## TITLE

# Why extreme events matter for species redistribution

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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 discuss processes by which EWCEs could contribute to range shifts, approaches for understanding these mechanisms, and implications of understanding these processes for conservation.

## ABSTRACT

Climate change is altering species' distributions globally. Increasing frequency of extreme weather and climate events (EWCEs), including heat waves, droughts, storms, floods, and fires, is one of the hallmarks of climate change. These events can trigger rapid shifts in species' distributions by impacting dispersal, establishment, and survival of organisms. Despite species redistribution being widely studied in response to longer-term trends of climate change, few studies consider the contribution of EWCEs to range shifts. With EWCEs impacting ecologically, economically, and culturally important species, we call for integrating EWCEs into the study of biodiversity redistribution. Advances in data availability and statistical methods are improving our capacity to understand and integrate these complex processes into adaptive conservation management efforts and biodiversity assessments.

## INTRODUCTION

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]. Climate change can cause conditions to become more or less suitable for organisms, either directly via impacts on organisms and the environment or indirectly via impacts on biotic interactions. 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** (see Glossary) when climatic conditions become more suitable beyond current distribution boundaries [4]. In general, species ranges are shifting toward higher latitudes, higher elevations, and deeper depths in response to warming temperatures [2,4–6] (Fig. 1). Yet, large variation occurs in the rate and direction of range shifts [7,8]. While the background rates of warming temperatures may facilitate gradual range shifts driven by (relatively) slow changes in population dynamics and colonisation/extirpation events, **extreme weather and climate events** (EWCEs) (see Glossary) may amplify sudden expansion and contraction dynamics via impacts on dispersal, establishment success, reproduction, and survival.

EWCEs are increasing in frequency and severity [9,10], with substantial impacts on ecologically, culturally, and economically important species [11]. The Intergovernmental Panel on Climate Change describes extreme weather events as "rare at a particular place and time of year", such as heat, rain, storms, or fires, while extreme climate events are "patterns of extreme weather that persist for some time, such as a season", including heat waves and droughts [9]. While extreme climate events can be associated with long-term meteorological cycles, such as the El Nino Southern Oscillation, they can also occur over shorter time scales [12]. The severity of EWCEs is described by their magnitude, duration, and spatial extent [13]. Meteorologically, they are considered extreme when their magnitude falls beyond a threshold (e.g., the 90th percentile) over a baseline time period for a given location [9,13] (but see Box 1 for ecological definitions of extreme events). EWCEs lasting longer, covering larger areas, or occurring simultaneously or in rapid succession to produce **compound EWCEs**, are likely to have larger ecological impacts, including altering range dynamics and impacting the extent to which range shifts correspond with the rate and direction of long-term climate change.

As the frequency and magnitude of EWCEs is projected to increase further [9,10], understanding, quantifying, and predicting their impacts on range dynamics could inform adaptive conservation management, as well as biodiversity assessments and projections. However, the role EWCEs play in range dynamics remains unclear, in part because attributing range shifts to a specific driver requires long-term evidence of species’ responses to EWCEs, often over large geographic extents [14]. Here, we discuss mechanisms by which EWCEs could affect expansion or contraction of species’ ranges, contributing to a mechanistic understanding of the potential role of EWCEs in range dynamics. We then discuss ways to better understand EWCEs' role in range shifts and highlight how insights into these mechanisms can inform conservation management.

## EXPANSION AND CONTRACTION DYNAMICS

### Expansion

EWCEs can facilitate range expansions by increasing the probability that individuals in a population disperse long distances. This change in dispersal dynamics can be statistically described by a shift in the **dispersal kernel** (see Glossary) [15] (Fig. 2). For example, individuals of 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). Similar dynamics occur amongst animals that engage in active dispersal, with the influence of climate and weather events influencing the initiation, direction, and duration of their dispersal dynamics [16]. Combined with species traits, environmental conditions thus impact the thickness and length of dispersal kernel tails. Increasing frequency of intense storms [17–19], such as hurricanes with high winds and floods, could increase both the distance of dispersal (tail length) and the probability and frequency that any propagule will disperse beyond the average range of dispersal (tail thickness) [15,20,21] (Fig. 2). A consequent increase in **propagule pressure** (see Glossary) beyond range edges increases the likelihood that populations will become self-sustaining over generations and contribute to range expansion [20,21] (Fig. 1).

