Title

Extreme events drive rapid and dynamic range fluctuations

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Highlights:

- Climate change is causing a global redistribution of species, but range shifts often occur at unexpected rates and directions considering gradual climate change.
- Extreme weather and climate events (EWCEs) are increasing in frequency and severity and can impact dispersal, establishment, and survival — processes that drive range shifts.
- Previous work has not fully considered the potential role of EWCEs on range shifts.
- To bridge the gap between research on range shifts and EWCEs, we outline processes by which EWCEs may impact range shift dynamics, as well as approaches and implications of understanding these processes for management.

Abstract

Climate change is altering species' distributions globally. Increasing frequency of extreme weather and climate events (EWCEs) is one of the hallmarks of climate change. Despite species redistribution being widely studied in response to longer-term climate trends, the contribution of EWCEs to range shifts is not well understood. We outline how EWCEs can trigger rapid and unexpected range boundary fluctuations by impacting dispersal, establishment, and survival. Whether these mechanisms cause temporary or persistent range shifts depends on the spatiotemporal context and exposure to EWCEs. Using the increasing availability of data and statistical tools to examine EWCE impacts at fine spatiotemporal scales on species redistribution will be critical for informing conservation management of ecologically, economically, and culturally important species.

Climate-induced range shifts

Climate change is causing species to shift their distributions globally, with consequences for biodiversity and ecosystem functioning, as well as for the economy, food security, and human health and culture [1,2]. Species' geographic ranges are determined by a combination of abiotic and biotic factors that influence the dispersal, reproduction, and survival of individuals in a population [3]. When climate becomes less suitable, populations decline due to lower recruitment and higher mortality, causing range contraction at the **trailing edge** (see Glossary) [4]. In contrast, range expansion usually occurs at the **leading edge** as climatic conditions become more suitable beyond current distribution boundaries [4]. Overall, species ranges are shifting toward higher latitudes, elevations, and depths in response to warming temperatures [2,4–6] (Fig. 1). Yet, shifts often lag behind rates of climate change and can occur in unexpected directions [7,8]. While background rates of warming may facilitate gradual range shifts driven by (relatively) slow changes in population dynamics and colonisation/extirpation events, **extreme weather and climate events** (EWCEs) may affect range shift rates by amplifying expansion and contraction dynamics. As a result, range edges can experience rapid fluctuations in expected or unexpected directions that may result in temporary or persistent range shifts depending on the degree of exposure and the spatiotemporal context of the EWCE.

EWCEs are characterized by their magnitude, duration, and spatial extent and following a meteorological definition, are categorized as extreme when their magnitude falls beyond a threshold (e.g., the 90th percentile) over a baseline time period for a given location [9,10] (Box 1). While EWCEs can be associated with long-term meteorological cycles, such as the El Niño Southern Oscillation, they can also occur over shorter time scales [11]. EWCEs are increasing in frequency and severity [9,12], with potentially substantial impacts on distributions of ecologically, culturally, and economically important species [13]. While EWCEs can contribute to defining range edges [14], the role EWCEs play in range dynamics remains unclear [but see 15–17,18; Box 2]. This is in part because attributing range shifts to a specific driver requires long-term and spatially widespread evidence of population responses to climate fluctuations [19]. Here, we outline how EWCEs can amplify expansion and contraction dynamics, causing rapid and/or unexpected range shifts or range edge fluctuations. We then discuss how increasing availability of data at fine spatiotemporal resolutions and statistical techniques for understanding impacts of climate variability can improve our understanding of these dynamics and inform conservation management.

