





# Conservation implications of ecological responses to extreme weather and climate events

Sean L. Maxwell<sup>1</sup>  | Nathalie Butt<sup>2</sup>  | Martine Maron<sup>1</sup>  | Clive A. McAlpine<sup>1</sup> | Sarah Chapman<sup>1</sup>  | Ailish Ullmann<sup>3</sup> | Dan B. Segan<sup>4</sup> | James E. M. Watson<sup>1,5</sup> 

<sup>1</sup>School of Earth and Environmental Sciences, The University of Queensland, Brisbane, Queensland, Australia

<sup>2</sup>School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia

<sup>3</sup>Dana and David Dornsife College of Letters, Arts, and Sciences, University of Southern California, Los Angeles, California

<sup>4</sup>Tahoe Regional Planning Agency, Stateline, Nevada

<sup>5</sup>Wildlife Conservation Society, Global Conservation Program, Bronx, New York

## Correspondence

Sean L. Maxwell, School of Earth and Environmental Sciences, The University of Queensland, Brisbane, Qld, Australia.  
Email: smaxwell@uq.edu.au

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## Abstract

**Aim:** Many conservation efforts now focus on mitigating biodiversity loss due to climate change. While a focus on impacts from mean, long-term changes in climate is warranted, the vast majority of conservation plans largely ignore another key factor of climate change—changes in the frequency and intensity of extreme weather and climate events. A typology of the full range and severity of ecological responses to extreme events would help underpin tracking of their impacts.

**Location:** Global.

**Methods:** Here, we review 519 observational studies of ecological responses to extreme events between 1941 and 2015. We include responses from amphibians, birds, fish, invertebrates, mammals, plants and reptiles to cyclones, drought, flood, cold waves and heat waves.

**Results:** Negative ecological responses were the most commonly reported, accounting for 57% of all documented responses. There were over 100 cases of a >25% population decline and 31 cases of local extirpation. Sixty per cent of the studies in our review observed ecological responses for more than 1 year, and of the studies that monitored species or ecosystem recovery following exposure to an extreme event, 38% showed species or ecosystems did not recover to pre-disturbance levels.

**Main conclusions:** Extreme weather and climate events have profound implications for species and ecosystem management. We discuss current conceptual challenges associated with incorporating extreme events into conservation planning efforts, which include how to quantify species sensitivity and adaptive capacity to extreme events, how to account for interactions between extreme events and other stressors, and how to maximize adaptive capacity to more frequent and intense extreme events.

## KEYWORDS

adaptation plan, climate change, cyclone, drought, impact, vulnerability assessment

## 1 | INTRODUCTION

Understanding what makes species and ecosystems vulnerable to climate change has become integral to the field of conservation science. To date, climate change vulnerability assessments have predominantly focused on how species and ecosystems will respond to mean, long-term changes in climate (Chapman et al., 2014; Jones, Watson, Possingham, & Klein, 2016), including regional warming (van Gils et al., 2016), seasonal shifts (Asch, 2015) and sea level rise (Runting, Wilson, & Rhodes, 2013). This focus has improved our overall understanding of how climate change is shaping the environment (Scheffers et al., 2016) but has left many conservation plans unprepared for changes in the frequency and distribution of extreme weather and climate events (Chapman et al., 2014; Jones et al., 2016). Moreover, it is increasingly recognized that changes in climate extremes can have greater environmental consequences than changes in climate means (Bailey & van de Pol, 2016; Gutschick & BassiriRad, 2003; Harris et al., 2018; Maron, McAlpine, Watson, Maxwell, & Barnard, 2015; Vasseur et al., 2014).

Extreme weather and climate events (weather or climate events that are rare within their statistical reference distributions at a particular place (IPCC, 2014); herein “extreme events”), such as cyclones, floods, heat waves and drought, have become more frequent and intense in many regions of the world as a consequence of anthropogenic climate change (Seneviratne et al., 2012; Ummenhofer & Meehl, 2017). This pattern is likely to accelerate. For example, increases in daily temperature and precipitation extremes are likely to continue, more extreme rainfall is expected in southern Africa, increased drought intensity is expected in central America, north-east Brazil and the Mediterranean, and drought and heat waves are expected to become more frequent in Australia, northern Africa and south-western America (Handmer et al., 2012; Pohl, Macron, & Monerie, 2017; Russo, Marchese, Sillmann, & Imme, 2016; Seneviratne et al., 2012).

Our knowledge of ecological responses to extreme climate stress is predominantly based on laboratory or field experiments (Bailey & van de Pol, 2016; Hoffmann & Parsons, 1997). Fundamental ecological insights gleaned from such studies, including thermal tolerance of a species or tipping point for an ecosystem, can potentially aid in the design of effective conservation interventions. However, the utility of experimental studies for conservation intervention design is limited, because experimental studies rarely replicate the variable and highly nuanced bioclimatic conditions species face in unmodified ecological systems (Chevin & Hoffmann, 2017).

Observational studies of species' or ecosystems' responses to extreme events can highlight particular events or taxonomic groups that may benefit from focused vulnerability research (Altwegg, Visser, Bailey, & Erni, 2017; Smith, 2011). Some dramatic ecological responses to extreme events have been observed across individual, population and ecosystem scales. For example, cyclones can alter the onset of sexual maturity in turtles (Dodd & Dresliik, 2008), prolonged droughts have caused population collapse in koalas (Seabrook et al., 2011), flooding can reduce plant

species richness (Miller, Gornish, & Buckley, 2010), and heat waves can alter the structure of marine ecosystems (Wernberg et al., 2013).

Previous reviews of observed responses to extreme events in ecological systems have focused on a specific taxonomic group (Orsenigo, Mondoni, Rossi, & Abeli, 2014; van de Pol et al., 2010), extreme event (Cech & Cech, 2013; Lugo, 2008), or set of responses (Moreno & Moller, 2011), or indicate potential responses to extreme events without quantifying the magnitude of the impacts over time (Bailey & van de Pol, 2016; Easterling et al., 2000; Jiguet, Brotons, & Devictor, 2011; Parmesan, Root, & Willig, 2000). To our knowledge, there has been no formal review and categorization of the full range of observed responses to extreme events in ecological systems, which could be used to inform effective conservation strategies.

Here, we categorize and quantify observed ecological responses to extreme events. We build on the existing literature by reviewing studies spanning 70 years of how seven taxonomic groups (birds, mammals, fish, amphibians, reptiles, invertebrates and plants) have responded to five types of extreme event (drought, cyclones/hurricanes/typhoons, floods/storm surges, heat waves, and cold waves/extreme winters/ice storms). We also collected information on study duration and whether studies report on species or system recovery following exposure to an extreme event. We discuss future research needs and conceptual challenges associated with incorporating extreme events into conservation vulnerability assessments and adaptation plans.

## 2 | METHODS

We performed a literature search in the ISI Web of Science database in July, 2015 and included all literature published prior to that date. Key search terms were set according to a “taxon” AND “event” structure and changed iteratively until all combinations of taxa and event included in our review were searched. Additional search terms were used to better refine search results (see Supporting Information Table S1). Search results ( $n = 4,896$ ) were screened for our inclusion criteria: (a) an observational study; (b) from peer-reviewed literature published in a national or international journal; and (c) documenting an ecological response during, or in the years following an extreme event. Studies reporting on responses to seasonal flooding (e.g., in the Brazilian Pantanal) or non-climate-induced flooding events (e.g., dam decommission) were excluded, as were studies of commercially farmed or produced species.