For expansion to occur following dispersal, individuals must be able to establish, survive, and reproduce at or beyond current range boundaries. While background rates of climate warming may increase climatic suitability of novel areas, EWCEs can improve establishment success through increased climate suitability as well as reducing competition. For example, wildfires can facilitate range expansion of understory plants toward higher latitudes or elevations via the removal of adult vegetation [22,23]. As disturbance frequency increases with EWCEs, reduced competition may therefore facilitate the establishment of range-expanding species that are light- and nutrient-demanding [24–26].

Yet impacts of EWCEs on expansion dynamics will not be consistent across species. In some cases, these processes may lead to shifts that are in disequilibrium with climate change [27,28], while EWCEs could also hinder dispersal or establishment by increasing mortality [29] or altering species interactions [30].

## Contraction

Range contractions can occur when EWCEs cause mass mortality at range edges by exceeding physiological tolerances [31]. While declines in population abundance are more common, extirpation has occasionally been observed in direct response to EWCEs [32]. For example, extreme fires have caused geographically restricted plant species to lose up to 95% of their range [33], marine heatwaves have caused loss of habitat-forming corals and seaweeds at the warmest portions of their range [34–36], and extreme droughts have caused rapid contraction of the ponderosa pine, *Pinus ponderosa* [37]. Impacts of EWCEs on range contraction are likely to be most severe for species that live close to their critical thermal limits, including marine ectotherms and tropical insects [38,39].

EWCEs can also cause retractions at leading edges, causing highly fluctuating range boundaries (Fig. 1). For instance, minimum winter temperatures play a key role in defining poleward range limits in terrestrial ecosystems [40]. While reductions in the frequency of cold events in many regions will facilitate establishment following dispersal to higher latitudes or elevations [41,42], winter low temperature extremes have become more frequent in the mid-latitudes of the eastern US and Eurasia [43,44]. Reduced survival and reproduction, population declines, and local extirpation of expanding populations could consequently cause range retraction [29,45,46].

Fine-grained spatial and temporal climatic variability can play a vital role in reducing species' exposure to EWCEs, and thus explain unexpectedly limited or counterintuitive responses to them [47,48]. For example, many species that live in, or can retreat to, microrefugia are buffered from macroclimatic conditions, mitigating the impact of extreme events [25,49]. Within their current distributions, populations may therefore be constrained to topographic features such as valleys and patches of dense vegetation, or “nurse objects", such as logs and rocks, which reduce exposure to climatic extremes [22,50]. As species expand their range, microrefugia can similarly prevent range retraction and facilitate establishment and survival by reducing exposure to cold winter extremes, fires, or drought [e.g., 51].

## Compound EWCEs could amplify impacts on range shifts

**Compound EWCEs** (see Glossary) [9,52], including preconditioned events, temporally and spatially compounding events, and multivariate events [52], can amplify the impacts of EWCEs on range dynamics. **Preconditioned events** (see Glossary) occur when a pre-existing climate condition, such as saturated soils, results in a stronger outcome when an extreme event, such as high precipitation, occurs. In this case, precipitation may increase flood severity due to soil saturation, increasing long-distance water dispersal and possibly range expansion. Alternatively, range contraction may be more likely to occur following EWCEs when physiological adaptations to a period of favourable climate conditions amplify negative responses (Box 2). **Multivariate and spatially compounding EWCEs** (see Glossary) involve simultaneous events amplifying species responses [52]. For example, simultaneous extreme heat and drought events cause large-scale tree diebacks and contraction at range edges [53], and unusually high temperatures and calm waters cause contraction toward deeper depths in marine algae [54]. In contrast, spatially compounding EWCEs may aid range expansion if an extreme event in one region facilitates dispersal, while an extreme event in a neighboring region facilitates establishment by reducing competition. **Temporally compounding EWCEs** (see Glossary), such as successive heat waves or storms, amplify impacts by occurring in quick succession [52], which may prevent population recovery, leading to range contraction [55] or strengthen propagule pressure beyond current range boundaries by increasing the frequency of long-distance dispersal, leading to range expansion.

## ADVANCES IN UNDERSTANDING EWCES IMPACTS ON RANGE SHIFTS

Improving our understanding of EWCEs impacts on range shifts requires accurately measuring and predicting impacts on populations, species, and ecosystems. This is a challenging task, as EWCEs operate at statistical fringes and data at fine spatiotemporal scales are scarce. To address these challenges, ecologists must combine advances in climate modelling and forecasting with long-term monitoring and experimental approaches.

