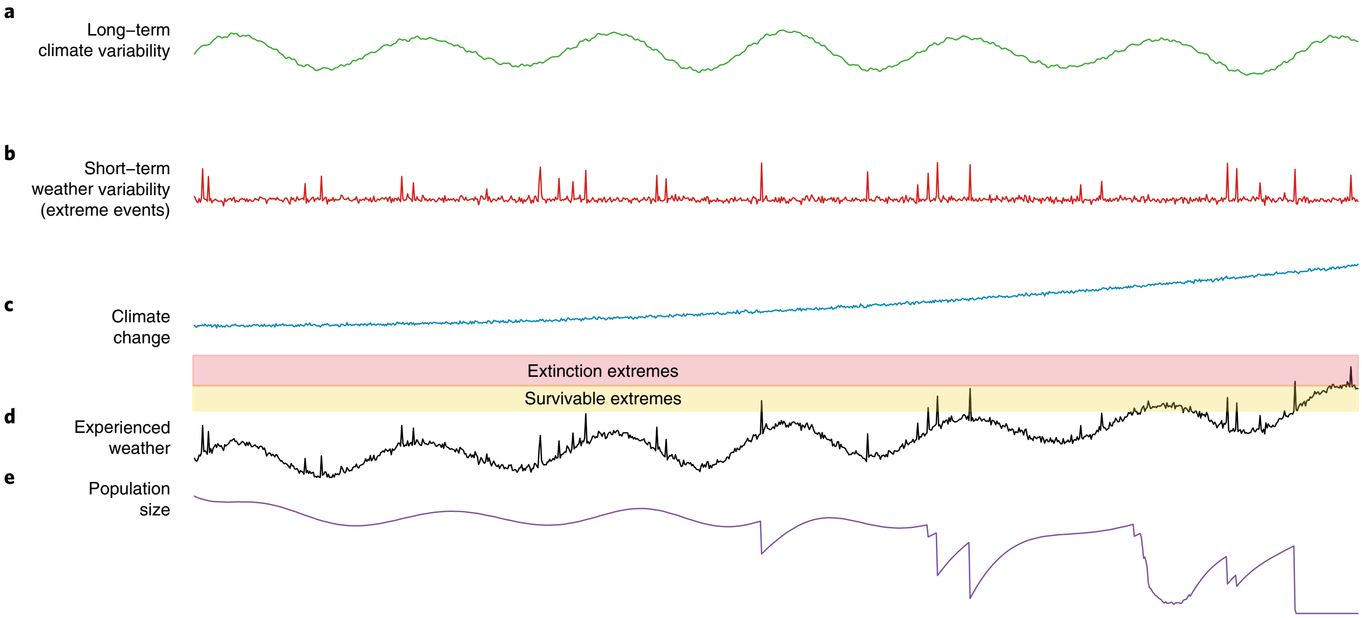

Fig. 1 | The press–pulse framework, showing the components of climate change and climate variability experienced by biological systems. a–d, Many organisms have adapted to cope with long-term (**a**) and short-term climate variability (**b**), but as the climate change trend increases (**c**), both the magnitude and frequency of extreme events is expected to increase (**d**). The threshold between survivable extreme weather events (yellow) and extinction extremes (pink) is therefore crossed more frequently, preventing recovery to previous population size. **e**, The cumulative effects of the climate press and extreme pulses may have long-term consequences for population size, and potentially for persistence.

Table 1 | Summary of the climate presses and pulses associated with each case study, outlining the direct and indirect impacts, social consequences and potential management responses