We read studies that met our inclusion criteria ( $n = 584$ ), and recorded the documented ecological response, the focal species (if applicable), the ecosystem in which the response was studied, whether responses were observed across multiple years, and whether studies were designed to monitor species or ecosystem recovery following exposure to an extreme event. After initial review, 65 studies were excluded because they did not meet the inclusion criteria, which left 519 studies for review (see Supporting Information Table S2 for the complete list of studies). There were 205 journals represented in our

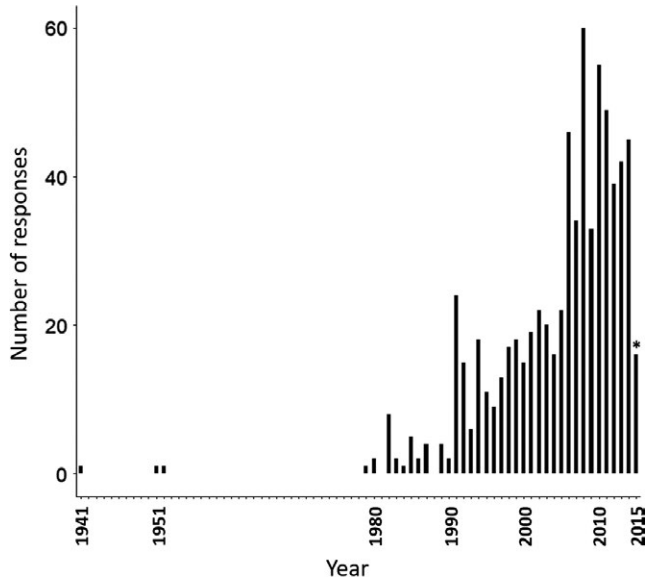
**TABLE 1** Description of 19 alternative ecological responses to extreme events that have observed in ecological systems between 1941 and July, 2015

Response	Description
<b>Positive</b>	
Improved body condition	Increase in biomass or growth. Increase in per cent canopy cover or leaf production. Lower rates of mortality
Increase in species richness	Increase in the number of species inhabiting an area
Increased fecundity	Decline in nest predation. Increase in nestling success or seed production
Population increase	Any increase in estimate population abundance or density
<b>Ambiguous</b>	
Change in behaviour	Change in diet, foraging behaviour, reproductive strategy or migratory behaviour
Change in phenology	Temporal shifts in flowering or breeding
Change in social organization	Change in social hierarchy or interactions
Change in species composition	Change in the range of species inhabiting an area
Change in morphology or physiology	Change in morphology or development. Morphological abnormalities
Change in occupied range	Increase or shift in the area occupied by a species
<b>Negative</b>	
Decline in body condition	Decline in biomass or productivity. Structural damage (including uprooting, loss of stem density, loss of basal area and increased herbivory). Desiccation. Increased stress levels or reduced immune function
Decline in fecundity	Destruction of breeding sites. Decline in recruitment or breeding attempts
Decline in species richness	Decline in the number of species inhabiting an area
Habitat loss	Loss of habitat or decline in area occupied by species
Increased mortality	Increased rates of predation. Decline in adult or juvenile survival
Local extirpation	Complete loss of population from a study area after an extreme event occurred, and had not re-established by the end of the study
Population decline <25%	Decline in estimated population abundance of less than 25%, or any unspecified per cent loss in population abundance
Population decline >25%	Decline in estimated population abundance of greater than 25%
Little impact	Rapid recovery or no response following exposure to extreme event

review, with *Biotropica*, *Ecology* and *Hydrobiologia* the dominant journals (12.8% of responses collectively).

Similar ecological responses to extreme events were grouped together and categorized (Table 1). Responses were further classified as being positive, neutral, negative or ambiguous, where ambiguous responses were those that could imply adaptation or maladaptation

to an extreme event. Extreme events with similar definitions were grouped into a single category (i.e., cyclones, hurricanes and typhoons; floods and storm surges; and cold waves, extreme winters and ice storms). Many studies documented more than one ecological response. As such, our review includes more responses ( $n = 698$ ) than studies ( $n = 519$ ; Figure 1).



**FIGURE 1** The number of ecological responses to extreme events (cyclones, drought, floods, heat waves and cold waves) documented in peer-reviewed literature between 1941 and July, 2015 (\* denotes that responses in 2015 were reviewed till July only)

### 3 | RESULTS

Our review revealed nineteen different types of responses (hereafter, response categories) (Table 2; Supporting Information Table S3). Four of these response categories were positive responses, six were ambiguous, eight were negative, and one category included cases where little or no response to an extreme event was observed. Plants were the most commonly studied taxonomic group (number of responses,  $n = 189$ ), followed by birds (143), invertebrates (123), fish (97), mammals (93), reptiles (27) and amphibians (26) (Figure 2). Responses were most commonly observed in terrestrial (385) and freshwater (140) ecosystems. Marine (48), coastal (40), riparian (32), estuarine (28) and wetland (25) ecosystems shared similar

numbers of observed responses (Figure 3; Supporting Information Table S4).

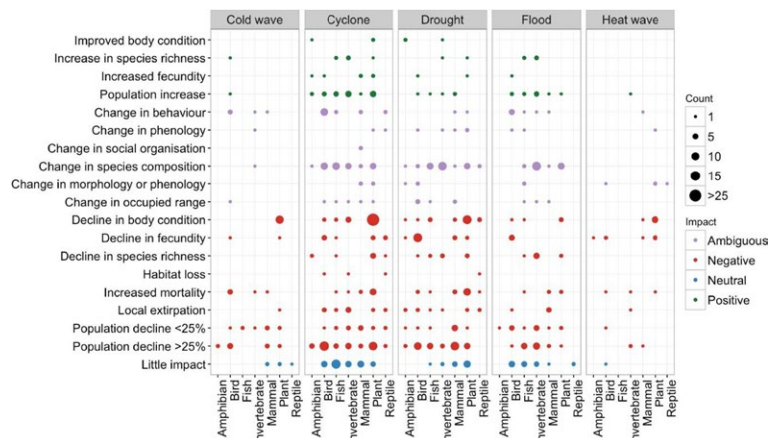
Sixty per cent of the studies in our review observed ecological responses for more than one year ( $n = 416$ ). Studies that focused on drought, cold waves and floods generally spanned more than 1 year, whereas more than half of cyclone and heat wave studies were completed within 1 year (Supporting Information Table S5). We found no discernible differences in the type or frequency of responses to extreme events observed from studies carried out within 1 year compared to studies carried out across multiple years (Supporting Information Table S6).

Only 40% of studies monitored species or ecosystem recovery following exposure to an extreme event (Supporting Information Table S7). Of these studies, 38% showed species or ecosystems that did not recover to pre-disturbance levels after extreme event exposure, while full or partial recovery was observed in 62% of cases. Recovery usually occurred within 2 years, but in some cases, species or ecosystems took over 10 years to recover fully to pre-disturbance levels (Supporting Information Table S7).

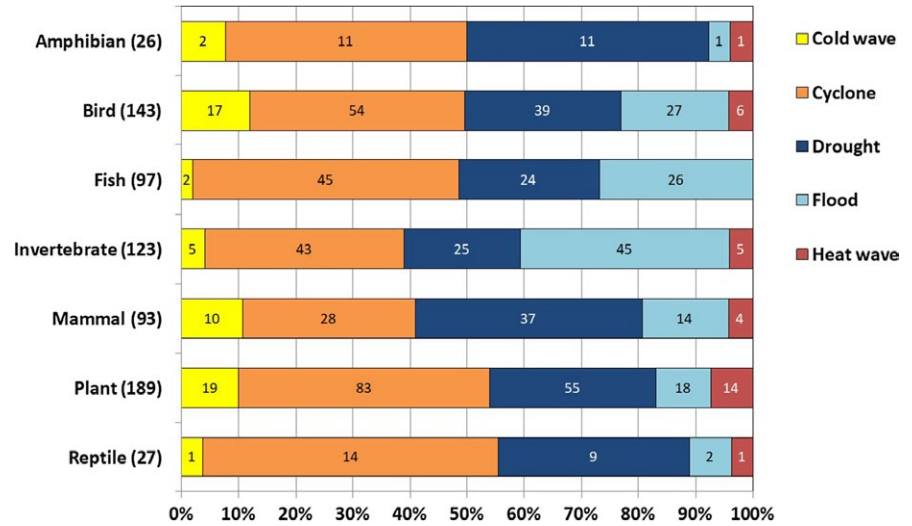
Negative ecological responses were the most commonly reported, accounting for 57% of all documented responses ( $n = 395$ ; Figure 4). There were 31 cases of local extirpation, and of the 18 cases where recovery was assessed, 12 cases of local extirpation were found to be persistent. There were four cases of mammal populations becoming locally extinct after a flood event, and five cases of invertebrate populations becoming locally extinct following a cyclone. There were 117 cases of >25% population decline following an extreme event—the most frequently documented ecological response. The majority of these responses were documented after a cyclone or drought ( $n = 46$  and  $n = 38$ , respectively). There were also 44 cases of fecundity declines and 27 cases of species richness declines following an extreme event.