Expansion and contraction mechanisms

EWCEs can amplify range expansion by increasing the probability and frequency of long-distance dispersal and establishment, or by pushing individuals toward range edges [16,18]. The change in dispersal dynamics can be described by a shift in the **dispersal kernel** [20] (Fig. 2). Passively dispersed sessile organisms, such as wind- or water-dispersed plants and marine larvae, often disperse short distances, while the probability of dispersing long distances (the tail of the dispersal kernel) is typically low (Fig. 2). Storms with high winds and currents can contribute to long-distance dispersal and allow establishment of ephemeral populations far beyond range edges [15,21,22; Box 2]. Active dispersers may decide when and how to respond to EWCEs. For example, individuals may move to range edge habitat or beyond in response to reduced habitat suitability caused by EWCEs in the range core [18; Box 2]. As the magnitude and frequency of EWCEs increases [12,23–25], active and passive dispersers may travel longer distances, extending the dispersal distance (tail length) and increasing the probability and frequency of propagules dispersing beyond the average dispersal range (tail thickness) [26,27] (Fig. 2). Greater **propagule pressure** beyond range edges would increase the likelihood that populations become self-sustaining over generations and contribute to range expansion [26,27] (Fig. 1).

EWCEs can also facilitate establishment and reproduction phases of expansion by improving abiotic and biotic conditions beyond range edges [16,28,29]. When EWCEs, such as heat waves, last over the duration of a species' lifecycle, reproduction in abnormally favorable climate conditions beyond the leading range edge can improve establishment success [16]. EWCEs can also improve establishment via competitive release [30]. For example, wildfires remove adult vegetation, allowing light- and nutrientdemanding understory plants to expand their range [28,29], while marine heatwaves that reduce kelp cover have facilitated range expansions of corals and turf-forming algae [31; Box 2].

Conversely, EWCEs can amplify range contractions by causing population mortality when conditions exceed critical physiological thresholds [32]. For example, extreme fires have caused geographically restricted plant species to lose up to 95% of their range [33], marine heatwaves have caused mass mortality of habitat-forming coral and kelp, leading to 100 km range contractions off the western coast of Australia [17,34–36], and extreme droughts have caused rapid contraction of the ponderosa pine, *Pinus ponderosa* [37].

Impacts of EWCEs on expansion and contraction processes are highly variable across species, depending on both intrinsic and extrinsic factors [38]. For instance, species traits, including critical thermal limits [39,40], hygric traits associated with water loss and desiccation rates [41], and body/leaf size [42,43], as well as habitat quality [44] impact **resistance** to negative impacts of EWCEs that may cause range contraction. For example, species living near their critical thermal limits, including marine ectotherms and tropical insects, exhibit lower resistance to EWCEs than species with larger thermal safety margins [39,40]. Furthermore, low dispersal, slow-paced life histories, and low habitat connectivity [44,45] limit **resilience** to EWCEs as well as expansion probability. When resilience is high despite low resistance, temporary range contractions may occur, while recovery prevents persistent range shifts. In contrast, low resistance and resilience will likely cause persistent contractions.

Rapid, unexpected, and fluctuating range dynamics

EWCEs can cause rapid and persistent range shifts or rapidly fluctuating range edge dynamics in both expected and unexpected directions depending on the spatiotemporal context and exposure to EWCEs, via the aforementioned expansion and contraction processes.

The spatial context of EWCEs describes the location and extent of impact with respect to a species' range. When EWCEs facilitate expansion processes at the leading edge and contraction processes at the trailing edge, they may amplify rates of range shifts in directions expected by background climate change. However, when expansion and contraction processes occur elsewhere, shifts may be ephemeral or occur in unexpected directions. For instance, when cold extremes, which have become more frequent in the mid-latitudes of the eastern US and Eurasia [46,47], exceed physiological tolerances of expanding populations, retraction may occur at the leading edge [48–50] (Fig. 1). Alternatively, EWCEs could reduce competition and cause expansion at the trailing range edge, where biotic factors often impose range boundaries [51,52].