Case study	Press	Pulse	Biological impacts		Social consequences	Management Response
			Direct	Indirect		
Riverine forest decline (2003–2009)	Decreased river flows; increasing surface air temperatures; decreased rainfall	Large rainfall deficits accompanied by more intense heatwaves	Mortality, reductions in forest canopy cover	Reduced avifaunal and mammal abundance; decreased recruitment; changes to riverine nutrient availability	Loss of aesthetic values, pollination services, water quality and timber resources	Maintain environmental flows; thinning to reduce water competition
Kelp forest regime shift (austral summer 2011)	Increasing sea surface temperatures	Extended large-scale marine heatwave	Mortality in kelp forests, fish, lobster, abalone and coral; range contraction of coastal kelp forests	Propagule limitation, competition from turfs and grazing by tropical species prevents kelp re-establishment	Fisheries collapse; reduced tourism	Translocation of warm adapted genotypes; assisted recolonization of kelp forests
Arid zone boom and bust (2011–2012) Fires burnt more than a third of the continent	Increasing air temperatures	Extreme wet season rainfall linked to La Niña	Massive plant growth; rodent outbreaks; fires	Explosion of introduced predator populations; soil destabilization; dune movement	Dust storms; loss of livestock and pasture	Fire risk and predator management
Obligate seeder forest collapse (2003–2014)	Increasing air temperatures; increasing frequency of dry lightning storms	Multiple wildfires in short succession; high temperatures; radiation frosts	Extensive immature forest; reduced tree growth, seed production, seedling establishment	Increased insect defoliation; increased erosion impacting soils and seedbanks	Loss of forest resources, carbon storage, water supplies, and tourist amenity values	Aerial sowing; thinning or resowing with resprouting eucalypts; protect unburnt mature forests from fire
Mangrove dieback (austral spring 2015–2016)	Increasing air and sea surface temperatures; sea-level rise	Weak monsoon, leading to below average rainfall; significant water deficits; hyper-salinity likely	Mangrove dieback; hypersalinization of saltpans; primary productivity loss	Biodiversity loss; increased erosion and sedimentation; reduced water quality	Declining fisheries and indigenous use	Reseeding/replanting
Fire in Gondwanan refugia (2016)	Increasing fire weather associated with warming and drying	Extreme lightning storm	Loss of palaeo-endemic community	Destruction of organic soils; loss of biodiversity	Increase in public awareness of climate risks; infrastructure loss; loss of tourism	Hazard reduction burning; seed storage

climate change (the press) is therefore crucial to predict and quantify climate extremes (the pulses), which may tip ecosystems beyond survival thresholds.

The press. Even against a background of high natural variability, substantial changes to Australia's baseline climate are evident in sea surface temperatures (SSTs) and surface air temperatures (SATs) between the periods 1961–1988 and 1989–2015 (Fig. 2). These periods were selected to incorporate both positive and negative phases of Pacific decadal variability, minimizing the influence of natural variability on the differences between these periods and maximizing the likelihood of identifying anthropogenically induced changes.

There has been a distinct warming over the entire region, with temperatures during the recent period being on average 0.5 °C warmer than the earlier period (Fig. 2). Land warming is strongest over central-eastern Australia (a difference of ~0.75 °C), and weakest over the south-west (a difference of ~0.3 °C). Observed ocean warming is lower than land warming, but also displays a clear signal (0.4 °C warmer). This trend is evident in the temperature distributions for the south-eastern Australian case studies (Fig. 2d–f), although warming is weaker in the northern and western regions (Fig. 2a–c).

Changes in rainfall are dominated by seasonal and regional trends. Northern and central Australia have experienced increased rainfall in the wet season (October–March) since the 1970s[42]. This is reflected in the rainfall distributions for the Mangrove and Arid zone case studies (Fig. 2a,c), although these changes are not significant due to the influence of climate variability and the monsoon[40,43]. While the frequency of extreme rainfall has increased over much of the continent since 1900, the southeast and southwest regions are exceptions, displaying no significant change and a rainfall decrease respectively[40] (Fig. 2d–f). Cool season rainfall (April–September) has declined significantly over some regions, most notably southwest Western Australia and the southeast, attributed to a decline in rain-bearing systems at this time of year[33,44].

Mean sea-level rise for Australia between 1993 and 2009 was estimated at 3.1 ± 0.6 mm yr^{-1} and is projected to track global trends[45]. However, sea-level rise along the northern coastline is significantly higher than the continental mean, increasing by 4–8 mm yr^{-1}, and by 9 mm yr^{-1} in the Gulf of Carpentaria[45], the location of the mangrove dieback event (Fig. 2a).