Ambiguous ecological responses, in which it was unclear whether the changes were positive or negative, were the second most prevalent response documented by the studies ( $n = 159$ , 23%). Change

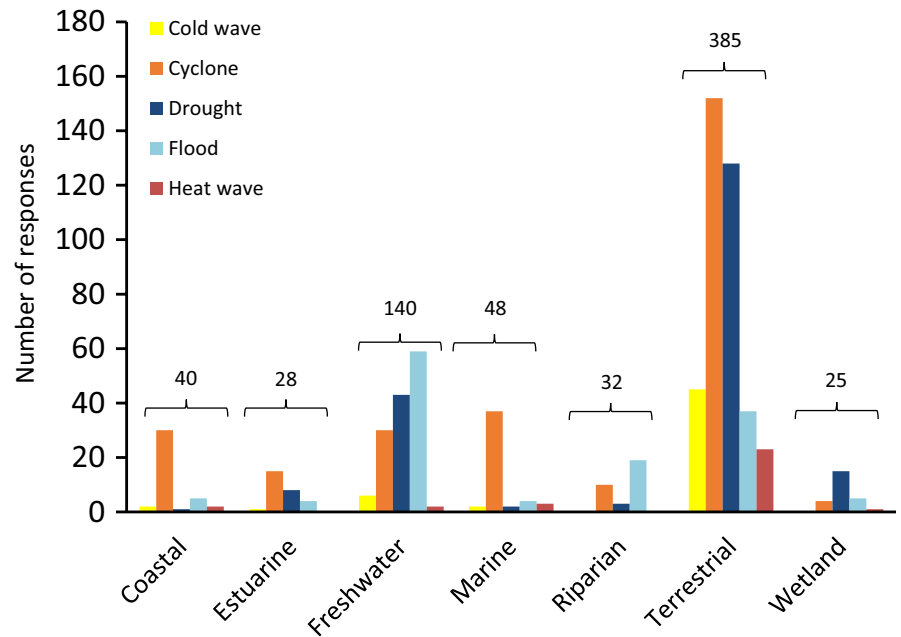
**TABLE 2** Categorization and quantification of ecological responses to extreme events that were observed in ecological systems between 1941 and July, 2015. The review synthesizes 534 observational studies from 205 different journals



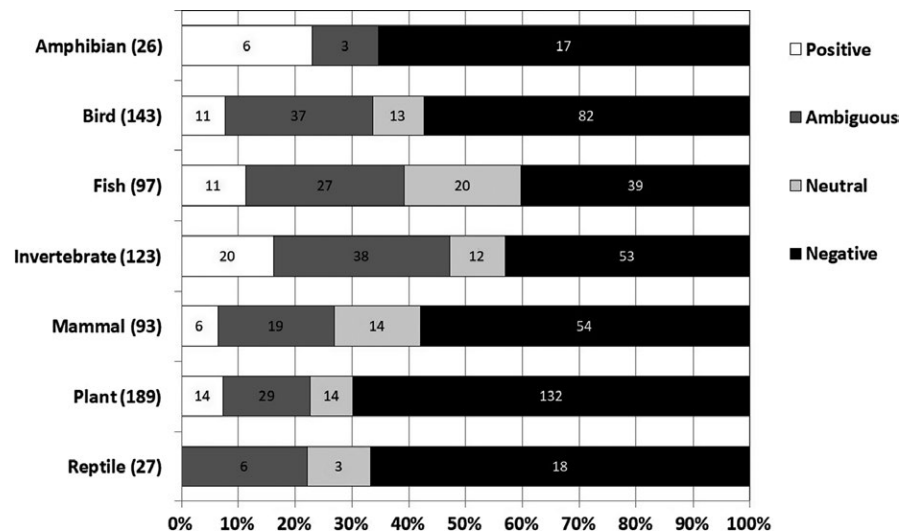
**FIGURE 2** The relative prevalence of cyclones, drought, flood, cold waves and heat waves to species and ecosystem responses to extreme events observed between 1941 and July, 2015. Bracketed numbers beside taxon labels represent the total number of observed responses to extreme events for each taxon. The values in bars represent the total number of observed responses per extreme event documented for each taxon



**FIGURE 3** Number of ecological responses to extreme events observed in different ecosystems between 1941 and July, 2015. Numbers above brackets represent the total number of observed responses in each ecosystem



**FIGURE 4** The relative contribution of positive, ambiguous, neutral and negative responses to extreme events observed between 1941 and July, 2015. Bracketed number beside taxon labels represent the total number of observed responses to extreme events for each taxon. The values in bars represent the total number of responses per impact type documented for each taxon



in species composition was the most prevalent ambiguous response ( $n = 87$ ), with changes in invertebrate communities accounting for 32% of these responses ( $n = 28$ ). Of the 44 responses monitored for recovery following an extreme event, 18 studies showed persistent compositional change. We identified 76 cases of little-to-no ecological response following an extreme event.

Positive responses to extreme events were the least frequent of all impact categories ( $n = 68$ ). Over half of these positive responses were population increases ( $n = 39$ ), which primarily followed a cyclone or flood event. There were very few positive responses to cold waves ( $n = 2$ ) and heat waves ( $n = 1$ ), and no positive reptilian responses to any extreme event.

Cyclones were the most prevalent extreme event for birds, fish, plants and reptiles. Among these taxa, reptiles seem to be particularly responsive to cyclones ( $n = 14$ , 52% of all reptile responses to extreme events), with the majority of these responses being negative ( $n = 11$ , 79%). Cyclones also led to 15 cases of a >25% population decline in bird populations (58% of all negative bird responses to cyclones). There were 27 cases of plants declining in body condition following a cyclone, with eight of these responses persisting long after the event.

Mammals and amphibians were most responsive to drought events, with drought leading to 12 cases of >25% population decline in mammals. Drought events also led to 13 cases of fecundity declines in bird populations and 12 cases of compositional change in invertebrate communities. Invertebrates had the most recorded responses to flooding events ( $n = 45$ ), yet these responses included negative ( $n = 19$ ), ambiguous ( $n = 15$ ), neutral ( $n = 4$ ) and positive ( $n = 7$ ) responses. Cold waves, extreme winters and ice storms accounted for around 11% of impacts on birds and mammals and around 7% of impacts on amphibians. There were no documented fish responses to heat waves. For all other taxa, heat waves accounted for around 4% of responses, except plants, for which heat waves accounted for around 7% of responses.

## 4 | DISCUSSION

Collectively, the studies in our review suggest that extreme weather and climate events have profound implications for species and ecosystem management. Ecological responses were observed across all ecological levels, from individuals to ecosystems, and over half were found to be negative. Some of the more severe negative responses identified in our review were prevalent and persisted long after an extreme event. There were, for example, over 100 cases of a >25% population decline and 31 cases of local extirpation of a species. The numerous declines in fecundity and species richness documented further justify the inclusion of extreme event impacts in conservation planning frameworks.

Plant species had the highest proportion of negative responses to extreme events (70%). Many of these involved structural damage (e.g., uprooting, loss of stem density, increased herbivory) following cyclones—which in many cases would be impermanent—but there were also numerous cases of plant communities suffering increased

mortality rates and reduced species diversity following a cyclone. Reptile and amphibian species also had a high proportion of negative responses to extreme events (both 67%). Declines in fecundity after cyclones and reduced body condition following drought were prevalent in reptilian species, while populations of amphibian species suffered large declines following cyclone events. Species located in coastal ecosystems had the highest proportion of negative responses (65%), which included fecundity declines and population declines of >25% following cyclones. Large population declines following drought events were also numerous in terrestrial ecosystems.

Many of the studies we reviewed observed ecological responses for <1 year and did not monitor species or ecosystem recovery following extreme event exposure. This constrains our understanding of how changing patterns of extreme events may impact species over the coming decades. Many long-term studies reveal how extreme events can drive drastic changes in ecosystem structure and fundamental shifts in key life history stages of some species. For example, the intensification of extreme flooding events since the turn of the century reduced the biomass and species richness of macrobenthic communities in the Mondego estuary in Portugal (Cardoso, Raffaelli, Lillebo, Verdelhos, & Pardal, 2008). In another example, one major flood event resulted in rapid, wholesale reorganization of a desert rodent community in Portal, Arizona (Thibault & Brown, 2008). Over a 30-year period, drought intensity led cliff swallows (*Petrochelidon pyrrhonota*)—a long-distance migrant bird—to initiate breeding colonies earlier in warmer and drier years (Brown & Brown, 2014). Finally, drought and increasing temperatures in Yellowstone National Park over the last decade caused drastic reductions in wetland habitat and subsequently reduced amphibian species diversity and abundance (McMenamin, Hadly, & Wright, 2008).

