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BIODIVERSITY REVIEW

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Conservation implications of ecological responses to extreme weather and climate events

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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, northeast 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 & Dreslik, 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
Positive	
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
Ambiguous	
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
Negative	
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).

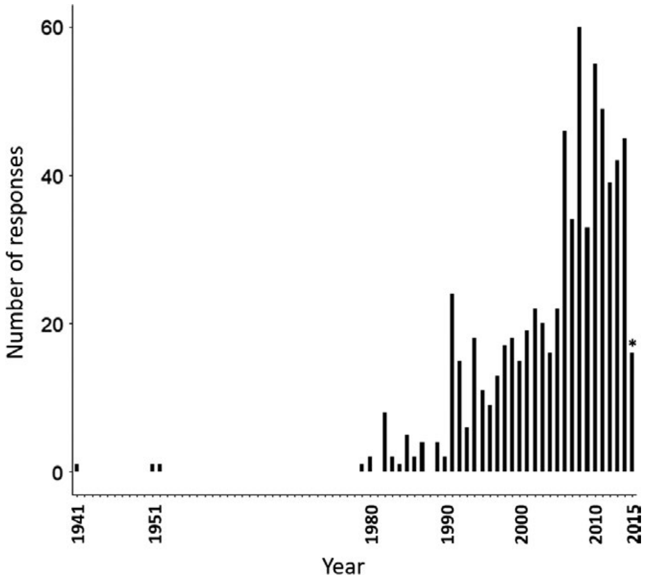


FIGURE 1 The number of ecological responses to extreme events (cyclones, drought, floods, heat waves and cold waves) documented in peer-reviewed literature between 1941 and July, 2015 (* denotes that responses in 2015 were reviewed till July only)

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).

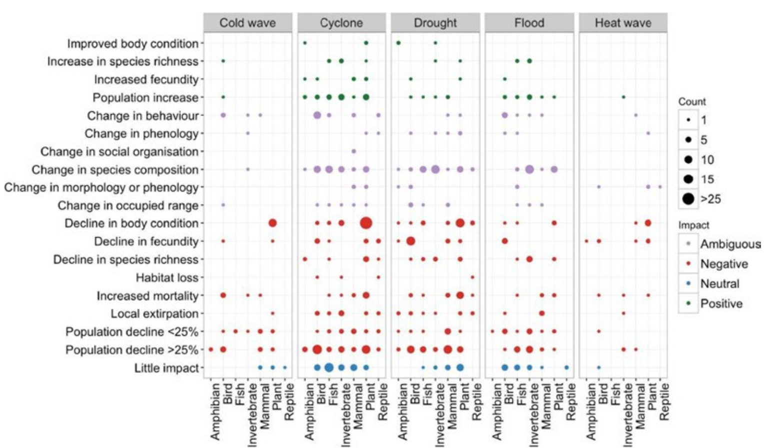
Sixty per cent of the studies in our review observed ecological responses for more than one year ($n = 416$). Studies that focused on drought, cold waves and floods generally spanned more than 1 year, whereas more than half of cyclone and heat wave studies were completed within 1 year (Supporting Information 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



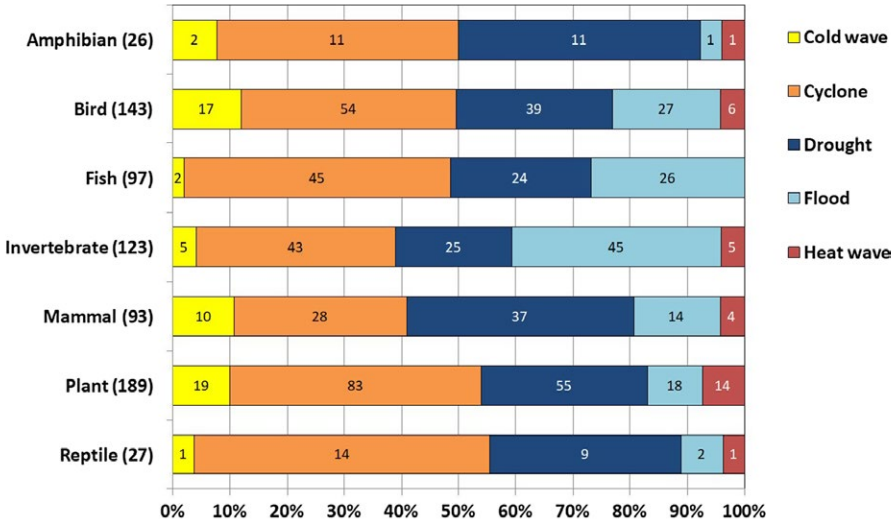


FIGURE 2 The relative prevalence of cyclones, drought, flood, cold waves and heat waves to species and ecosystem responses to extreme events observed between 1941 and July, 2015. Bracketed numbers beside taxon labels represent the total number of observed responses to extreme events for each taxon. The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