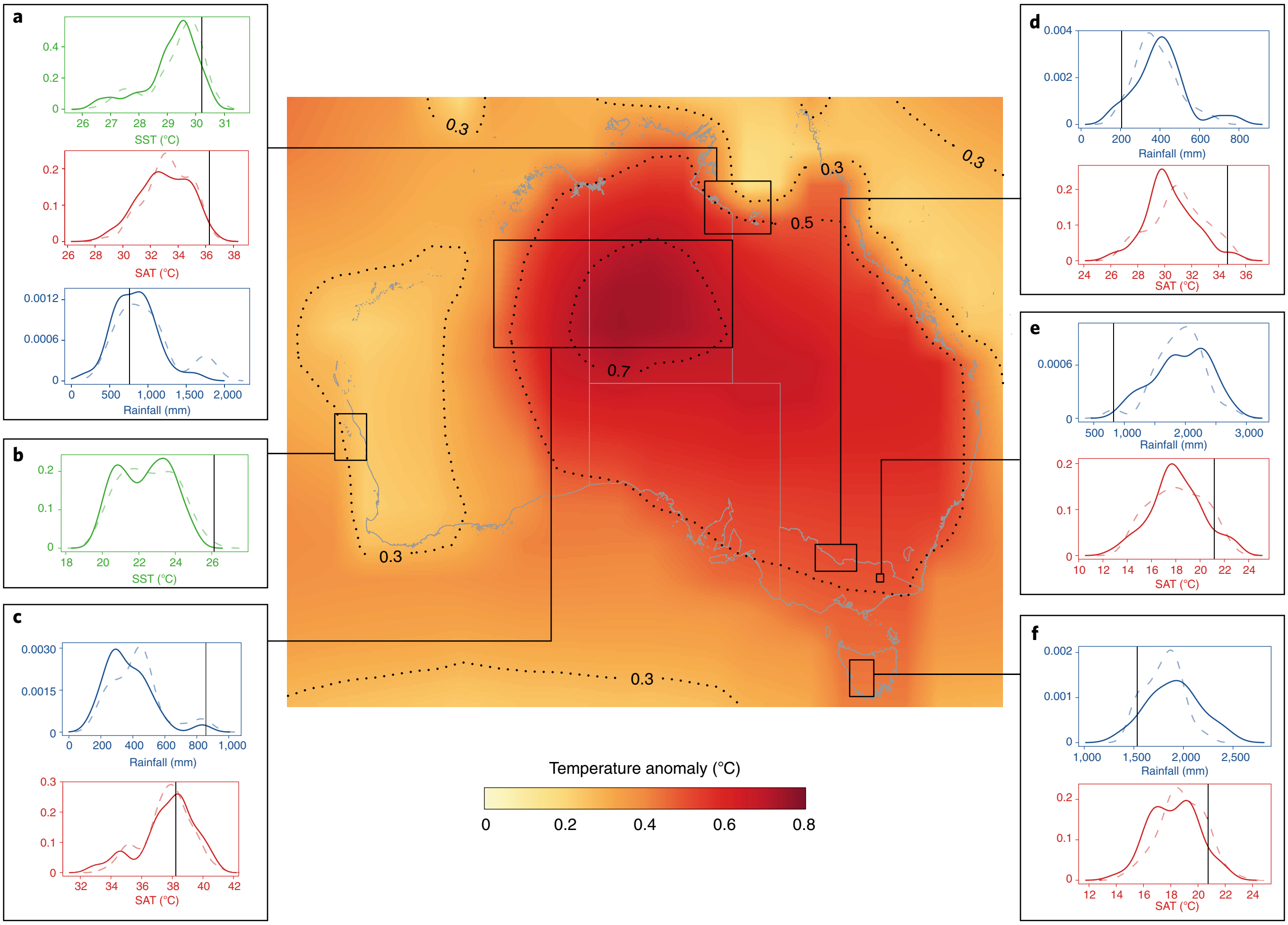

Fig. 2 | Case study locations overlaid on SAT and SST anomalies. The mapped temperature anomaly calculated between the press (1989–2015) and baseline (1961–1988) periods is shown in the main panel. Data from refs [91,92]. **a**–**f**, Case study pdfs of the climatological baseline (solid line), press (dashed line) and pulse (vertical line indicates climate conditions before the 'event' year(s) during which biological responses occurred for: 2015 (**a**), 2010–2011 (**b**), 2010–2011 (**c**), 2003–2009 (**d**), 2003, 2006, 2009, 2013, 2014 and 2016 (**e**) and 2015 (**f**). The meteorological data used to generate the pdfs are taken from the Australian Bureau of Meteorology's Australian Data Archive for Meteorology[93]. Seasonal boundaries used to calculate pdfs were as follows: northern wet season for Gulf mangroves (**a**; September–May SST, SAT, rainfall), arid zone (**b**; July–June rainfall; Dec–Jan SAT), marine heatwave (**c**; October–March SST); southern wet season and following summer SAT for riverine forest (**d**; May–October rainfall; summer (DJF) SAT), obligate forest (**e**) and Gondwanan refuge (**f**; January–December rain and summer (DJF) SAT).

