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Extreme events and habitats as comparative tools for assessing scaled ecosystem responses to stressors in aquatic systems

Katherine E. Dale[1]*, Evie S. Brahmstedt[2☯], Joshua Culpepper[3☯], Kyle A. Emery[4☯], Alexander W. Mott[5☯], Walter A. Rich[6☯], Xinyu Sun[7☯], Audrey Thellman[8☯], Tianfei Xue[9☯], Atefeh Hosseini[10☯], Hadis Miraly[11☯]

1 Department of Biology, East Carolina University, Greenville, North Carolina, United States of America, **2** New York State Water Resources Institute, Cornell University, Ithaca, New York, United States of America, **3** Department of Biology, York University, Toronto, Ontario, Canada, **4** Marine Science Institute, University of California, Santa Barbara, California, United States of America, **5** Department of Biological Sciences, Southeastern Louisiana University, Hammond, Louisiana, United States of America, **6** King Abdullah University of Science and Technology, Thuwal, Saudi Arabia, **7** Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, United States of America, **8** Department of Earth, Marine, and Environmental Sciences, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, United States of America, **9** GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany, **10** Department of Civil, Environmental, and Architectural Engineering, University of Kansas, Lawrence, Kansas, United States of America, **11** College of Environmental Science and Forestry, State University of New York Syracuse, New York, United States of America

☯ These authors contributed equally to this work.
* dalek22@ecu.edu

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Abstract

Two types of extremes are often used as indicators of future change: Extreme climate events and extreme habitats. These extremes can be useful gauges of environmental change, but only if biological, spatial, and temporal scopes are aligned between the extreme and the future change it is hypothesized to mirror. In general, short-lived extreme events provide insights towards acute responses but are not as suitable for assessing long-term ecological or evolutionary change. Extreme habitats can reveal potential long-term adaptations, but community structure and trophic interactions can be challenging to assess due to species often following habitat-dependent evolutionary paths, and these environments tend to undergo gradual rather than rapid ecological change. Community structure and species interactions may further differ for both types of extremes between biological response levels. In cases of a mismatch between the size of an extreme habitat or event and its comparative system, it will be more appropriate to study biological responses at smaller geographic scales than the habitat or event occurs. Here, we explore the opportunities and limitations of a variety of extremes in marine and freshwater systems.

Introduction

"We tend to pick the most notable cases out of general pools, often for idiosyncratic reasons that can only distort a proper scientific investigation...Our strong and biased predilection for focusing on extremes (and misconstruing their trends as surrogates for a totality), rather than documenting full ranges of variation, generates all manner of deep and stubborn errors." - S.J. Gould (Gould, 1997).

Anthropogenic stressors continue to shift both aquatic and terrestrial systems away from their historical baselines, intensifying the need for comparative tools that can offer windows into how biological systems might respond in the future [1]. Two potential comparative approaches are extreme events affecting "status quo" ecosystems, and habitats that have developed environmental conditions that lie at boundary levels for that system (e.g., extremely high temperatures, low dissolved oxygen) [2]. Definitions on what constitutes an "extreme" vary widely in the literature, and are often qualitative [3,4]. Here, we define extreme events and habitats as having measurable environmental conditions that are in the 90–99th percentile of baseline (or historically average) conditions, with the understanding that baselines have been shifting in aquatic ecosystems [5]. Both events and habitats can be geographically defined and have a distinct area of impact. Extreme events further have a well-defined start and end. Extreme events and habitats are thus defined by their environmental conditions, spatial scale, and temporal scale (Fig 1), rather than their impacts [3].

Both extreme events and habitats are appealing as natural comparative tools for how biological systems may respond to future change, versus experimental, mesocosm, or hypothetical modeling experiments that may offer a more limited, restricted, or idealistic view. Extreme habitats and events represent rare or outlier conditions that are expected to become more common under climate change [6], but have not been generally considered together as complementary tools for examining the impacts of global change, with extreme events more commonly studied. In general, aquatic systems under future global change are projected to have higher temperatures, lower oxygen, and more variability [6]. Extreme events such as aquatic heatwaves, storms, and high-precipitation events are predicted to become the new normal and increase in frequency and duration, along with more gradual long-term changes in temperature, salinity, precipitation, and oxygen. Extreme habitats can be potential examples of endpoints for systems experiencing ramp pressure from global change, such as high-temperature reefs and oxygen minimum zones, or examples of stable systems that could act as refugia, such as peatlands. In some cases, extreme ecosystems themselves are experiencing ramp change, and "baseline" habitats represent a potential endpoint, such as Arctic habitats [7]. Crucially, the usefulness of extreme habitats and events varies based on the temporal, spatial, and biological scales of the extreme, its "typical" counterpart, and the future change it is an analog for (Fig 2). Temporal scales (durations and rates of change) for extremes vary from the acute (seconds to minutes) to decadal, while spatial scale varies from microscopic to continental/basin-wide (Fig 1). Biological scales are similar to classic ecological levels of biological organization, from cellular to ecosystem (Fig 2), in addition to trophic level. We discuss the opportunities and limitations of a variety