The spatial context of an EWCE can also impact the persistence of range shifts by affecting metapopulation dynamics [44]. When EWCEs negatively impact populations that act as sources of individuals and genes for metapopulation recovery, mortality is more likely to cause rapid and persistent range contraction. The abundant centre hypothesis and complementary rare edge hypothesis suggest species abundance is highest in the center and declines toward range edges [53,54]. Despite mixed support for these hypotheses [55], when such patterns occur, EWCEs that negatively impact core populations could amplify future range contraction by depleting source populations, which reduces potential for demographic rescue at trailing edges [56]. However, immediate impacts on range shifts may not be apparent when EWCEs do not occur at range edges. On the other hand, EWCEs that cover large extents of a range or are **spatially compounding** may amplify the rate and persistence of range contraction by causing mass mortality, particularly in low quality and poorly connected habitat where recovery potential declines [44]. Effects may be particularly severe for small-ranged and highly endemic species, because extirpation risk will increase in the face of EWCEs for a relatively larger proportion of populations within their range [57].

The temporal context of EWCEs refers to their time of occurrence with respect to other climate events can also have important implications for range dynamics. Exposure to **temporally compounding EWCEs** that occur with high frequency can amplify expansion and contraction processes [58]. For example, successive marine heatwaves from 2014 to 2016 combined with anomalous poleward currents led to range expansions for a number of coastal marine taxa by increasing propagule pressure beyond range edges, with populations of some species establishing 300-500 km beyond the leading edge [16]. Where contraction occurs, high frequency EWCEs may exceed the recovery period of the affected species and cause persistent contraction. Alternatively, recovery following lower frequency events can cause rapidly fluctuating range edges [44]. Multiple types of EWCEs occurring simultaneously (**Multivariate EWCEs**) may also increase the likelihood of mass mortality and consequent range contractions [58]. For example, simultaneous extreme heat and drought events have caused tree diebacks at range edges [59], and unusually high temperatures and calm waters have caused contraction toward deeper depths in marine algae [60]. When these EWCEs are **preconditioned**, they may amplify mortality and range contraction [58]. For example, adaptation to a long period of wet climate conditions or early spring onsets that deplete soil moisture may amplify mortality and range contraction (Box 2) [58,61].

Overall, whether EWCEs impact range dynamics depends on organismal exposure, which is moderated by microclimate variability and compensatory mechanisms, including thermoregulatory behavior and phenological adjustments [38,62,63]. Climatic buffering effects of topography and vegetation produce **microclimatic refugia** within landscapes, such as the understories of forests with tall and dense canopies or convergent topographic environments (e.g., valley bottoms), that reduce exposure to extreme heat, cold, and drought [64,65]. Populations that live in or disperse to these refugia during EWCEs may persist, preventing rapid range contraction and promoting range expansion. However, the extent to which microrefugia can reduce exposure to EWCEs depends on the capacity for vegetation to buffer extreme climate conditions over time [65]. For example, water availability is critical for maintaining high buffering capacity [66,67]. Heat and drought extremes that increase water deficit could therefore reduce buffering capacity and increase exposure to extreme climate conditions [66]. Tree mortality due to drought, wildfire, and insect outbreaks, as well as anthropogenic disturbances, may compound reductions in microclimate buffering in the long term by increasing canopy openness [66,68]. Understanding the temporal consistency in microclimate buffering during EWCEs is urgently needed to assess exposure and possible impacts on range shifts.

Advancing our understanding of EWCE impacts on range shifts

Improving our understanding of EWCE impacts on range shifts requires quantifying climate variation at biologically relevant spatial and temporal scales and its impacts on population dynamics across large spatial extents. This is a challenging task, as climate data often face trade-offs between high spatial (e.g., 1 km^2 CHELSA climate data [69]) or temporal resolution (e.g., 1 hour for ERA5 climate data [70]), while temporally resolved demographic data covering large spatial extents is rare [71]. Coarse resolutions across either axis represent average measurements over space or time that may overlook short-term or localized extremes and risk underestimating daily maximum or overestimating daily minimum temperatures - both of which can have vital impacts on demography and range dynamics [72–74]. Mechanistic microclimate models that downscale temporally resolved macroclimate data, as well as statistical microclimate models based on globally distributed *in-situ* microclimate loggers, offer paths forward, but may require substantial computational capacity when implemented across large spatial and temporal extents [75,76]. Furthermore, spatiotemporally resolved occurrence data are becoming increasingly available and can be obtained through large-scale and long-term monitoring initiatives (e.g., GLORIA, MIREN) [77,78]), citizen science databases (e.g. eBird and iNaturalist [48]), and airborne remote sensing [e.g., 79].