The pulse. An extreme event is a weather event that is rare at a particular place and time of year[46]. Changes in extreme events can be assessed against the background of climate trends and variability using a range of extreme event indices and methods[14]. An extreme event may be described in terms of an absolute threshold, such as the number of days exceeding 35 °C (ref. [47]), but it is also frequently defined in relative terms. As organisms are adapted to local levels of climate variability, the magnitude of the deviation from the mean has the greatest biological impact[47]. Extreme events are therefore often operationally defined as falling within the 10th or 90th percentile of the probability density function (pdf) based on historical observations[46].

Relatively small shifts in the distribution of climate variables can result in major changes to the frequency and magnitude of extreme events. Additionally, changes in the shape, or variance, of the distribution may have a larger effect on the frequency of extremes than just a simple shift in the mean[14]. The shape and the tails (frequency of extreme values) of the rainfall distribution in northern and southeastern Australia (Fig. 2a–d) have both shifted in the recent period relative to the baseline considered here. In contrast, the tails of the temperature distribution do not show substantial changes (Fig. 2).

More generally, the intensity, frequency and duration of heatwaves have increased over Australia since 1950, although the magnitude of change is location-specific. Night-time temperatures are increasing faster than daytime temperatures[48,49], while record-breaking warm events are outnumbering record-breaking cold events 12 to 1[50]. Fire danger has increased over Australia as temperatures have risen, particularly in the south and east, with weather conditions conducive to extreme fire danger and the duration of the fire season increasing since the 1970s[51].

Several recent attribution studies have detected an increase in the likelihood of specific observed extreme temperature events in Australia due to anthropogenic climate change[52]. The 'angry summer' of 2013 was found to be six times more likely due to human influence on the climate[53], whereas the May heatwave of 2014 was found to be 23 times more likely[54]. In contrast, it is more difficult to determine the human influence behind recent Australian extreme rainfall events, because of the dominating influence of natural climate variability[55].