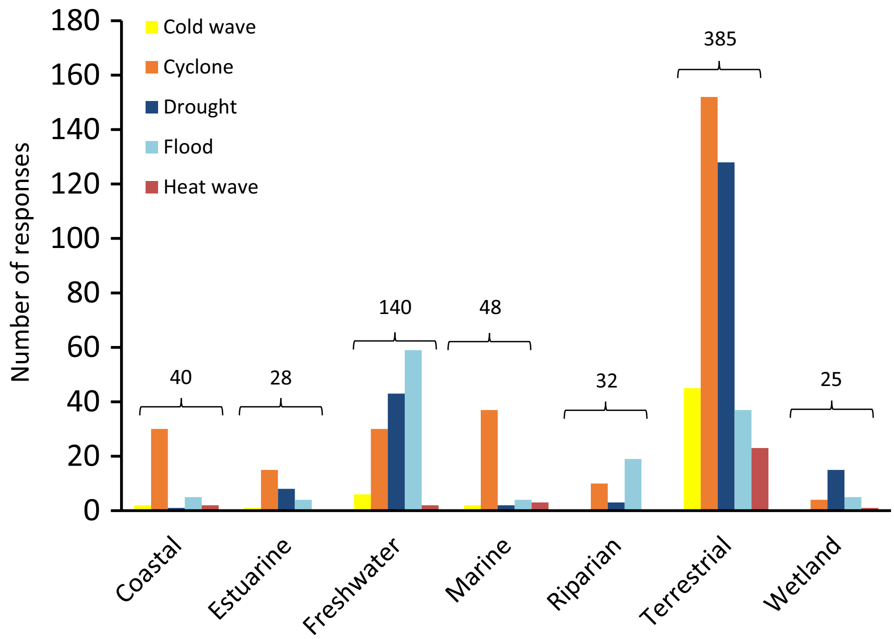


FIGURE 3 Number of ecological responses to extreme events observed in different ecosystems between 1941 and July, 2015. Numbers above brackets represent the total number of observed responses in each ecosystem

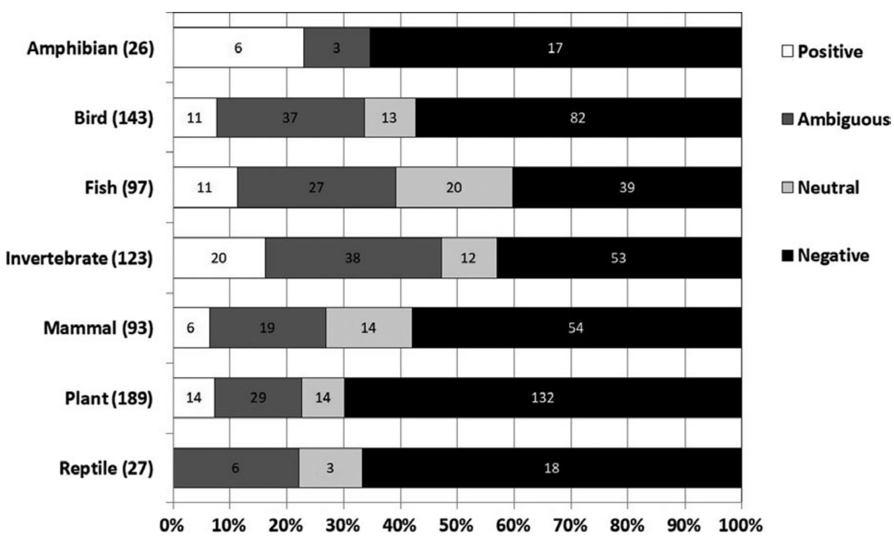


FIGURE 4 The relative contribution of positive, ambiguous, neutral and negative responses to extreme events observed between 1941 and July, 2015. Bracketed number beside taxon labels represent the total number of observed responses to extreme events for each taxon. The values in bars represent the total 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 Woesik, 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 pittosporum (*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, Cowlishaw, Cornforth, & Pettorelli, 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, Cowlishaw, & Pettorelli, 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 (Pacifici 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 & Murdiyarso, 2009). Furthermore, intact habitats retain soil, stabilize slopes and control flooding, and wind erosion during extreme events (Alila, Kuraś, 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.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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