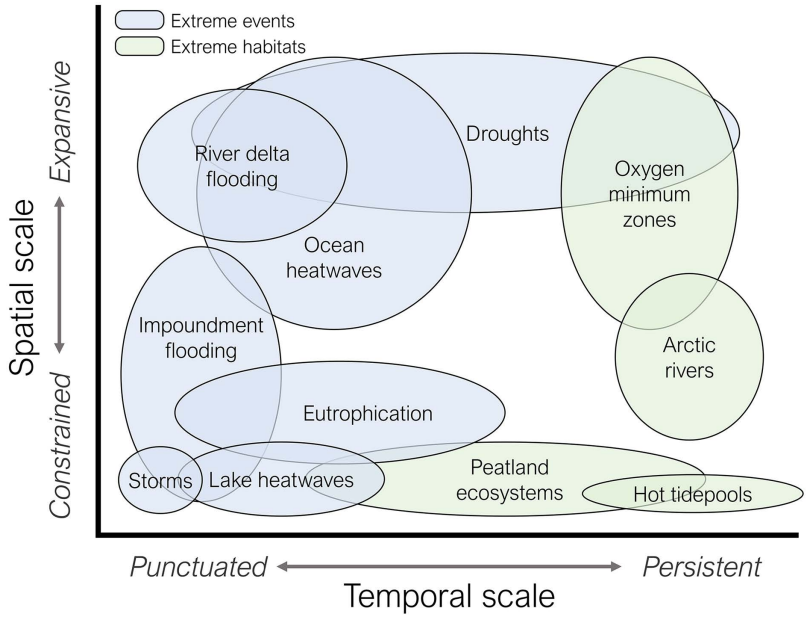

Fig 1. The case studies presented in this study and their qualitative spatial scale (from small to expansive) and temporal scale (from punctuated to persistent). Case studies represent a breadth of temporal and spatial scales.

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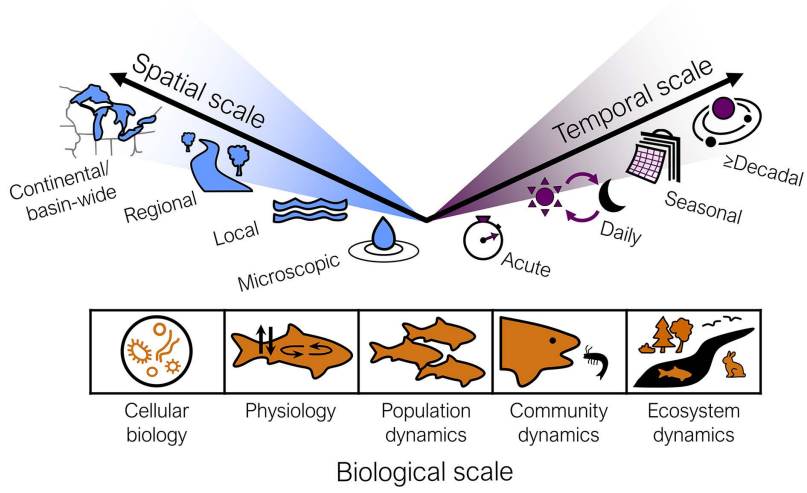

Fig 2. We defined three scales to consider when leveraging extreme events or habitats in global change studies. Spatial scale encompasses the area of effect of the event/habitat and the size of the research study. Temporal scale includes the duration, seasonality, and the interval between events. Biological responses, including evolutionary responses, can be measured at a variety of scales defined by classic ecological definitions, from microscopic to community-wide. The map of North American used for the Great Lakes drawing is available at https://commons.wikimedia.org/wiki/File:North_America_blank_map_with_state_and_province_boundaries.png.