### Data limitations

Attributing range shifts to EWCEs requires temporally and spatially fine resolution data covering large spatial extents on both climate conditions and species occurrences and population dynamics. Coarse-resolution data, representing average measurements over space or time, may overlook short-term or localized extremes. Traditional climate data sources are not tailored for tackling these issues, as they face the trade-off between relatively high spatial (e.g., 1 km$^2$ CHELSA climate data [56]) or temporal resolution (e.g., 1 hour for ERA5 climate data [57]). Navigating this trade-off involves the risk of underestimating, e.g. daily maxima and overestimating daily minima temperatures - both of which can have vital impacts on demography and range dynamics [58–60]. Obtaining microclimate data at both high spatial and temporal resolutions remains challenging beyond local scales, particularly in some of the most diverse areas of the planet, such as tropical montane regions [61]. Recent advances, including mechanistic microclimate models and a global database of *in-situ* measured microclimate data offer paths forward [62–65].

## Methodological approaches

Approaches integrating observational and experimental data with predictive models will be critical to overcome current data limitations [66].

Observational approaches can be used to examine correlations between EWCEs and shifts in distributions across large spatiotemporal extents, e.g. by harnessing data from large-scale and long-term monitoring initiatives [66]. Citizen science databases, such as eBird and iNaturalist can provide species occurrence data at high spatial and temporal resolutions, facilitating analysis of EWCE impacts [e.g., 45,67]. However, big-data approaches can be hampered by biases from opportunistic data collection [66]. Long-term monitoring initiatives (e.g., GLORIA, MIREN) [68,69] establish protocols and provide structured data collection capable of detecting population- and species-level responses to EWCEs, focusing on areas at and beyond range edges of target species. In addition, intensifying monitoring efforts after an EWCE could improve our understanding of short-term impacts and be accomplished through citizen science initiatives, such as bio-blitzes.

On the other hand, experimental approaches can be used to interrogate mechanistic links between EWCEs and range shifts, as well as evaluate the success of management actions [66,70]. These may include transplant experiments [71] and measuring performance responses to short-term variation under simulated climate conditions [72]. Yet, these approaches are typically limited in spatial and/or taxonomic extent [66].

Finally, forecasting ecological responses using predictive models will help anticipate future impacts of EWCEs on species' range shifts [73]. However, most ecological forecasts are plagued by unpredictability due to: (i) high uncertainty in the future incidence of EWCEs (though the extent of uncertainty will vary based on the type of event and the time horizon), (ii) taxon-specific variation in responses, and (iii) limited biological knowledge [72]. Despite these challenges, near-term ecological forecasts have the potential to inform adaptive management plans because they are at relevant time scales and can be iteratively evaluated as more observations become available [74,75]. For example, near-term forecasts can predict distributional shifts in crop pests in response to extreme droughts [75]. By applying similar methods to other economically or ecologically important species, and communicating findings along with predictive uncertainty to decision makers, spatially, temporally, and taxonomically targeted efforts for management and biodiversity research and assessment can be proactively designed to address potential impacts of EWCEs on range shifts.

## Implications for Conservation Management

Uncertainties in estimating and predicting the impacts of EWCEs on species' redistribution hampers accurately informing management actions. We therefore suggest management approaches be spatially and taxonomically targeted and prioritize building and maintaining ecological resilience across multiple spatial scales [76]. Management and research efforts should prioritise areas at high risk of EWCEs, such the Amazon, North Africa, SE Asia, and Northern Australia, where the number of extreme heat events are increasing [42] (see also [77] for identifying regions in the United States highly impacted by EWCEs). In addition, efforts should be targeted to quantify EWCE impacts on the ranges of economically important species, disease vectors, and invasive species, which can alter ecosystem structure and function and may experience less negative impacts from EWCEs [1,78].

At local scales, efforts should be made to identify, protect, and create microhabitats that buffer species from impacts of EWCEs, which may, for example, prevent rapid contraction at warm range edges following extreme heat waves [79]. Furthermore, we must recognize the potential impact of EWCEs on range shifts when designing and managing protected areas, e.g. by allowing previously absent species to enter if they disperse to the area or managing species that disperse to the area as the result of an EWCE and threaten species already present. At regional scales, dispersal in response to EWCEs can be either limited or enhanced by human development. For example, deforestation and urban infrastructure can impede dispersal pathways that may allow individuals to reduce exposure to EWCEs [80,81]. Management efforts should thus consider the interaction between human actions and species responses to EWCEs and work toward strategic habitat protection and restoration that can improve connectivity between areas that are highly impacted by EWCEs and areas with suitable habitat beyond the leading range edge.