While widespread ecological changes following extreme events may prove to be lasting or even irreversible (Harris et al., 2018; Pisaric et al., 2011), long-term observational studies also provide valuable insights into how ecosystems can recover following an extreme event (Capon et al., 2015). For example, near Glacier Bay, Alaska, the density of pink salmon (*Oncorhynchus gorbuscha*) decreased by 90% following a major rainfall event that caused substantial geomorphic change to stream channels. Within two generations, however, salmon densities recovered to pre-disturbance levels (Milner, Robertson, McDermott, Klaar, & Brown, 2013). Bird communities in far north Queensland, Australia can also recover to a pre-disturbance state within 12 months of a tropical cyclone by modifying their foraging behaviour and movement patterns within a landscape (Freeman, Pias, & Vinson, 2008). Hence, the markedly different responses to extreme events observed in long-term studies show that caution is required when predicting likely responses to future events. The information gleaned from long-term studies will be critical for improving predictions of species responses to extreme events; however, such studies are rare.

We found a larger-than-expected number of positive or neutral responses to extreme events ( $n = 144$ ; 21% of all responses). These responses serve as a reminder that natural disturbances from

extreme events often play a critical role in maintaining the structure and function of many ecosystems and life history strategies (Attiwill, 1994; McMahon et al., 2017; Whittaker, Willis, & Field, 2001). Some positive responses that were common yet temporary included cyclone events leading to increased abundances of bird species that prefer regenerating habitat (e.g., Brown, Sherry, & Harris, 2011; Freeman et al., 2008), and cyclones and floods leading to increased richness of fish and invertebrate species (e.g., Gerisch, Dziock, Schanowski, Ilg, & Henle, 2012; Horrocks, Cunningham, O'Dowd, Thomson, & Mac Nally, 2012; Kano et al., 2011). Increases in fish and invertebrate richness were typically due to higher food availability in disturbed areas, or flooding events facilitating colonization by species downstream. Marine ecosystems had the highest proportion of positive responses following an extreme event (21%). Examples of such responses included an increase in surface deposit feeders in the immediate aftermath of Hurricane Isabel (Hughes, Richardson, Luckenbach, & Seed, 2009) and increased densities of striated surgeonfish (*Ctenochaetus striatus*) after major cyclones had disturbed the reefs in the Cook Islands (Rongo & van Woosik, 2013).

In the studies we reviewed, species that benefited from extreme events were typically invasive (e.g., green sunfish (*Lepomis cyanellus*) in California (Beche, Connors, Resh, & Merenlender, 2009); sweet pit-tosporum (*Pittosporum undulatum*) in Jamaica (Bellingham, Tanner, & Healey, 2005); *Phragmites australis* in wetlands along the Atlantic and Gulf Coasts of the United States (Bhattarai & Cronin, 2014)), or native species that are mobile or have rapid population turnover times (e.g., molluscs in Germany (Ilg et al., 2008); fish communities in the interior lakes of central North America (Starks, Cooper, Leavitt, & Wissel, 2014)). However, we also found cases of range-restricted species benefiting from extreme event exposure. For example, reductions in rainforest canopy cover caused by cyclone events can decrease the risk of endangered rainforest frogs becoming infected by a fungal pathogen, chytrid fungus (*Batrachochytrium dendrobatidis*) (Roznik, Sapsford, Pike, Schwarzkopf, & Alford, 2015). Drought also reduces chytrid fungus intensity and mortality in adult crawfish frogs (*Lithobates areolatus*) (Terrell, Engbrecht, Pessier, & Lannoo, 2014). In these cases, cyclones and drought conditions act to create microhabitat conditions that exceed the critical maximum temperature for chytrid fungus and hence help anuran resistance to the disease.

#### 4.1 | Assessing vulnerability to extreme events

Vulnerability assessments can identify species or ecosystems that are likely to require conservation intervention. A widely adopted framework for assessing vulnerability to climate change that measures species' exposure, sensitivity and adaptive capacity (Foden et al., 2013) is also applicable to measurements of species' vulnerability to extreme events. Exposure is a measure of the nature and degree to which a system is exposed to significant climatic variations. Sensitivity is a measure of how a species will be affected by particular changes in climate variables, and is predominantly governed by intrinsic factors (e.g., phenology, physiological traits). Adaptive capacity is the ability of a species to adjust to altered climate and

weather patterns, and is influenced by both intrinsic (e.g., strict habitat dependencies) and extrinsic factors (e.g., habitat loss).

Of the three components of vulnerability, our ability to measure exposure to extreme events is arguably the most advanced. For example, over 30% of threatened terrestrial mammals have experienced significant exposure to cyclones, droughts or a combination of both (Ameca y Juárez, Mace, Cowlshaw, Cornforth, & Petteorelli, 2013). Measurements of exposure should not, however, rely solely on historical patterns of extreme events. Under climate change, heat waves are likely to be more intense, more frequent and last longer, particularly in Amazon and Congo basins (Seneviratne et al., 2012). The frequency of tropical cyclones may remain unchanged but they are predicted to become more intense in some ocean basins (Seneviratne et al., 2012). Moreover, the duration and intensity of droughts will increase in some regions of the world, including southern and central Europe, central North America, Central America and Mexico, north-east Brazil and southern Africa (Handmer et al., 2012; Pohl et al., 2017; Russo et al., 2016; Seneviratne et al., 2012).

The infrequent and short-term nature of extreme events makes it difficult to predict their local frequency and intensity (Bailey & van de Pol, 2016; Flato et al., 2013). Predictions are also constrained by incomplete data on the historical frequency of extreme events for some regions (Flato et al., 2013). Of the extreme events included in this review, predictive modelling is least developed for heat waves that affect marine ecosystems (Frölicher, & Laufkötter, 2018), whereas predictions for extreme precipitation and heat events have improved dramatically in recent years (e.g., Baker et al., 2018; Tabari & Willems, 2018). Regardless of the type of event, however, species vulnerability assessments can be made more robust to uncertain predictions if they consider the range of plausible extreme event patterns predicted by model simulations.

Biological traits, including home-range size (Ameca y Juárez, Mace, Cowlshaw, & Petteorelli, 2014), and individual demographic factors, including age, are likely to mediate sensitivity to extreme events (Beehner, Onderdonk, Alberts, & Altmann, 2006). For example, older female baboons (*Papio cynocephalus*) in Kenya are less likely to have successful pregnancies during drought (Beehner et al., 2006). But despite a long history of experimental research on ecological responses to climatic stress (Bailey et al., 2017; Hoffmann & Parsons, 1997; Pardo, Jenouvrier, Weimerskirch, & Barbraud, 2017; Parmesan, 2006; White, Campbell, Kemp, & Hunt, 2000), key questions on species' sensitivity and adaptive capacity to extreme events remain. Such questions include those around limits to phenotypic plasticity, the capacity for genetic change in individuals, and how individual responses to extreme events influence ecosystem function (Palmer et al., 2017). Sessile species with slow reproductive rates and specialized habitat and dietary requirements are commonly flagged as being highly vulnerable to anthropogenic climate change (Pacifci et al., 2015). These same traits are also likely to exacerbate vulnerability to more frequent and intense extreme events. However, research that continues to explore this important research gap will help clarify the preconditions for successful adaptation to extreme events among different taxonomic groups.

Studies exploring species' sensitivity and adaptive capacity to extreme events will inevitably require large investments of both money and time, and hence should target areas of most need. Our findings suggest priorities for this research include ecological responses to cold and heat waves, given their predominantly negative impacts (73% and 74% of responses were negative, respectively) and the comparatively few studies focusing on these events. Responses in coastal, estuarine, marine, riparian and wetland ecosystems were mostly negative and relatively poorly studied (Figure 3; Supporting Information Table S8). Other less-studied topics include reptile responses to cyclones, and mammal and bird responses to drought. Future studies should also examine ambiguous responses, including changes in behaviour and species composition, to help clarify their long-term implications. Changes in the composition of invertebrate communities following drought and flood events, and changes in avian species behaviour following cyclones and floods were particularly prominent.

#### 4.2 | Accounting for threat interactions in vulnerability assessments

Understanding how multiple threats interact to influence species' vulnerability to extinction is difficult (Cote, Darling, & Brown, 2016), but can be of critical importance to the success of conservation efforts (Brook, Sodhi, & Bradshaw, 2008). Assessments of species' vulnerability to extreme events should consider how interactions between threats may exacerbate or attenuate vulnerability levels. Such interactions include those between multiple extreme events or between extreme events and other threatening processes.