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of extreme events and habitats (Table 1, Fig 2), taking into consideration the impact of temporal, spatial, and biological scales. Though we focus on aquatic systems due to our own areas of expertise, many of our suggestions apply to terrestrial systems as well.

Table 1. List of case studies mentioned, with key limitations and opportunities provided, along with a selection of relevant citations and other systems or events that may have related environmental conditions or similar challenges/uses.

Type	Case study	Limitations	Limitation citations	Opportunities	Opportunity citations	Related systems or events
Extreme event	Aquatic heatwaves	Rapid temperature increases do not mirror slower future rates of change	[8–10]	Identification of organisms vulnerable to rising temperatures Exploring impacts of temperature changes on community composition Mapping habitat and range shifts with temperature	[11–15]	Terrestrial heatwaves
	Consecutive drought-flood events	Different types of aquatic systems vary greatly in hydrological buffering capacity, making it difficult to generalize findings across systems	[16]	Assessing impacts of multiple stressors Evaluating recovery and resiliency capacity of ecosystems	[17]	Rain-on-snow events; saltwater intrusion
	Storms	Difficult to construct generalized impacts due to being highly context-dependent	[18]	Evaluating recovery and resiliency capacity of many types of aquatic ecosystems	[19]	Hurricanes; tornadoes
	Impoundment flooding	Only short-term effects can be considered in cases examining initial impoundment. In cases of long-term water level management, extrapolations may be highly system-specific and layered on other disturbances (e.g., managed water levels; land use change in basin).	[20]	Comparing acute responses to rapid precipitation & reduced-flow/drought events	[21]	Storms or other high-precipitation events; dam releases
	Extreme eutrophication	Effects on higher trophic levels are more challenging to assess, due to increasing ecological complexity and lagged, indirect effects	[22–24]	Predicting responses at lower trophic levels, such as primary producers and microbial communities	[25]	Nutrient pollution; short-term pulse disturbances
Extreme habitat	Hot tide pools	Small physical size leads to communities that are subsets of a typical reef. Responses may not be applicable to broader ecological questions and may be difficult to disentangle effects of other co-occurring unusual environmental conditions.	[26]	Identifying physiological or genetic adaptations/responses to thermal stress	[26,27]	Hot springs; shallow lagoons; vernal pools
	Peatlands	Context-dependent when used to examine refugia	[28,29]	Identifying refugia (in peatlands with specific characteristics) and microrefugia (in late-succession peatlands)	[30–32]	Mangrove forests; groundwater-fed swamps and fens; anoxic and waterlogged soils
	Arctic rivers	High-latitude rivers have different innate photoperiods than lower-latitude rivers Permafrost causes Arctic river systems to function and freeze differently and is a confound when directly comparing to lower-latitude rivers	[7,33,34]	Comparing to temperate rivers when permafrost is lost; constructing comparison studies among Arctic rivers	[35]	Rain-on-snow events; midwinter ice breakups on aquatic systems; terrestrial and aquatic heatwaves
	Tidal and marsh habitats	Organisms that occupy these habitats are likely adapted to oscillations in salinity and inundation, and adaptations and community dynamics may not carry over to systems that do not regularly experience similar variability Disentangling effects of environmental variability from long-term change (such as sea-level rise) can be challenging	[36,37]	Assessing organismal growth, survival, and distribution in relation to regular fluctuations or changes to cyclical patterns	[38]	Tidally-influenced systems and marine shoreline; monsoons; high precipitation events
	Oxygen minimum zones	Slower, long-lasting deoxygenation may not mirror rates of future change Due to divergent evolutionary strategies, species interactions may not be challenging to examine	[39]	Identifying potential evolutionary pathways and tolerances for adapting to low-oxygen conditions	[40,41]	Deep sea vent systems; benthic zones of lakes; swamps, bogs, and other low-oxygen environments

(Continued)

Table 1. (Continued)

Type	Case study	Limitations	Limitation citations	Opportunities	Opportunity citations	Related systems or events
	Hypereutrophic lakes	Species composition and evolutionary history are context-dependent	[42]	Identifying potential evolutionary pathways for long-term adaptation to high-nutrient conditions	[43]	Terminal lakes; shallow coastal lagoons and estuaries
	Terminal lakes	Stability and magnitude of salinity levels varies across systems of different sizes and locations	[44]	Identifying potential adaptations to hypersaline and drying environments Assessing short-term responses to sudden inundations	[45]	High-salinity environments; salt flats; inland seas