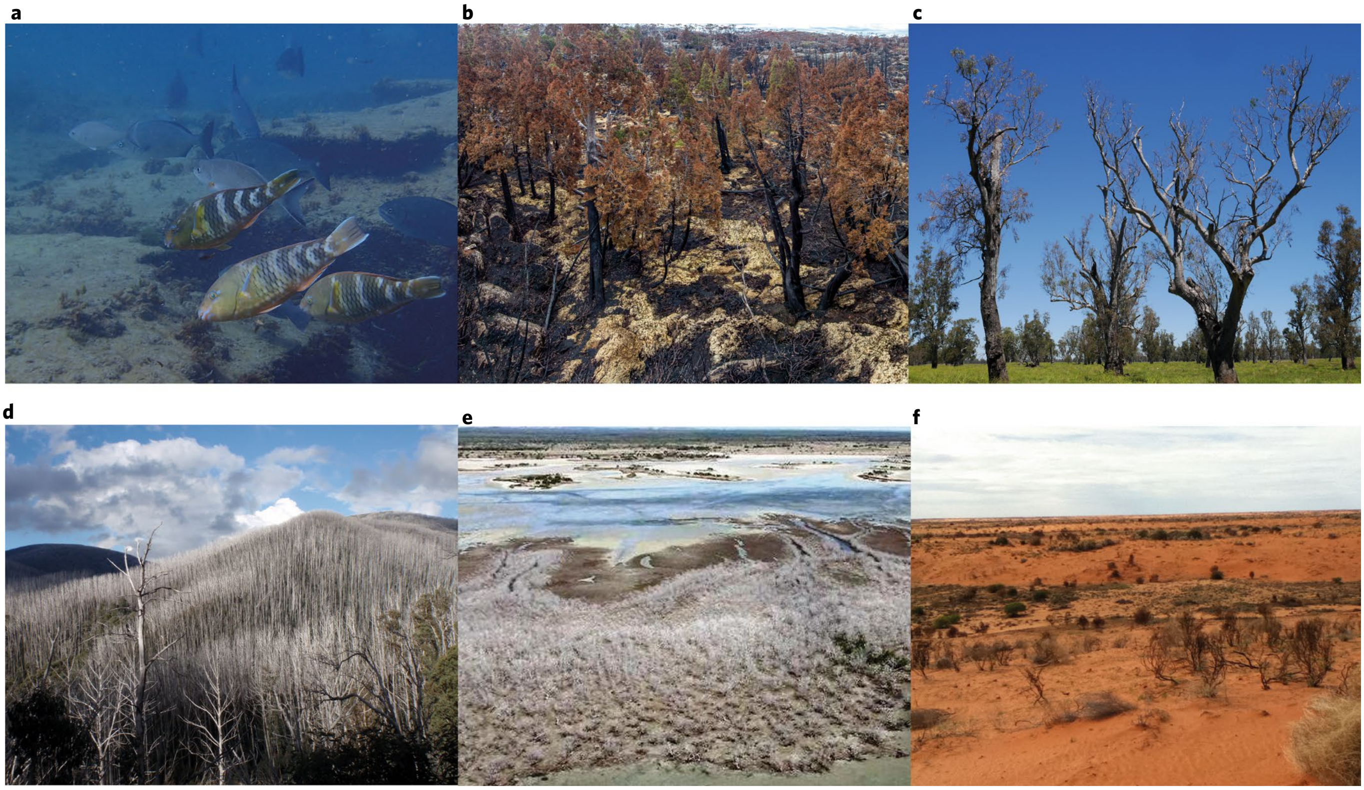

Fig. 3 | Extreme biological responses to extreme weather events. a, Kelp forests after the 2011 marine heatwave. **b**, The largest remaining palaeo-endemic pencil pine forest growing in sphagnum, killed by lightning-ignited fires in 2016. **c**, Dieback of floodplain forests during unprecedented drought from 2003–2009. **d**, Obligate seeder forest burnt three times resulting in the local extinction of *E. delegatensis* (taken in 2014). **e**, Mangrove dieback (taken in 2015). **f**, Aftermath of large-scale wildfires in the Strzelecki Desert in 2013 due to fuel accumulation following extreme rainfall events that were linked to the La Niña Phase of ENSO in 2010/2011. Credits: **a**, J. Costa and S. Bennett; **b**, R. Blakers; **f**, M. Letnic.

Australian case studies

Many Australian ecosystems are governed by, and have adapted to, interannual and interdecadal climate variability. Climate reconstructions from palaeo proxies show that extreme pulse events are not unprecedented[56–58], and extreme responses during periods of climate change in the Holocene have been documented[59]. However, internal variability is now superimposed on longer-term climate change[60]. As the interval between extreme events declines, negative impacts on biodiversity are increasing — even in systems that have adapted to extremes and high natural variability. We report six cases that have occurred since 2000, drawn from temperate marine, tropical intertidal, arid, temperate and montane terrestrial environments (Table 1, Fig. 3). These are not formal detection and attribution studies as defined by the IPCC[61] (the challenges of which are discussed elsewhere[22]), but were chosen to identify commonalities and differences in recent observed responses.

In each case the response is associated with identifiable climate presses and pulses (summarized in Table 1, see Supplementary Information for further details), and collectively they demonstrate how the ongoing press of climate change can lead to ecological catastrophe given climatic pulse events at critical periods (Fig. 2). Of the case studies reviewed, only one — the Riverine forest — has experienced previous anthropogenic impacts. The others have had negligible exposure to disturbance or other stressors, highlighting that undisturbed systems are not necessarily more resilient to climate change.

Against the backdrop of warming and precipitation change, the years in which three of the case study events occurred represented extreme values not previously seen in the observational record (mean annual SST: Western Australia marine heatwave, >99th percentile of baseline period; mean annual rainfall: Arid zone boom and bust and Obligate seeder forest collapse, >99th and <1st percentile of baseline period, respectively) (Fig. 2). The fires in the Gondwanan refuge occurred in a year that represented extreme values for both annual rainfall and maximum summer temperature (7th and 90th percentiles of baseline period, respectively).

The years during which the other case study events occurred (indicated by the vertical lines in Fig. 2) were at the upper end of natural variability, but not necessarily at the most extreme values. When seasonal values were considered, however, at least one important climate variable for each case study was within the highest or lowest 10th percentile, and thus represented 'pulse' events. For example, values for annual rainfall in the mangrove case study region were not extreme (37th percentile of baseline period), but SST for October to March was in the 92nd percentile, and maximum temperature for September to May was in the 98th percentile. Similarly, annual rainfall in the riverine forest decline study was in the 18th percentile for the baseline period, but March to October rainfall was in the 3rd percentile.

A single extreme event can be sufficient to cause irreversible regime shift or an ecosystem 'tipping point'[29]. For instance, the kelp forest regime shift off south-western Australia is clearly attributable to a single heatwave event superimposed on the press of increasing SSTs (Supplementary Section 1.1). Summer ocean temperatures between 2011 and 2013 were the hottest in over 140 years. The warmest year was 2011, with temperatures 2 and 5 °C above the long-term mean, extending over 2,000 km of coastline for more than 10 weeks[27,43]. This event led directly to mortality in kelp, abalone, coral, fish and lobster populations. Permanent range contraction of kelp forest resulted from competition with turf seaweeds and grazing by tropical fish species — patterns established during the heat wave.