Multiple extreme events are likely to act in synergistic ways to exacerbate risk of species' extinction. For example, the co-occurrence of drought and heat waves has greater impacts on bird abundance changes than if these events occur in isolation (Albright et al., 2010). The combination of heat waves and low summer rainfall also has severe impacts on koala populations (*Phascolarctos cinereus*), either directly by causing physiological stress or indirectly by affecting the nutrient and water content in eucalypt leaves (Seabrook et al., 2011). Synergistic interactions between extreme events have also been documented in marine systems. For example, heat waves increase demand for carbon in a temperate seagrass species (*Amphibolis antarctica*) found in Shark Bay, Western Australia. Yet, this demand cannot be met through photosynthesis when turbid floodwaters reduce light availability, resulting in a negative carbon balance in plants for more than 2 years after the co-occurrence of heat waves and flooding events (Fraser et al., 2014).

Interactions with non-climate-related threats are also likely to influence species' overall vulnerability to extreme events. For example, habitat fragmentation can limit the ability of butterflies to cope with, and recover from, heat waves (Piessens, Adriaens, Jacquemyn, & Honnay, 2009). Toxic compounds in agricultural runoff are also less diluted in years of drought, which can elevate

toxicity levels in fish liver tissue (e.g., in striped bass (*Morone saxatilis*) in the San Francisco Bay estuary (Bennet, Ostrach, & Hinton, 1995)). Drought can also promote a complex interaction between diseases that are tolerable in isolation, but with co-infection cause catastrophic mortality in lion populations (*Panthera leo*) (Munson et al., 2008). Sustained browsing by introduced ungulates during drought events has been linked to declines of a critically endangered seed specialist bird (*Loxioides bailleui*) in Hawaii (Banko et al., 2013).

Ecological responses are likely to be more pronounced when extreme events co-occur with other events or threatening processes, particularly where species exist near upper thermal tolerance limits (Fraser et al., 2014), are resource-limited (Maron et al., 2015) or have specialized habitat requirements (Banko et al., 2013; Hinojosa-Huerta, Nagler, Carrillo-Guererro, & Glenn, 2013). Accounting for threat interactions is likely to improve predictions of responses to extreme events, such as for population decline (Vasseur et al., 2014). Further research that reviews or elucidates when extreme events act additively, synergistically or antagonistically with other threats will therefore improve the reliability of species vulnerability assessments. To advance on current knowledge of threat interactions, such research should be long term and include measures of threat intensity. However, we caution that research focusing on interactive effects should not detract from efforts to clarify how species are likely to respond to altered extreme event patterns, which remains a key uncertainty in most vulnerability assessments.

#### 4.3 | Promoting adaptation to extreme events through conservation action

Just as they promote adaptation to climate change, actions that enhance habitat connectivity, access to climate refugia and intra-species genetic variation are also likely to benefit species threatened by extreme events. The most effective way to achieve these aims is through the conservation of intact habitats (Martin & Watson, 2016; Watson et al., 2018).

Intact habitats on land are typified by large, contiguous areas of native vegetation that often span environmental gradients, such as altitude, rainfall or temperature (Watson et al., 2018). Marine intact habitats (Jones et al., 2018) are seascapes mostly free of human disturbance that perform key functional roles (D'agata, 2016) and maintain high levels of ecological and evolutionary connectivity (Jones, Srinivasa, & Almany, 2007). The characteristics of intact habitats across land and sea help to maximize species dispersal, gene flow and genetic adaptation (Alberto et al., 2013; Lawler et al., 2015; Sgro, Lowe, & Hoffmann, 2011). Intact habitats also act as important refuges for plant and animal communities dependent on long time intervals between disturbance processes, including drought and wildfire (Laurance, 2004; Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011). Degradation and loss of intact habitats can decrease daily rainfall intensity, increase drought duration during El Niño years and increase the number of dry and hot days (McAlpine et al., 2018; Sheil & Murdiyarsa, 2009). Furthermore, intact habitats retain



soil, stabilize slopes and control flooding, and wind erosion during extreme events (Alila, Kuraš, Schnorbus, & Hudson, 2009; Brookhuis & Hein, 2016). Intact habitats are also likely to be more resilient to large-scale disturbances from extreme events. For example, exotic seedling germination following cyclone damage is higher and more diverse inside fragmented habitats than intact habitats (Catterall, McKenna, Kanowski, & Piper, 2008).

Where intact habitat protection is not available to conservation practitioners, ecological restoration efforts can also help species to adapt to extreme events (Reside, Butt, & Adams, 2017). For example, sustained restoration efforts (i.e., 15+ years) in brackish marshes help plant and animal communities to cope with drought events (Kinney, Quigg, & Armitage, 2014). Ecological restoration that helps species to adapt to extreme events can also benefit human communities with immediate adaptation needs (Maxwell, Venter, Jones, & Watson, 2015). There are now important examples of using oyster or seagrass beds to protect coastal areas from flooding offers substantial dual benefits for climate-vulnerable biodiversity and human communities (Borsje et al., 2011).

In fragmented landscapes, re-establishing native vegetation and regulating incompatible land uses will facilitate species mobility during extreme events and provide critical food and shelter resources to aid recovery after events (e.g., Steenhof, Kochert, Carpenter, & Lehman, 1999). Populations that face resource bottlenecks during or following extreme events would benefit from feed supplement programmes (Maron et al., 2015; Turton, 2012) or removing competition from invasive ungulates (Banko et al., 2013). It may not be possible, however, to restore ecosystem stability and community assemblages to better cope with extreme events and other stressors in areas that have been heavily degraded (Cardoso et al., 2008).

Restoring environmental flows or improving management of groundwater withdrawals during drought periods will become increasingly important to maintain many freshwater populations and systems threatened by drought and heat wave events (Baker & Jennings, 2005). Importantly, the success of such restoration efforts will depend on also re-establishing natural temperature regimes in river and stream systems—an effect that is difficult to achieve if water is simply released from dams or reservoirs at periodic intervals (Rader, Voelz, & Ward, 2008).

More intensive conservation interventions could be necessary for critically endangered species that are vulnerable to extreme events. Such actions could involve pre-emptive translocation or relocation of populations following successive extreme flood events (e.g., Sousa et al., 2012). Populations that are regularly exposed to extreme events, or inhabit highly variable environments, may be suitable source populations for ex-situ conservation efforts as such populations typically show higher phenotypic plasticity and may be preadapted to more frequent and intense extreme events (Chevin & Hoffmann, 2017).

#### 4.4 | Concluding remarks

Our review provides an overview of contemporary ecological responses to extreme events, and lays a foundation for future

long-term studies to improve the understanding of species sensitivity and adaptive capacity to extreme events. Predicting the occurrence of individual extreme events and subsequent ecological responses is likely to remain a challenge. Less-documented phenomena include ecological responses to heat and cold waves, reptilian responses to cyclones, mammalian and bird responses to drought, and clarifying ambiguous ecological responses. Incorporating extreme events into climate change vulnerability assessments and adaptation plans will be challenging, but by doing so we have a greater chance of arriving at conservation interventions that truly address the full range of climate change impacts.

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#### AUTHOR CONTRIBUTIONS

JW, NB, MM, CM, DS and SM conceived the idea and designed methodology; SM, SC and AU collated and reviewed studies; SM and JW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### DATA ACCESSIBILITY

The studies included in this review are listed Supporting Information Table S2. Data to populate Table 2 in this review are made available in Supporting Information Table S3.