Expanding climatological and biological data allow ecologists to interrogate mechanisms impacting EWCE-driven range shifts across taxa and regions globally using diverse modelling techniques. Longitudinal process-based models (e.g., occupancy dynamics models, demographic distribution models, abundance dynamics models) can provide spatially explicit predictions of demographic dynamics, including colonization and extinction, in response to short-term climate variability, which may impact range shifts over short or long time periods [71,73]. When temporally replicated biological data is absent, eco-physiological models (i.e., mechanistic models) that estimate organismal responses to temporally variable climate conditions based on physiological first-principles offer a promising alternative for predicting EWCE impacts on range shifts [71,80]. Additionally, before-after-control-impact (BACI) designs can attribute biological responses to single EWCEs, which may contribute to a mechanistic understanding of range fluctuations, though challenges in predicting EWCEs may provide obstacles to obtaining the necessary data [81]. Correlative species distribution models can also improve our understanding of EWCE impacts on range edges when they incorporate environmental stochasticity using statistical distributions that capture information on the frequency and intensity of EWCEs (e.g., the generalised extreme value distribution) [14,82]. Experimental approaches can supplement these models to detect mechanisms by which EWCEs influence range dynamics, but are typically limited to local spatial extents [83].

Implications for Conservation Management

Recognizing that EWCEs often accelerate range expansion and contraction processes pushes participatory and anticipatory planning to the fore [84]. While uncertainties in estimating and predicting the impacts of EWCEs on species' redistribution hampers accurately targeting conservation actions, improvements in near-term ecological forecasting offer a promising avenue for informing anticipatory conservation actions [85]. Boult [86] suggests adopting a forecast-based action approach that is used regularly for planning and mounting rapid recovery efforts, such as deploying on-the-ground actions, to buffer sensitive species to single EWCEs (e.g., installing shading of sea turtle nests in anticipation of extreme heat events; [86]). Knowledge of how EWCEs affect individuals across their geographical range can help inform where forecasting and management efforts should focus. For example, when a species' range core is subject to an EWCE event, the habitat within its range edges can take on enhanced importance as it serves as an extreme weather refuge [e.g., 18,87]. Similarly, anticipating the arrival of native and non-native outlier populations beyond range edges can improve identification and monitoring efforts of population growth and impacts on local ecosystems [84]. Monitoring can then inform population management plans as well as strategic habitat protection and restoration initiatives that facilitate expansion by connecting outliers to primary range or habitat predicted to become suitable in the future [84,88]. Employing these approaches will be critical for ecologically and economically important species, including habitat-forming species, invasive species, disease vectors, and key fishery species.

Concluding Remarks

EWCEs may be catalysts for, or inhibitors of, substantial shifts in species' distributions under a changing climate (see Outstanding Questions). While the probability of an EWCE occurring at a duration, frequency, and spatial position to have an impact on species' ranges may be relatively low, increasing examples of EWCEs on range dynamics highlight the importance of understanding these processes [e.g., 16]. To accurately forecast species redistributions, it will be essential to recognise the complex interactions between extreme events, habitat loss, and gradual changes in climate trends on populations at biologically relevant spatial and temporal scales. Though incorporating EWCEs remains challenging due to data limitations, predictive uncertainties in ecological forecasts, and the inherent complexity of ecological and climatological systems, advancements in data availability and methodological approaches are growing rapidly. Using these avenues to begin exploring the mechanisms we propose will improve our ability to forecast EWCE impacts on range shifts, which can inform proactive conservation management planning.