Likewise, a single fire was sufficient to threaten the core refugia of the endemic Gondwanan conifer, *Athrotaxis cupressoides*, which is restricted to environments in which fire is historically rare (Supplementary Section 1.2). However, in this case, the increasing press of a changing climate resulted in the emergence of novel pulse events. Background warming and drying has created soil and vegetation conditions that are conducive to fires being ignited by lightning storms in regions that have rarely experienced fire over the last few millennia. This pulse fire event led to the loss of ancient conifer communities and the destruction of organic soils that are unlikely to redevelop under future drier and warmer conditions.

In other cases, a single extreme event is only sufficient to tip the ecosystem over the edge when gradual declines in populations have already occurred. Declines in the health of riverine forest across the southern Murray Darling Basin occurred under the ongoing presses of decreased river flows and groundwater levels due to water extraction, declining rainfall and increasing surface air temperatures. However, severe mortality followed the combined pulses of acute drought and more intense heatwaves in 2002–2003 and 2007–2008, resulting in dieback across 70% of the forest (Supplementary Section 1.3).

An increased frequency of extreme events can also lead to population collapse if the population does not have sufficient time to recover before the event recurs[28]. Multiple wildfires in short succession, resulting from increased dangerous fire weather, have resulted in localized conversion of obligate seeder *Eucalyptus delegatensis* forest to shrubland in the Australian Alps, a process that potentially threatens the entire species' range (Supplementary Section 1.4).

However, not all examples are clearly attributable to a single climate event, or series of events, and are most probably caused by multiple interacting climate presses and pulses. Extensive mangrove dieback in Northern Australia followed a warm period in 2015–2016, when SSTs and air temperatures exceeded the 95th percentile of temperature data since 1910 (Supplementary Section 1.5). In isolation, this event cannot explain such an extreme biological response, even in concert with the background presses of increasing temperatures. The pulse was twofold. First, weak monsoons led to below average rainfall and low cloud cover, resulting in high radiation levels, high air temperatures, extreme vapour pressure deficits and high evaporation rates. Second, a 20 cm drop in sea level across the Gulf of Carpentaria in October 2015, driven by weak equatorial trade winds associated with a strong El Niño event[62,63], is likely to have caused hypersalinization of mangrove sediments. Together, these factors imposed sufficient hydric, thermal and radiant stresses to cause the near-complete mortality of mature mangroves along 1,000 km of coastline[64].

Finally, extreme biological responses do not always manifest through impacts on the dominant species. Cascading interactions and feedbacks can trigger ecosystem-wide responses to extreme events, as in the arid zone case study (Supplementary Section 1.6). In 2010, extreme rainfall triggered rapid plant growth, resulting in rodent plagues that in turn led to ` of introduced predators (such as feral cats). Additionally, extremes of heat, drought and flooding cycles alter fire regimes, vegetation cover and species interactions in arid zones, exceeding fundamental physiological thresholds and transforming ecosystems.

A future of stronger presses and pulses

The strength of all influential presses and pulses are projected to increase across Australia through the century, regardless of the emissions scenario followed. Average temperature is projected to increase by up to 5 °C under a high emissions scenario by 2100[40]. The frequency and intensity of extreme temperatures are projected to increase, with up to 50% more warm nights[48], and between 10 (southern Australia) and 50 (northern Australia) more heatwave days annually[65]. Daily maximum and minimum temperatures are projected to increase similarly to the mean, whereas heatwave intensity will increase the most over central southern Australia[40,65].

Projections of average rainfall across Australia are mixed. Model projections differ regarding increases or decreases in annual rainfall, yet there is general agreement that the frequency and intensity of extreme rainfall will increase[40,48,66]. One-day events are projected to increase in intensity by 5–40%, with very extreme events occurring up to twice as often by 2100[40].

Fire danger is projected to continue increasing under warmer, drier conditions[67–69]. By 2090, the number of severe fire danger days may increase by 160–190% across eastern Australia and south-east Queensland[40]. Projections are less clear for inland arid areas, where fire danger is determined by fuel availability linked to episodic rainfall. There are no clear indications that atmospheric instability conducive to lightning will increase in the future[70], but more frequent ignitions are expected with drier soils.