## Concluding Remarks

EWCEs may be catalysts for, or inhibitors of, substantial shifts in species' distributions under a changing climate. To accurately forecast species redistributions, it is essential to recognise the complex interactions between extreme events 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, and the inherent complexity of ecological and climatological systems, data availability and advancements in technical and methodological approaches are growing rapidly. Using these avenues to begin exploring the mechanisms we propose will improve our understanding of EWCE impacts on range shifts.

## OUTSTANDING QUESTIONS

- To what extent do 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?

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## 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 [83–85]. In this paper, we 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 [9,13]. 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 [85,86]. When the focus is on a specific species, thresholds may be defined relative to physiological limits [87], 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 [88].

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 [84]. 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 [84,87]. 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 [87].

At the ecosystem level, the response may be altered forest structure, carbon cycling, or hydrological dynamics e.g.. 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 mangroves**

Mangroves are one of the few ecosystems for which empirical evidence exists to show impacts of increasing frequency of EWCEs on both the expansion and contraction of ranges (Figure I). While the constant pressure imposed by climate warming is likely causing poleward expansion of mangroves globally, EWCEs may mediate the rate of range shifts [89]. Tropical storms increase the dispersal distance of mangrove propagules, which are buoyant and carried by tides, ocean currents, and storm surges [90]. For example, hurricanes have facilitated expansion at the poleward range limit of mangroves in Florida where hurricane season overlaps with mangrove propagule production, increasing the probability of long-distance dispersal [90–92]. Extreme cold events are unlikely to inhibit poleward range shifts, but may slow the rate of expansion because they cause leaf damage [93]. 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 [94]. Drought also has inhibited mangrove recovery following hurricanes in the North Atlantic Basin [95], which may lead to range contraction under persistent increased disturbance from hurricanes.

## Glossary

**Compound EWCEs:** Two or more weather or climate events that occur in short succession of each other or simultaneously in one or multiple nearby regions leading the impacts that are larger than the sum of the impacts if each event were to occur in isolation

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

**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 [9]. Patterns of extreme weather events persisting for some time, such as a season, form an extreme climate event [9]. However, EWCEs can also be defined based on ecological thresholds (Box 1).

**Leading edge:** The geographical location(s) that describe(s) the current distribution limit along the expanding range front of a range-expanding species

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

**Preconditioned events**: A pre-existing climate condition results in a stronger ecological outcome when an extreme event occurs

**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.

**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

**Trailing edge:** The geographical location(s) that describe(s) the current distribution limit along the non-expanding or the contracting range front of a species