Outstanding Questions

- To what extent do extreme weather and climate events (EWCEs) alter the dispersal kernel and propagule pressure of a species?
- How do EWCEs change the relative rate and magnitude of range expansion and contraction?
- What is the long-term impact of EWCEs on species range shifts?
    - Do mass mortality events induced by EWCEs frequently cause long-term range contraction?
    - Do EWCE-facilitated long-distance dispersal events often lead to range expansion?
- What is the relative impact of individual versus compound EWCEs on range shifts?
- Besides thermal tolerances and dispersal, what species' traits will mitigate or exacerbate impacts of EWCEs on range dynamics?

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Figures

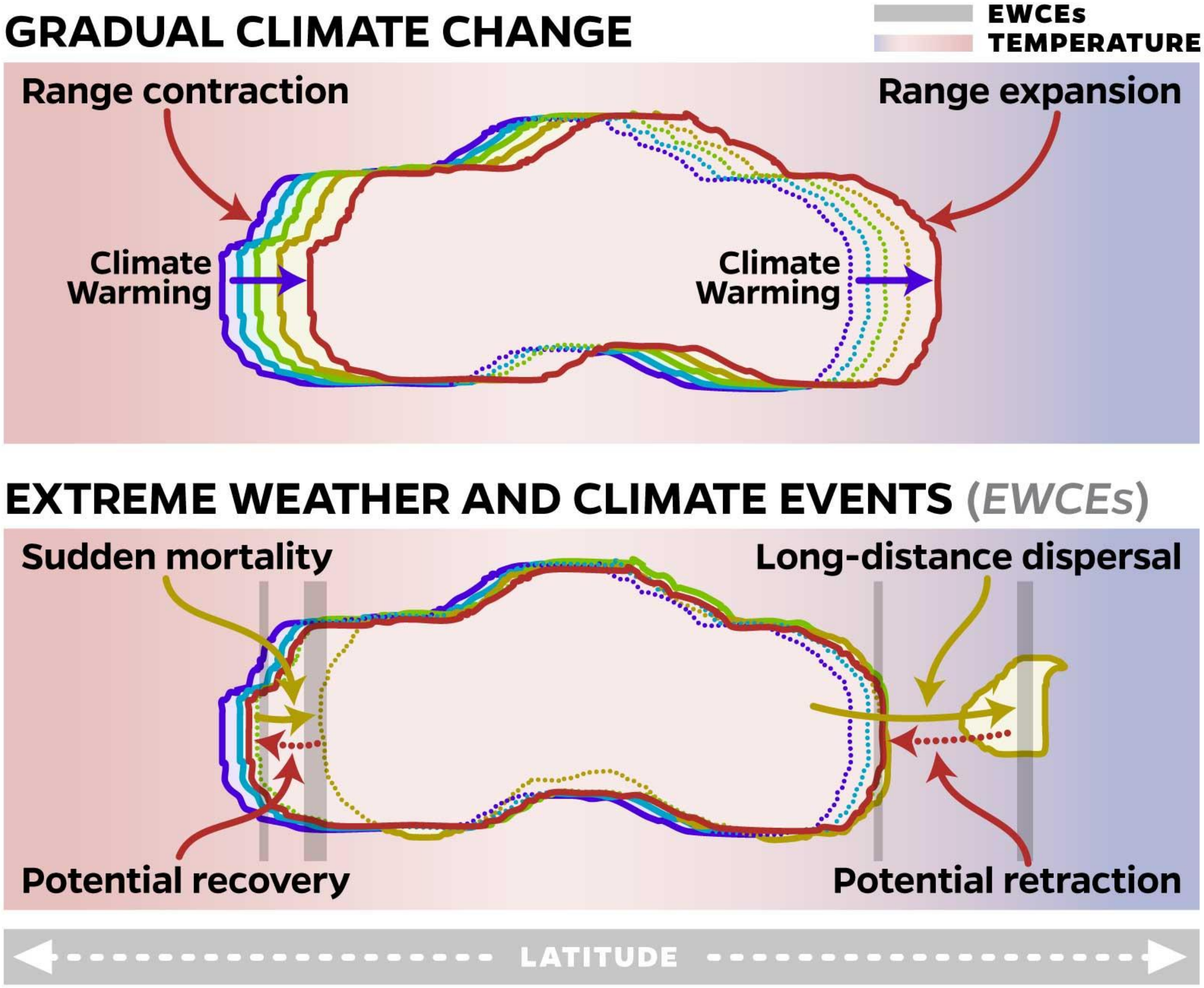

Figure 1 Impacts of gradual climate change and EWCEs on species' range shifts. (a) The traditional view of range shifts, which shows climate warming gradually causing redistribution toward higher latitudes (although range shifts can also occur toward higher elevations and deeper depths) via gradual expansion at the leading edge and gradual contraction at the trailing edge. Colors of ranges indicate shifts in the range over time. (b) The potential impact of EWCEs on range shifts. At the trailing edge, EWCEs can cause high mortality, leading to range contraction. However, populations may recover to the previous range boundary. At the leading edge, EWCEs may cause rapid expansion via long-distance dispersal. However, subsequent EWCEs could cause retraction toward the previous leading edge boundary.