Although changes to El Niño/South Oscillation (ENSO)-driven pulses may have already emerged[71–73], current research suggests that ENSO is unlikely to change significantly in the future[71]. However, the atmospheric impact of ENSO events is expected to increase[74] as changes in the background state of the Pacific Ocean allow the meridional collapse of the regions' rainbands onto the equator[75]. This means that the climatic pulses associated with ENSO events in the future may be larger than those of an event of the same magnitude now.

Implications for conservation management

We have focused on six case studies, but there are myriad examples from around the world of recent extreme biotic responses to extreme events (for example, mass mortality of sea fans in the Ligurian Sea after repeated extreme SST events, altering the benthic trophic food web[76]; forest collapse across California[77]). These recent examples suggest that future responses to extreme events will be taxonomically and geographically idiosyncratic[78] and, consequently, difficult to predict. Nevertheless, understanding how pulse and press events interact to drive abrupt ecological change may (1) improve detection of climate change impacts on biological systems; (2) improve our theoretical understanding of how ecological processes respond and communities change in response to climate change and (3) promote better mitigation and adaptation strategies. We have described shifts in ecosystem state with a focus on structurally dominant plant taxa, but the press–pulse framework is equally applicable to populations or species belonging to any taxonomic group.

Although the temporal context of the press–pulse framework will vary across different ecosystems, extreme biological responses are likely to be characterized by abrupt ecological changes and long recovery times. As the frequency of extreme events increases, the return interval between events may prevent recovery occurring, even with substantial intervention. Pulse events result in strong ecosystem responses over short response times, which can be highly nonlinear when compared with responses to a climatic press[79]. Pulses may also induce lag and legacy effects in ecosystem processes[80]. Management success will therefore be influenced by the timescale at which impacts are manifest and recovery occurs.

Considering the impact of pulse events in the context of climate presses can help to identify when and where management intervention might be necessary and most likely to succeed. In some cases, proactive intervention after an extreme event may prevent system collapse or mitigate the impact of the next extreme event. Fire-killed regeneration in Alpine Ash forest has been re-established by the aerial sowing of seed[81], for example, although it is expensive, dependant on seed availability and long-term establishment will be compromised by subsequent fires and reduced growth rates[28]. In other instances, however, management responses will be limited because the ecosystems are too remote, intervention would be too expensive, or success would be low (for example, replanting mangroves in the Gulf of Carpentaria). Such cases highlight the importance of landscape-scale conservation to reduce habitat loss and fragmentation and to bolster system resilience. We have shown that relatively undisturbed environments are not immune to the impacts of extreme events. However, the more natural habitat that is retained, the greater the chance that some areas will not be affected by a localized extreme event. Populations from unaffected areas are important sources of seeds and populations for dispersal or translocation, improving rates of recolonization and genetic diversity following an extreme biological response.

Management may be improved by identifying the important climate presses. Although many presses, such as sea-level rise, ocean acidification and warming temperatures, are outside the influence of management, the impacts of others may be minimized. For example, reducing nutrient loads and water extraction could mitigate the impact of drought and extreme heat events in marine and riverine environments. Similarly, hazard-reduction burning and the construction of firebreaks to exclude fire from fire-sensitive communities can help to reduce the impacts of extreme fire weather events.

It is widely accepted that the effective management of climate-related risks requires robust quantification of the likelihood of extreme events under current and future conditions[82]. However, the interacting effects of climate presses and pulses challenge our ability to quantify the probability of biological responses to extreme events, and limit our ability to predict or mitigate them. A key lesson of the case studies considered here is that management may not always be successful, particularly as the frequency of extreme events increases. Our ability to predict ecological responses could still be improved in several ways, however.

Ecosystem models, which are currently calibrated for equilibrium conditions, would be greatly improved by incorporating a better mechanistic understanding of the impacts and responses to interacting climate presses and pulses. Recent advances in remote sensing and instrumental networks for monitoring environmental conditions at increasing spatial and temporal resolutions should substantially improve our ability to capture and understand pulse events[83]. Greater comprehension of adaptive capacity (genetic, behavioural and phenotypic plasticity) and physiological tolerances of taxa would also improve our ability to identify the most vulnerable species and systems[84]. Better mechanistic knowledge of 'keystone' or 'habitat-forming' species is foundational to forecasting community-level responses to both presses and pulses. Deeper insight into large-scale plant propagation, captive breeding and (re)introductions is a prerequisite to improving the success of management actions such as assisted migration, translocation and rehabilitation.