#### ORCID

Sean L. Maxwell  <https://orcid.org/0000-0002-0533-2659>

Nathalie Butt  <https://orcid.org/0000-0003-1517-6191>

Martine Maron  <https://orcid.org/0000-0002-5563-5789>

Sarah Chapman  <https://orcid.org/0000-0002-3141-8616>

James E. M. Watson  <https://orcid.org/0000-0003-4942-1984>

#### REFERENCES

- Alberto, F. J., Aitken, S. N., Alía, R., González-Martínez, S. C., Hänninen, H., Kremer, A., ... Whetten, R. (2013). Potential for evolutionary responses to climate change: Evidence from tree populations. *Global Change Biology*, 19(6), 1645–1661. <https://doi.org/10.1111/gcb.12181>
- Albright, T. P., Pidgeon, A. M., Rittenhouse, C. D., Clayton, M. K., Wardlow, B. D., Flather, C. H., ... Radeloff, V. C. (2010). Combined effects of heat waves and droughts on avian communities across

- the conterminous United States. *Ecosphere*, 1(5), 1–22. <https://doi.org/10.1890/es10-00057.1>
- Alila, Y., Kuraś, P. K., Schnorbus, M., & Hudson, R. (2009). Forests and floods: A new paradigm sheds light on age old controversies. *Water Resources Research*, 45(8), W08416. <https://doi.org/10.1029/2008WR007207>
- Altwegg, R., Visser, V., Bailey, L. D., & Erni, B. (2017). Learning from single extreme events. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 372(1723), 20160141. <https://doi.org/10.1098/rstb.2016.0141>
- Ameca y Juárez, E., Mace, G. M., Cowlshaw, G., & Pettorelli, N. (2014). Identifying species' characteristics associated with natural population die-offs in mammals. *Animal Conservation*, 17(1), 35–43. <https://doi.org/10.1111/acv.12053>
- Ameca y Juárez, E., Mace, G. M., Cowlshaw, G., Cornforth, W. A., & Pettorelli, N. (2013). Assessing exposure to extreme climatic events for terrestrial mammals. *Conservation Letters*, 6(3), 145–153. <https://doi.org/10.1111/j.1755-263X.2012.00306.x>
- Asch, R. G. (2015). Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, 112(30), e4065–e4074. <https://doi.org/10.1073/pnas.1421946112>
- Attwill, P. M. (1994). The disturbance of forest ecosystems: The ecological basis for conservative management. *Forest Ecology and Management*, 63(2–3), 247–300. [https://doi.org/10.1016/0378-1127\(94\)90114-7](https://doi.org/10.1016/0378-1127(94)90114-7)
- Bailey, L. D., Ens, B. J., Both, C., Heg, D., Oosterbeek, K., & van de Pol, M. (2017). No phenotypic plasticity in nest-site selection in response to extreme flooding events. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 372(1723), 20160139. <https://doi.org/10.1098/rstb.2016.0139>
- Bailey, L. D., & van de Pol, M. (2016). Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology*, 85(1), 85–96. <https://doi.org/10.1111/1365-2656.12451>
- Baker, H. S., Millar, R. J., Karoly, D. J., Beyerle, U., Guilloid, B. P., Mitchell, D., ... Allen, M. R. (2018). Higher CO<sub>2</sub> concentrations increase extreme event risk in a 1.5 °C world. *Nature Climate Change*, 8(7), 604–608. <https://doi.org/10.1038/s41558-018-0190-1>
- Baker, T. L., & Jennings, C. A. (2005). Striped bass survival in Lake Blackshear, Georgia during drought conditions: Implications for restoration efforts in Gulf of Mexico drainages. *Environmental Biology of Fishes*, 72(1), 73–84. <https://doi.org/10.1007/s10641-004-6585-z>
- Banko, P. C., Camp, R. J., Farmer, C., Brinck, K. W., Leonard, D. L., & Stephens, R. M. (2013). Response of palila and other subalpine Hawaiian forest bird species to prolonged drought and habitat degradation by feral ungulates. *Biological Conservation*, 157, 70–77. <https://doi.org/10.1016/j.biocon.2012.07.013>
- Beche, L. A., Connors, P. G., Resh, V. H., & Merenlender, A. M. (2009). Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography*, 32(5), 778–788. <https://doi.org/10.1111/j.1600-0587.2009.05612.x>
- Bellingham, P. J., Tanner, E. V. J., & Healey, J. R. (2005). Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. *Journal of Vegetation Science*, 16(6), 675–684. [https://doi.org/10.1658/1100-9233\(2005\)016\[0675:HDAIBT\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2005)016[0675:HDAIBT]2.0.CO;2)
- Bennet, W. A., Ostrach, D. J., & Hinton, D. E. (1995). Larval striped bass condition in a drought-stricken estuary: Evaluating pelagic food-web limitation. *Ecological Applications*, 5(3), 680–692. <https://doi.org/10.2307/1941977>
- Beehner, J. C., Onderdonk, D. A., Alberts, S. C., & Altmann, J. (2006). The ecology of conception and pregnancy failure in wild baboons. *Behavioral Ecology*, 17(5), 741–750.
- Bhattacharai, G. P., & Cronin, J. T. (2014). Hurricane activity and the large-scale pattern of spread of an invasive plant species. *PLoS ONE*, 9(5), e98478. <https://doi.org/10.1371/journal.pone.0098478>
- Borsje, B. W., van Wesenbeeck, B. K., Dekker, F., Paalvast, P., Bouma, T. J., van Katwijk, M. M., & de Vries, M. B. (2011). How ecological engineering can serve in coastal protection. *Ecological Engineering*, 37(2), 113–122. <https://doi.org/10.1016/j.ecoleng.2010.11.027>
- Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, 23(8), 453–460. <https://doi.org/10.1016/j.tree.2008.03.011>
- Brookhuis, B., & Hein, L. (2016). The value of the flood control service of tropical forests: A case study for Trinidad. *Forest Policy and Economics*, 62, 118–124. <https://doi.org/10.1016/j.forpol.2015.10.002>
- Brown, C. R., & Brown, M. B. (2014). Breeding time in a migratory songbird is predicted by drought severity and group size. *Ecology*, 95(10), 2736–2744. <https://doi.org/10.1890/14-0425.1>
- Brown, D. R., Sherry, T. W., & Harris, J. (2011). Hurricane Katrina impacts the breeding bird community in a bottomland hardwood forest of the Pearl River basin, Louisiana. *Forest Ecology and Management*, 261(1), 111–119. <https://doi.org/10.1016/j.foreco.2010.09.038>
- Capon, S. J., Lynch, A. J. J., Bond, N., Chessman, B. C., Davis, J., Davidson, N., ... Humphrey, C. (2015). Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Science of the Total Environment*, 534, 122–130. <https://doi.org/10.1016/j.scitotenv.2015.02.045>
- Cardoso, P. G., Raffaelli, D., Lillebo, A. I., Verdelhos, T., & Pardal, M. A. (2008). The impact of extreme flooding events and anthropogenic stressors on the macrobenthic communities' dynamics. *Estuarine Coastal and Shelf Science*, 76(3), 553–565. <https://doi.org/10.1016/j.ecss.2007.07.026>
- Catterall, C. P., McKenna, S., Kanowski, J., & Piper, S. D. (2008). Do cyclones and forest fragmentation have synergistic effects? A before-after study of rainforest vegetation structure at multiple sites. *Austral Ecology*, 33(4), 471–484. <https://doi.org/10.1111/j.1442-9993.2008.01902.x>
- Cech, M., & Cech, P. (2013). The role of floods in the lives of fish-eating birds: Predator loss or benefit? *Hydrobiologia*, 717(1), 203–211. <https://doi.org/10.1007/s10750-013-1625-3>
- Chapman, S., Mustin, K., Renwick, A. R., Segan, D. B., Hole, D. G., Pearson, R. G., & Watson, J. E. M. (2014). Publishing trends on climate change vulnerability in the conservation literature reveal a predominant focus on direct impacts and long time-scales. *Diversity and Distributions*, 20(10), 1221–1228. <https://doi.org/10.1111/ddi.12234>
- Chevin, L. M., & Hoffmann, A. A. (2017). Evolution of phenotypic plasticity in extreme environments. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 372(1723), 20160138. <https://doi.org/10.1098/rstb.2016.0138>
- Cote, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B-Biological Sciences*, 283(1824), 20152592. <https://doi.org/10.1098/rspb.2015.2592>
- D'agata, S., Mouillot, D., Wantiez, L., Friedlander, A. M., Kulbicki, M., & Vigliola, L. (2016). Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications*, 7, 12000. <https://doi.org/10.1038/ncomms12000>
- Dodd, C. K., & Dreslik, M. J. (2008). Habitat disturbances differentially affect individual growth rates in a long-lived turtle. *Journal of Zoology*, 275(1), 18–25. <https://doi.org/10.1111/j.1469-7998.2007.00402.x>
- Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling and impacts. *Science*, 289(5487), 2068–2074. <https://doi.org/10.1126/science.289.5487.2068>
- Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S. C., Collins, W., ... Rummukainen, M. (2013). Evaluation of climate models. In T. F. Stocker, D. D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & M. P. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate*