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Extreme events

Ecosystems can experience extreme events, where one or more environmental factors dramatically increase or decrease over a short timeframe. Many of these extreme events, including aquatic heatwaves, algal blooms, droughts, and floods are predicted to increase in scale, frequency, and duration under future conditions [46]. Extreme events that span a broad range of spatiotemporal scales may be especially useful tools for understanding how ecosystems may respond to changing conditions (Fig 1, Table 1). Aquatic heatwaves are one example, ranging from short-lived and spatially constrained to long-lasting and expansive. Marine heatwaves are defined as an extreme temperature event that lasts at least five days with temperatures exceeding the 90th percentile of a 30-year baseline, with a spatial extent set by these thresholds [47]. Long-lasting heatwaves that encompass ocean basins, like the 2014–2016 North Pacific warm "blob" [11] can provide informative opportunities for projecting the impacts of rapidly rising temperatures on a broad scale, such as widespread mass mortality events across a range of taxa, and thus which species are potential "winners and losers" under more frequent heatwaves and long-term warming [10]. Shorter, smaller aquatic heatwave events have been used to examine the speed and magnitude of shifts in primary producer abundance, which can be compounded with long-term warming; for instance, extreme heatwaves in Australia triggered a transition from kelp forests to seaweed turfs [13] and heatwaves off Canada caused changes in zonation and abundance in a coastal community [12]. Researchers should select events that mirror the spatial, temporal, and biological scale of impacts they wish to study.

In particular, the duration of an event will determine if acute versus chronic biological responses can be reasonably measured. Long-lasting aquatic heatwaves have been used to assess both shorter-term effects such as algal blooms that closed shellfish fisheries [48] as well as the abrupt reorganization of communities, from changes in both bottom-up and top-down forcing [14] to range shifts [15]. However, the rapid increase in temperature that characterizes heatwaves may limit the inferences regarding more prolonged and gradual ocean warming that could result in evolutionary adaptations rather than mass mortality or migration [49]. Experimental evidence has demonstrated that the rate of warming is critical for understanding species' responses, and that rapid rates of warming may induce short-term impacts of greater magnitudes or mass mortality events [9]. The projected pace of warming and species' abilities to adapt is more gradual [50], though rapid evolution has been shown to occur under extreme events [51,52]. The ability to observe rapid adaptation can inform responses to longer-term climate impacts, but the interaction of these adaptations with long-term change remains unknown.

Another element of temporal scale to consider is the timing between consecutive extreme events. The recovery interval between events influences ecological memory and can determine the dominant effects, from short-term physiological

responses or plasticity to long-term community changes [53,54]. Thus, successive extreme events can provide useful information on the resilience of organisms and their communities. Drought-flood abrupt alternation events are one such example, defined as successive dry-wet periods that occur within a single year [16]. Though the individual effects of droughts or floods are often studied independently, the combined effects of consecutive extreme events can exceed those of the individual hazard disasters, severely altering the water quality and biota of habitats [55]. Organisms that survived prior droughts may be in suboptimal physiological states, decreasing their resilience to subsequent disturbances [19]. Droughts can also cause changes in community composition, which in turn influence community resilience to floods [19]. For instance, a European lake switched from being phytoplankton-dominated to being macrophyte-dominated under drought conditions, but reverted back once water levels rose [56]. However, due to the creation of a standing macrophyte seedbank, the system was hypothesized to be more likely to make the switch back to being macrophyte-dominated under weaker droughts in the future. A similar cascading phenomenon can be seen with aquatic heatwaves, where physiological assays of microbes demonstrate that while stable gradual warming can increase primary production, cyclical extreme heatwaves do not, largely due to the cooling phase, which can be an added stressor (rather than a recovery period) for microbes [8]. For storms over aquatic systems, more frequent events may benefit species that perform better in variable conditions or have high dispersal/colonization capabilities under turbulent conditions created by high winds [18]. These examples highlight the importance of considering the timing between successive disturbances in studying the biological impacts of extreme events.