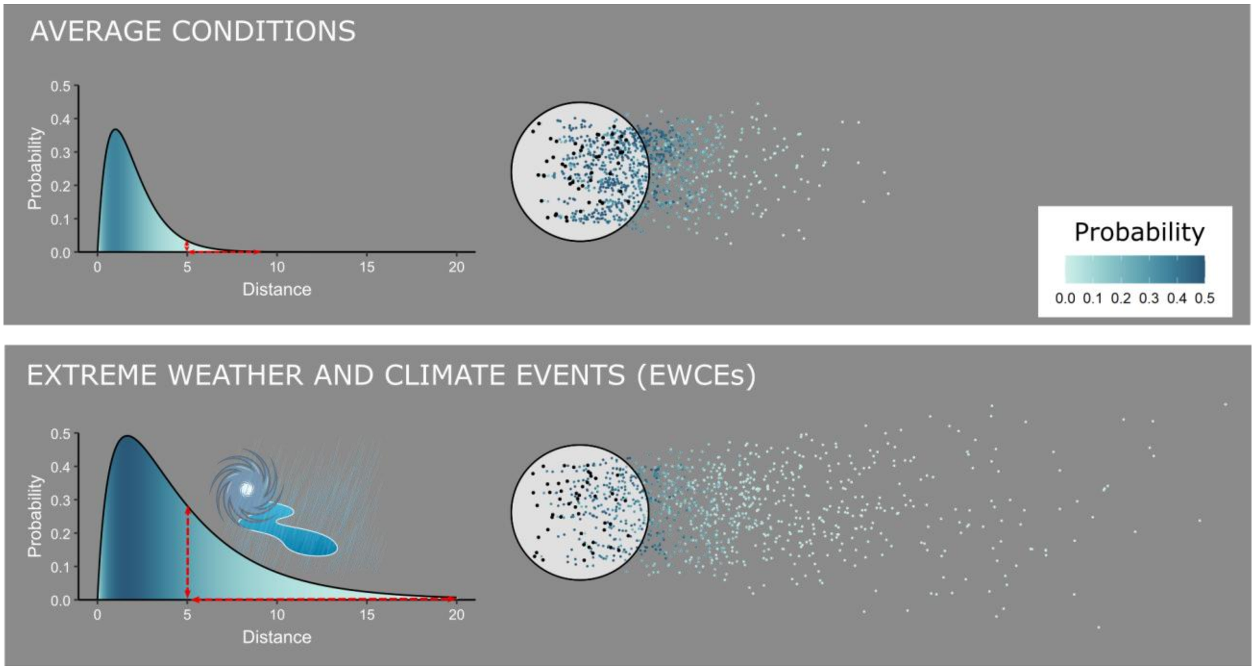

Fig. 2 Extreme events impact on dispersal kernels: When a source population (gray circle) is influenced by average conditions, the dispersal kernel will have a shorter and thinner tail resulting in most propagules (blue dots) dispersing close to the source. Extreme events can increase the length and thickness of the dispersal kernel tail, resulting in higher propagule pressure further from the source population. Red lines indicate the length and width of the dispersal kernel tail. Blue color gradient indicates the probability of dispersal. To simulate dispersal, populations were initialized with 50 individuals and 20 propagules dispersed from each source individual. Dispersal kernels were generated using a generalized normal distribution ($\frac{br}{a^2}\,\Gamma(\frac{2}{b})\,e^{-(\frac{r}{a})^b}$). Dispersal for average conditions were simulated with parameters a = 1 and b = 1, and dispersal for EWCEs were simulated with parameters a = 1 and b = 0.7. While dispersal could occur in other directions, we constrained dispersal to within 10° of the source point for visualization.

Text Boxes

Box 1: What is an extreme event ?

EWCEs occur at multiple spatial and temporal scales and can be defined based on biological responses or meteorological thresholds in reference to different environmental variables [89–91]. We have focused on meteorological thresholds, which define an extreme event as a weather or climate variable surpassing a threshold magnitude and/or duration for a specific area [9,10]. The threshold may be defined using the statistical distribution of events (e.g., 90th percentile) over a baseline time period or over a moving window of time to account for amplification of EWCEs by background climate change [91,92]. When the focus is on a specific species, thresholds may be defined relative to physiological limits [93], such as critical thermal minimum (CTmin) and maximum (CTmax), derived from experimental work. For example, an increasing frequency of EWCEs that surpass these thresholds may indicate that regular monitoring of a population should be initiated to increase detection probability of responses to EWCEs that are not immediately apparent. Regardless, not all EWCEs surpassing a predefined threshold lead to extreme biological responses [94].