- Change* (pp. 231–290). Cambridge, UK & New York, NY: Cambridge University Press.
- Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J. C., Akcakaya, H. R., Angulo, A., ... Mace, G. M. (2013). Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE*, 8(6), e65427. <https://doi.org/10.1371/journal.pone.0065427>
- Fraser, M. W., Kendrick, G. A., Statton, J., Hovey, R. K., Zavala-Perez, A., & Walker, D. I. (2014). Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. *Journal of Ecology*, 102(6), 1528–1536. <https://doi.org/10.1111/1365-2745.12300>
- Frölicher, T. L., & Laufkötter, C. (2018). Emerging risks from marine heat waves. *Nature Communications*, 9(1), 650.
- Freeman, A. N. D., Pias, K., & Vinson, M. F. (2008). The impact of Tropical Cyclone Larry on bird communities in fragments of the endangered rainforest Type 5b. *Austral Ecology*, 33(4), 532–540. <https://doi.org/10.1111/j.1442-9993.2008.01908.x>
- Gerisch, M., Dziock, F., Schanowski, A., Ilg, C., & Henle, K. (2012). Community resilience following extreme disturbances: The response of ground beetles to a severe summer flood in a Central European lowland stream. *River Research and Applications*, 28(1), 81–92. <https://doi.org/10.1002/rra.1438>
- Gutschick, V. P., & BassiriRad, H. (2003). Extreme events as shaping physiology, ecology, and evolution of plants: Toward a unified definition and evaluation of their consequences. *New Phytologist*, 160(1), 21–42. <https://doi.org/10.1046/j.1469-8137.2003.00866.x>
- Handmer, J., Honda, Y., Kundzewicz, Z. W., Arnell, N., Benito, G., Hatfield, J., ... Yan, Z. (2012). Changes in impacts of climate extremes: Human systems and ecosystems. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G. K. Plattner, S. K. Allen, M. Tignor, & P. M. Midgley (Eds.), *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change (IPCC)* (pp. 231–290). Cambridge, UK & New York, NY: Cambridge University Press.
- Harris, R., Beaumont, L., Vance, T., Tozer, C., Remenyi, T., Perkins-Kirkpatrick, S., ... Andrew, N. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, 8(7), 579. <https://doi.org/10.1038/s41558-018-0187-9>
- Hinojosa-Huerta, O., Nagler, P. L., Carrillo-Guererro, Y. K., & Glenn, E. P. (2013). Effects of drought on birds and riparian vegetation in the Colorado River Delta, Mexico. *Ecological Engineering*, 51, 275–281. <https://doi.org/10.1016/j.ecoleng.2012.12.082>
- Hoffmann, A., & Parsons, P. (1997). *Extreme environmental change and evolution*. Cambridge, UK: Cambridge University Press.
- Horrocks, G. F., Cunningham, S. C., O'Dowd, D. J., Thomson, J. R., & Mac Nally, R. (2012). Floodplain ants show a stronger response to an extensive flood than to variations in fallen timber load. *Austral Ecology*, 37(4), 518–528. <https://doi.org/10.1111/j.1442-9993.2011.02315.x>
- Hughes, C., Richardson, C. A., Luckenbach, M., & Seed, R. (2009). Difficulties in separating hurricane induced effects from natural benthic succession: Hurricane Isabel, a case study from Eastern Virginia, USA. *Estuarine Coastal and Shelf Science*, 85(3), 377–386. <https://doi.org/10.1016/j.ecss.2009.08.023>
- Ilg, C., Dziock, F., Fockler, F., Follner, K., Gerisch, M., Glaeser, J., ... Henle, K. (2008). Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands. *Ecology*, 89(9), 2392–2398. <https://doi.org/10.1890/08-0528.1>
- IPCC (2014). Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), (p. 1132). Cambridge, UK and New York, NY: Cambridge University Press.
- Jiguet, F., Brotons, L., & Devictor, V. (2011). Community responses to extreme climatic conditions. *Current Zoology*, 57(3), 406–413. <https://doi.org/10.1093/czoolo/57.3.406>
- Jones, G. P., Srinivasa, M., & Almany, G. R. (2007). Population connectivity and conservation of marine biodiversity. *Oceanography*, 20(3), 100–111. <https://doi.org/10.5670/oceanog.2007.33>
- Jones, K. R., Watson, J. E. M., Possingham, H. P., & Klein, C. J. (2016). Incorporating climate change into spatial conservation prioritisation: A review. *Biological Conservation*, 194, 121–130. <https://doi.org/10.1016/j.biocon.2015.12.008>
- Jones, K. R., Klein, C. J., Halpern, B. S., Venter, O., Grantham, H., Kuempel, C. D., ... Watson, J. E. M. (2018). The location and protection status of Earth's diminishing marine wilderness. *Current Biology*, 28(15), 2506–2512. e2503. <https://doi.org/10.1016/j.cub.2018.06.010>
- Kano, Y., Ohnishi, K., Tomida, Y., Ikeda, N., Iwawaki, N., Miyagawa, M., ... Watanabe, K. (2011). Fluctuation and variation in stream-fish assemblages after a catastrophic flood in the Miyagawa River. *Japan. Environmental Biology of Fishes*, 92(4), 447–460. <https://doi.org/10.1007/s10641-011-9861-8>
- Kinney, E. L., Quigg, A., & Armitage, A. R. (2014). Acute effects of drought on emergent and aquatic communities in a brackish marsh. *Estuaries and Coasts*, 37(3), 636–645. <https://doi.org/10.1007/s12237-013-9721-1>
- Laurance, W. F. (2004). Forest-climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), 345–352.
- Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., ... Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology*, 29(3), 618–629. <https://doi.org/10.1111/cobi.12505>
- Lindenmayer, D. B., Hobbs, R. J., Likens, G. E., Krebs, C. J., & Banks, S. C. (2011). Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences*, 108(38), 15887–15891. <https://doi.org/10.1073/pnas.1110245108>
- Lugo, A. E. (2008). Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Austral Ecology*, 33(4), 368–398. <https://doi.org/10.1111/j.1442-9993.2008.01894.x>
- Maron, M., McAlpine, C. A., Watson, J. E. M., Maxwell, S., & Barnard, P. (2015). Climate-induced resource bottlenecks exacerbate species vulnerability: A review. *Diversity and Distributions*, 21(7), 731–743. <https://doi.org/10.1111/ddi.12339>
- Martin, T. G., & Watson, J. E. M. (2016). Intact ecosystems provide best defence against climate change. *Nature Climate Change*, 6(2), 122–124. <https://doi.org/10.1038/nclimate2918>
- Maxwell, S. L., Venter, O., Jones, K. R., & Watson, J. E. (2015). Integrating human responses to climate change into conservation vulnerability assessments and adaptation planning. *Annals of the New York Academy of Sciences*, 1355(1), 98–116.
- McAlpine, C. A., Johnson, A., Salazar, A., Syktus, J. I., Wilson, K., Meijaard, E., ... Sheil, D. (2018). Forest loss and Borneo's climate. *Environmental Research Letters*, 13, 1–10.
- McMahon, K. M., Evans, R. D., van Dijk, K. J., Hernawan, U., Kendrick, G. A., Lavery, P. S., ... Waycott, M. (2017). Disturbance is an important driver of clonal richness in tropical seagrasses. *Frontiers in Plant Science*, 8, 1–14. <https://doi.org/10.3389/fpls.2017.02026>
- McMenamin, S. K., Hadly, E. A., & Wright, C. K. (2008). Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences*, 105(44), 16988–16993. <https://doi.org/10.1073/pnas.0809090105>
- Miller, T. E., Gornish, E. S., & Buckley, H. L. (2010). Climate and coastal dune vegetation: Disturbance, recovery, and succession. *Plant Ecology*, 206(1), 97–104. <https://doi.org/10.1007/s11258-009-9626-z>