Improved understanding of the changes in circulation, of the modes of variability and the teleconnections that lead to extreme weather events would improve the predictability of these events, which could be used as trigger points for management intervention. Extreme heatwaves, for example, are often associated with persistent blocking high-pressure systems[83]. Intervention could be targeted to respond to forecasted heat events — as is done by providing water to fruit bat colonies in an attempt to avert mass mortality[85], for example. Similarly, better understanding of antecedent conditions that increase the severity or impact of an extreme event (preconditioning)[83] could inform management. The relationship between winter rainfall, spring plant growth and higher fuel loads is a well-known example of this, but the links between other antecedent climate conditions are not well known. More extensive collaborations between climate scientists and ecologists would advance the application of such knowledge, resulting in improved climate–biodiversity adaptation strategies.

Long-term monitoring strategies in Australia and around the world have been far from adequate, but they are crucial if we are to understand the responses of these complex ecosystems to environmental stress[86]. The initiation of monitoring programmes following an extreme event is essential, to improve knowledge of underlying mechanisms, enable us to interpret these events and anticipate future events. This requires robust, long-term biological monitoring programmes with effective data storage and data sharing strategies. 'Before and after' monitoring is rarely possible, but better spatial controls could provide biological data for comparison from areas that did not experience the extreme event, and could also enable other important, non-climatic drivers to be identified[87]. Hypothesis-driven experiments should support observational studies to identify the mechanisms driving a response and establish casual relationships[87,88]. Although formal attribution of biological responses to climate change remains challenging[22], meta-analyses[89], in combination with observations, experiments, remote sensing and climate model output at increasingly fine resolutions, are likely to advance the field in the short term[83]. The press–pulse framework provides a useful organizing principle for such monitoring.

The interacting effects of climate presses and pulses suggest that management approaches will need to adapt in the future. Many interventions involve practices that remain controversial and for which there are few policy guidelines. Assisted colonizations, for example, or the translocation of warm-adapted genotypes, are not widely accepted practices[90]. The feasibility of other actions may be limited by economic costs, difficulties in accessing remote locations, or the spatial extent of the event. Management interventions will increasingly need to be decided on quickly and without full understanding of the ecological and evolutionary consequences. Focused consideration and planning, cross-disciplinary dialogues and the involvement of management practitioners and policymakers are all needed for successful mitigation strategies. The development of these strategies will require a considered debate about what natural values we desire, what a 'natural', 'pristine' or novel system is, and when active intervention is socially acceptable. The risk of non-intervention may outweigh the risk of intervention more often in the future.

Conclusions

The recent global constellation of extreme biotic responses suggests that many ecosystems are vulnerable to state change, and undisturbed systems are not immune. Even if global warming is limited to an average of 2 °C, recent events suggest that increased extreme events will have unprecedented effects on biota. Climatic presses and pulses are already causing complex and catastrophic responses, leading to population collapse, loss of relictual communities and shifts into novel ecosystems. Such extreme responses call for greater policy and philosophical fluidity in conservation management, greater capacity and appetite for interventions, and detailed documentation of the consequences of interventions.

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Author contributions

R.M.B.H. and D.M.J.S.B. conceived the study, with input from all authors. R.M.B.H. led the writing. M. L. suggested the application of the Press-Pulse framework in this context. All authors contributed to the formulation of the paper and contributed to the first manuscript draft and subsequent revisions. T.A.R. created Fig. 1. T.V. created Fig. 2, based on data and analyses contributed by C.T., S.E.P-K, S.M., P.J.M. and T.A.R. L.J.B and R.M.B.H. created Fig. 3 and compiled the Supplementary Material. P.J.M., D.M.J.S.B. and N.D.C. contributed images to Fig. 3. R.M.B.H., L.J.B., N.R.A. and A.B.N. wrote the Introduction and Discussion. T.V. led the writing of the Climate drivers section, with contributions from C.T., S.E.P-K, R.M.B.H., S.M. and P.J.M. D.M.J.S.B. led the writing of the obligate seeder forest collapse and fire in Gondwanan refugia case studies, with analyses contributed by G.W. M.F. contributed to the fire in Gondwanan refugia case study. L.B.H. led the writing of the mangrove dieback case study, with contributions from N.C.D. T.W. and L.E.C. wrote the kelp forest regime shift case study. M.L. and M.K. wrote the arid zone boom and bust case study. P.J.M. and C.W. wrote the riverine forest decline case study.

Competing interests

The authors declare no competing interests.

Additional information

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