EWCEs can alternatively be defined ecologically based on 'extremeness' of both the climatic driver and ecological response across varying levels of biological organisation from an individual to an ecosystem [90]. According to this definition, an EWCE is identified as a statistically uncommon climatic event that significantly disrupts ecological functions beyond what is considered normal variability [90,93]. At the individual or population level, the response, such as fecundity, survival rate, or leaf loss, depends on the actual climatic exposure (e.g., filtered by individual thermoregulatory behaviour or occupied microclimate), as well as on the extremeness of an event relative to the intrinsic species' sensitivity to climatic conditions [93]. At the ecosystem level, the response may be altered forest structure, carbon cycling, or hydrological dynamics. However, defining response-based EWCEs at larger levels of biological organisation may overlook population-level effects that could impact range shifts, as well as EWCEs that have no visible impact due to community resilience.

Given the complexities and context-specific nature of defining EWCEs, researchers must carefully select and explicitly report the definition they use in their studies. While species- and response-specific definitions can offer valuable insights for specific cases, we recommend adopting climatological thresholds, as these provide a consistent framework across systems enabling border comparisons that can help identify which EWCEs are most impactful and which ecological systems are most sensitive.

Box 2: Impact of EWCEs on range shifts

Mangroves

Mangroves are one of the few ecosystems for which the increasing frequency of EWCEs has impacted both range expansion and contraction. While background climate warming is likely causing poleward expansion of mangroves globally, EWCEs may mediate the rate of range shifts [95]. Tropical storms increase the dispersal distance of mangrove propagules, which are buoyant and carried by tides, ocean currents, and storm surges [96]. For example, hurricanes have facilitated expansion at the poleward range limit of mangroves in Florida where the hurricane season overlaps with mangrove propagule production, increasing the probability of long-distance dispersal [15,22,96]. In addition, while extreme cold events are unlikely to inhibit poleward range shifts, they may cause leaf damage and slow the rate of expansion [97]. In contrast, drought events following several decades of favourable climate conditions and physiological adaptations to the high moisture availability, led to an extreme dieback of mangroves and range contraction in Australia [61]. Drought also has inhibited mangrove recovery following hurricanes in the North Atlantic Basin [98], which may lead to range contraction under persistent increased disturbance from hurricanes.