- Milner, A. M., Robertson, A. L., McDermott, M. J., Klaar, M. J., & Brown, L. E. (2013). Major flood disturbance alters river ecosystem evolution. *Nature Climate Change*, 3(2), 137.
- Moreno, J., & Moller, A. P. (2011). Extreme climatic events in relation to global change and their impact on life histories. *Current Zoology*, 57(3), 375–389. <https://doi.org/10.1093/czoolo/57.3.375>
- Munson, L., Terio, K. A., Kock, R., Mlengeya, T., Roelke, M. E., Dubovi, E., ... Packer, C. (2008). Climate extremes promote fatal co-infections during canine distemper epidemics in African Lions. *PLoS ONE*, 3(6), e2545. <https://doi.org/10.1371/journal.pone.0002545>
- Orsenigo, S., Mondoni, A., Rossi, G., & Abeli, T. (2014). Some like it hot and some like it cold, but not too much: Plant responses to climate extremes. *Plant Ecology*, 215(7), 677–688. <https://doi.org/10.1007/s11258-014-0363-6>
- Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., ... Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5(3), 215–225. <https://doi.org/10.1038/nclimate2448>
- Palmer, G., Platts, P. J., Brereton, T., Chapman, J. W., Dytham, C., Fox, R., ... Thomas, C. D. (2017). Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 372(1723), 20160144. <https://doi.org/10.1098/rstb.2016.0144>
- Pardo, D., Jenouvrier, S., Weimerskirch, H., & Barbraud, C. (2017). Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 372(1723), 20160143. <https://doi.org/10.1098/rstb.2016.0143>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, 81(3), 443–450. [https://doi.org/10.1175/1520-0477\(2000\)081<0443:ioewac>2.3.co;2](https://doi.org/10.1175/1520-0477(2000)081<0443:ioewac>2.3.co;2)
- Piessens, K., Adriaens, D., Jacquemyn, H., & Honnay, O. (2009). Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. *Oecologia*, 159(1), 117–126. <https://doi.org/10.1007/s00442-008-1204-x>
- Pisaric, M. F., Thienpont, J. R., Kokelj, S. V., Nesbitt, H., Lantz, T. C., Solomon, S., & Smol, J. P. (2011). Impacts of a recent storm surge on an Arctic delta ecosystem examined in the context of the last millennium. *Proceedings of the National Academy of Sciences of the United States of America*, 108(22), 8960–8965. <https://doi.org/10.1073/pnas.1018527108>
- Pohl, B., Macron, C., & Monerie, P. A. (2017). Fewer rainy days and more extreme rainfall by the end of the century in Southern Africa. *Scientific Reports*, 7, 46466. <https://doi.org/10.1038/srep46466>
- Rader, R. B., Voelz, N. J., & Ward, J. V. (2008). Post-flood recovery of a macroinvertebrate community in a regulated river: Resilience of an anthropogenically altered ecosystem. *Restoration Ecology*, 16(1), 24–33. <https://doi.org/10.1111/j.1526-100X.2007.00258.x>
- Reside, A. E., Butt, N., & Adams, V. M. (2017). Adapting systematic conservation planning for climate change. *Biodiversity and Conservation*, 27, 1–29.
- Rongo, T., & van Woesik, R. (2013). The effects of natural disturbances, reef state, and herbivorous fish densities on ciguatera poisoning in Rarotonga, southern Cook Islands. *Toxicon*, 64, 87–95. <https://doi.org/10.1016/j.toxicon.2012.12.01>
- Roznik, E. A., Sapsford, S. J., Pike, D. A., Schwarzkopf, L., & Alford, R. A. (2015). Natural disturbance reduces disease risk in endangered rainforest frog populations. *Scientific Reports*, 5, 13472. <https://doi.org/10.1038/srep13472>
- Runting, R. K., Wilson, K. A., & Rhodes, J. R. (2013). Does more mean less? The value of information for conservation planning under sea level rise. *Global Change Biology*, 19(2), 352–363. <https://doi.org/10.1111/gcb.12064>
- Russo, S., Marchese, A. F., Sillmann, J., & Imme, G. (2016). When will unusual heat waves become normal in a warming Africa? *Environmental Research Letters*, 11(5), 054016. <https://doi.org/10.1088/1748-9326/11/5/054016>
- Scheffers, B. R., De Meester, L., Bridge, T. C., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., ... Dudgeon, D. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354(6313), aaf7671. <https://doi.org/10.1126/science.aaf7671>
- Seabrook, L., McAlpine, C., Baxter, G., Rhodes, J., Bradley, A., & Lunney, D. (2011). Drought-driven change in wildlife distribution and numbers: A case study of koalas in south west Queensland. *Wildlife Research*, 38(6), 509–524. <https://doi.org/10.1071/wr11064>
- Seneviratne, S., Nicholls, N., Easterling, D., Goodess, C., Kanae, S., Kossin, J., ... Zhang, X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G. K. Plattner, S. K. Allen, M. Tignor, & P. M. Midgley (Eds.), *Intergovernmental panel on climate change special report on managing the risks of extreme events and disasters to advance climate change adaptation* (pp. 109–231). Cambridge, UK: Cambridge University Press.
- Sgro, C. M., Lowe, A. J., & Hoffmann, A. A. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, 4(2), 326–337. <https://doi.org/10.1111/j.1752-4571.2010.00157.x>
- Sheil, D., & Murdiyarso, D. (2009). How forests attract rain: An examination of a new hypothesis. *BioScience*, 59(4), 341–347. <https://doi.org/10.1525/bio.2009.59.4.12>
- Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, 99(3), 656–663. <https://doi.org/10.1111/j.1365-2745.2011.01798.x>
- Sousa, R., Varandas, S., Cortes, R., Teixeira, A., Lopes-Lima, M., Machado, J., & Guilhermino, L. (2012). Massive die-offs of freshwater bivalves as resource pulses. *Annales De Limnologie-International Journal of Limnology*, 48(1), 105–112. <https://doi.org/10.1051/limn/2012003>
- Starks, E., Cooper, R., Leavitt, P. R., & Wissel, B. (2014). Effects of drought and pluvial periods on fish and zooplankton communities in prairie lakes: Systematic and asystematic responses. *Global Change Biology*, 20(4), 1032–1042. <https://doi.org/10.1111/gcb.12359>
- Steenhof, K., Kochert, M. N., Carpenter, L. B., & Lehman, R. N. (1999). Long-term prairie falcon population changes in relation to prey abundance, weather, land uses, and habitat conditions. *Condor*, 101(1), 28–41. <https://doi.org/10.2307/1370443>
- Tabari, H., & Willems, P. (2018). Lagged influence of Atlantic and Pacific climate patterns on European extreme precipitation. *Scientific Reports*, 8(1), 5748. <https://doi.org/10.1038/s41598-018-24069-9>
- Terrell, V. C. K., Engbrecht, N. J., Pessier, A. P., & Lannoo, M. J. (2014). Drought reduces chytrid fungus (*Batrachochytrium dendrobatidis*) infection intensity and mortality but not prevalence in adult crawfish frogs (*Lithobates areolatus*). *Journal of Wildlife Diseases*, 50(1), 56–62. <https://doi.org/10.7589/2013-01-016>
- Thibault, K. M., & Brown, J. H. (2008). Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, 105(9), 3410–3415. <https://doi.org/10.1073/pnas.0712282105>
- Turton, S. M. (2012). Securing landscape resilience to tropical cyclones in Australia's Wet Tropics under a changing climate: Lessons from Cyclones Larry (and Yasi). *Geographical Research*, 50(1), 15–30. <https://doi.org/10.1111/j.1745-5871.2011.00724.x>
- Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 372(1723), 20160135. <https://doi.org/10.1098/rstb.2016.0135>

- van de Pol, M., Ens, B. J., Heg, D., Brouwer, L., Krol, J., Maier, M., ... Koffijberg, K. (2010). Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology*, 47(4), 720–730. <https://doi.org/10.1111/j.1365-2664.2010.01842.x>
- van Gils, J. A., Lisovski, S., Lok, T., Meissner, W., Ozarowska, A., de Fouw, J., ... Klaassen, M. (2016). Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science*, 352(6287), 819–821. <https://doi.org/10.1126/science.aad6351>
- Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., ... O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B-Biological Sciences*, 281(1779), 1–8. <https://doi.org/10.1098/rspb.2013.2612>
- Watson, J. E. M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., ... Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, 2(4), 599–610. <https://doi.org/10.1038/s41559-018-0490-x>
- Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., ... Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, 3(1), 78–82. <https://doi.org/10.1038/nclimate1627>
- White, T. A., Campbell, B. D., Kemp, P. D., & Hunt, C. L. (2000). Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Global Change Biology*, 6(6), 671–684. <https://doi.org/10.1046/j.1365-2486.2000.00344.x>
- Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: Towards a general, hierarchical theory of

species diversity. *Journal of Biogeography*, 28(4), 453–470. <https://doi.org/10.1046/j.1365-2699.2001.00563.x>

#### BIOSKETCH

Sean Maxwell is a PhD student in the School of Earth and Environmental Sciences at The University of Queensland. Collectively, the authors have dedicated much of their research efforts this past decade to developing better planning approaches for short-term impacts of climate change.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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