## FIGURES

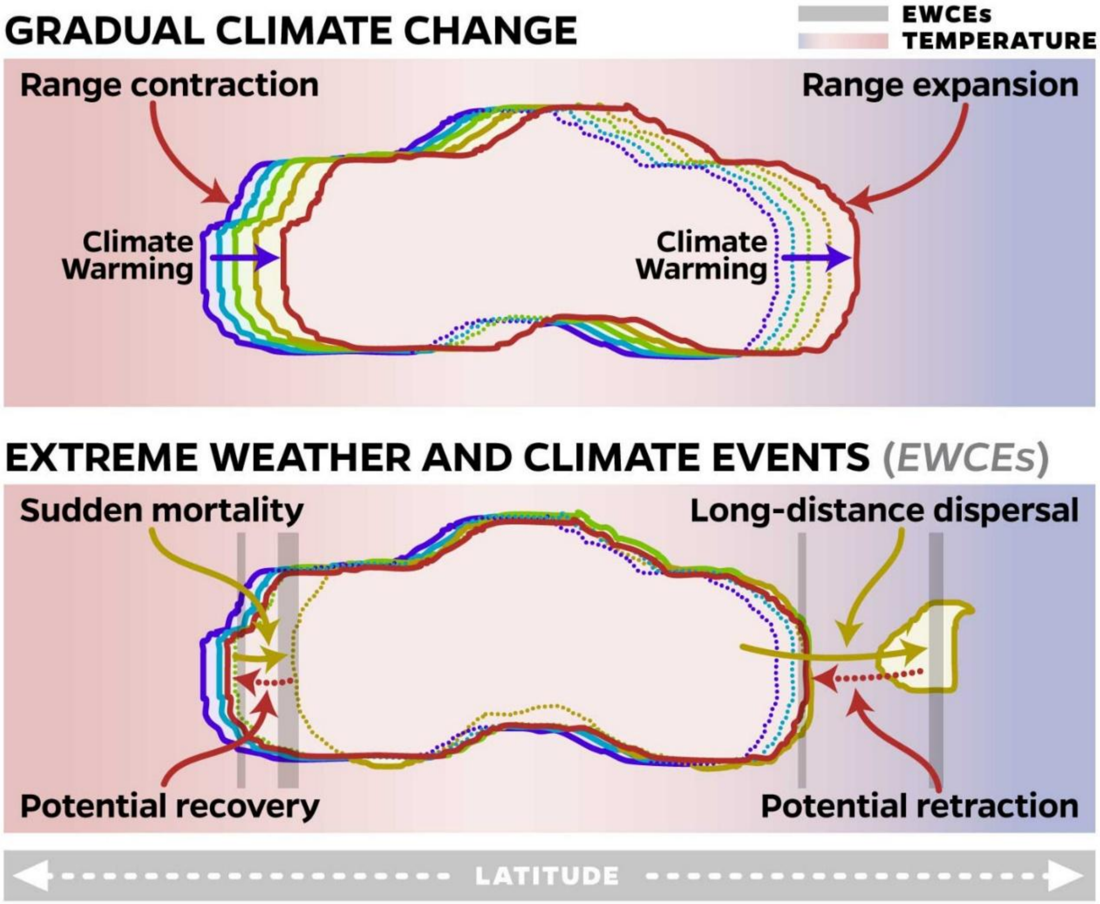

**Figure 1 Impacts of gradual climate change and EWCEs on species' range shifts**. (a) The traditional view of range shifts, which shows climate warming gradually causing redistribution toward higher latitudes (although range shifts can also occur toward higher elevations and deeper depths) via gradual expansion at the leading edge and gradual contraction at the trailing edge. Colours 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.

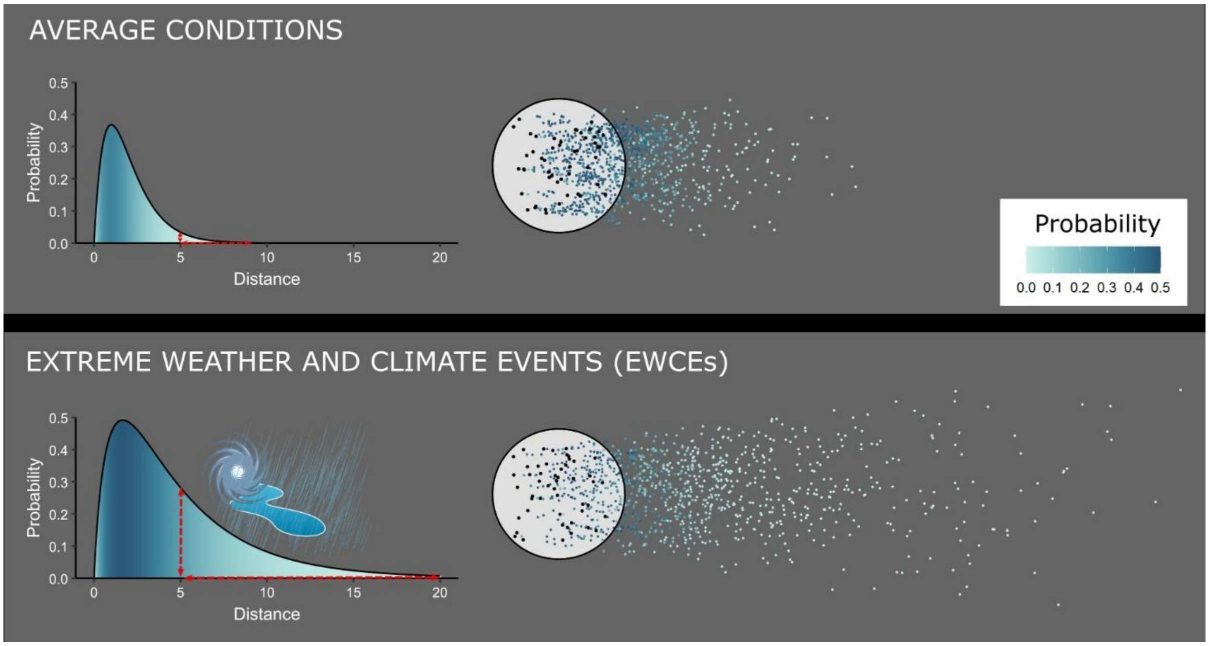

**Figure 2 Extreme events impact on dispersal kernels**: When a source population (gray circle) is influenced by average conditions, the dispersal kernel will have a shorter and thinner tail resulting in most propagules (blue dots) dispersing close to the source. Extreme events can increase the length 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.

**Figure I Florida mangroves:** 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.

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## DECLARATION OF INTERESTS

The authors declare no competing interests.