Mangroves have been a key system for understanding the consequences of extreme events and disturbance, including hurricane impacts, such as the mangroves shown here from Pine Island, FL which have been impacted by two significant hurricanes in 2022 and 2024.
© Florida Museum photo by Kristen Grace, March 25, 2017

Kelp

Kelp forests are declining globally, largely due to impacts of EWCEs rather than gradual climate change [17,99,100]. The magnitude of marine heat waves (MHWs) with respect to critical temperature thresholds impacts the degree of mortality [99]. While not all declines have resulted in range contractions, EWCEs may lead to temporary or persistent loss at warm range edges. For example, kelp populations off the Pacific coast of North America experienced severe declines at the southern range limit in the Baja peninsula, Mexico following an intense and prolonged heatwave from 2014-2016 with limited post-event recovery [100]. Similarly, a 100 km range contraction of kelp off the western Australian coast following the 2011 MHW persisted following returns to non-anomalous temperatures [17]. A shift to dominance by turf-forming seaweeds combined with poleward flowing currents that increased the proportion of subtropical and tropical taxa in the ecosystem prevented kelp recovery following the MHW [17].

Giant kelp (*Macrocystis pyrifera*) forests at their equatorial range limit off the coast of Baja California, México at a) Piedra Blanca (Punta Eugenia area) (credit: Rodrigo Beas) and b) near Asunción (credit: Roman Lopez from Cooperativa California en San Ignacio).

Dickcissel

The Dickcissel (*Spiza americana*) is a neotropical migrant bird with a widespread breeding range in the central U.S. An extreme drought in the range core caused temporary abundance increases at northern range edges [18]. These results suggest that range edge habitats can provide temporary refuge when core conditions become inhospitable, producing transitory poleward range shifts. Increasing frequency of EWCEs within the range core combined with background climate change that increases persistence of high abundances at range edges, could thus result in range shifts over time.

Dickcissel (*Spiza americana*) Image courtesy of Caleb Persia, https://www.inaturalist.org/people/cpersia

Glossary

Extreme weather and climate events (EWCEs): Meteorologically, extreme weather events are those that are “rare at a particular place and time of year”, where rarity is defined by a threshold, which can be determined statistically as a percentile (e.g., 90th percentile) of the distribution of events over a baseline time period. Patterns of extreme weather events persisting for some time, such as a season, form an extreme climate event. However, EWCEs can also be defined based on ecological thresholds.

Dispersal kernel: A probability density function that describes the likelihood of an individual dispersing a specific distance from its source location.

Leading and trailing edges: The leading edge is the geographical location that describes the current distribution limit along the expanding range front. The trailing edge is the geographical location that describes the current distribution limit along the non-expanding or contracting range front of a species.

Microclimatic refugia: Regions that are decoupled from macroclimate conditions, experiencing lower climatic fluctuations over time and therefore retaining historical climate conditions as the surrounding climate changes.

Multivariate EWCEs: Multiple EWCEs of different types (e.g., temperature and precipitation) that occur simultaneously in the same area.

Preconditioned events: An EWCE that causes an extreme impact due to a pre-existing climate condition, such as a long wet period or an early spring onset, both of which can amplify impacts of drought.

Propagule pressure: The combination of the number of individuals dispersing to an area at any given time and the number of times individuals disperse to that area.

Resilience: The capacity for a population or species to recover after being impacted by an EWCE.

Resistance: The extent to which an organism is not impacted by EWCEs.

Spatially compounding EWCEs: Multiple EWCEs occur simultaneously in geographically connected regions

Temporally compounding EWCEs: EWCEs occurring in quick succession, leading to larger impacts than if they were to occur in isolation