Temporal alignments between the extreme event and potential applications include the duration of anticipated impacts. Impoundment flooding after the construction of dams is one example. Impoundment flooding and flooding from elevated precipitation are both characterized by rapid freshwater buildup in an area that previously had no widespread standing water. However, comparisons between these high-water events (and reduced flow downstream of an impoundment, comparable to drought) are limited [21]. When comparing the filling phase to high-rainfall events, only ecological responses measured within hours to days should be used to predict impacts of future extreme flood events, since impoundment flooding ultimately creates a standing water body. Alternatively, the downstream, low-flow effects may be more relevant to study long-term, given the nature of droughts being ramp events characterized by extended periods of zero or low precipitation.

In addition to temporal aspects of scale, spatial scale in terms of magnitude and size should also be aligned between extreme events and potential applications. For instance, storms over aquatic systems vary based on timing, frequency, intensity, and biological characteristics of the communities they impact, potentially limiting their usefulness in applying to other systems such as tornados and hurricanes [18,19]. Studies of storm effects on seagrass have shown that the size and connectedness of seagrass patches, in combination with storm magnitude and duration, determined how likely meadows are able to recover [57], and damage to vegetation adjacent to streams and lakes following ice storms depended on the size of the system [58]. Returning to an earlier example, the cascading effects of drought-flood abrupt alternation have been primarily studied for larger spatial domains, such as river basins. Downscaling is listed as a priority for future work on successive drought-flood events [16], though at least one study has shown that smaller streams experienced larger fluctuations in their microbial communities in response to drought-flood abrupt alternation than larger rivers [59].

Sociological aspects may also influence the applicability of extreme events. Applying conclusions learned from dam impoundment flooding to other flooding (or drying) events depends upon whether or not the water releases are managed (i.e., consistent and regular) and if water level management mimics stabilizing flow vs. simulating natural variations [20]. In 2017, extreme flooding from heavy precipitation affected both Lake Ontario and the St. Lawrence River, an engineered riverine system with managed water levels [60]. The overlap and outward similarity of these parallel high-water events sparked stakeholder conflict over what was to blame for shoreline damage: Natural global variability, climate change, or management. The complex social and ecological contexts of impoundments illustrate how any opportunities for

comparison to flooding or low-flow/drought events under climate change must be contextualized due to differences across river ecosystems and the varied drivers of management.

Extreme events may have variable impacts on biological responses at different trophic levels and organism sizes. Extreme eutrophication events and storms can cause increases in toxic cyanobacteria, declines in zooplankton biomass, and changes in phytoplankton-zooplankton interactions [18,61]. At the same time, higher trophic-level organisms such as fish and macroinvertebrates are indirectly affected by blooms and storms, and impacts vary based on the location-specific food web, geomorphology, and type of water body [22,23]. In one study, fish biomass was positively correlated with eutrophication in freshwater but negatively correlated in a brackish system, primarily due to trophic variations in prey fields driven by salinity differences between the two habitats [24]. Few studies have linked the abiotic effects of extreme storms to resultant biological responses at higher levels [18]. This limited evidence suggests that extreme events may be most powerful for predicting the impacts of future change on lower trophic levels.

Habitats with stable extreme baselines

Ecosystems at the edges of their environmental range, such as for salinity, temperature, or rainfall, serve as valuable but imperfect tools for understanding long-term anthropogenic change (Table 1). Extreme habitats are typically stable and persistent, unlike extreme events, and offer a different lens for examining future change. However, like extreme events, misaligned temporal, biological, and spatial scales may also result in unforeseen confounds when using extreme habitats to study other systems in a changing climate. American Samoa is home to unusually hot tide pools that have been used to examine the effects of prolonged elevated temperatures on corals, primarily coral genetic responses, plasticity, and cellular processes [26,62]. However, these geographically small extreme habitats are not perfect analogies for typical reefs that are experiencing long-term warming related to climate change, as their small size results in co-occurring environmental or physical factors that are also unusual or extreme, beyond just temperature alone. Water flow in tide pools is typically restricted due to how tide pools are structured and their small size. Heat tolerance in corals is partially driven by water flow, with reduced flow leading to lower survival and recovery of corals from bleaching [63]. Thus, conclusions regarding the effect of temperature on coral physiology may be hard to separate from other size-dependent conditions to which hot tide pool corals have adapted.

Differences in spatial scales between tide pools and reef also lead to challenges in comparing community dynamics. Many tropical macroalgae have higher thermal tolerances than corals, so one might hypothesize that algae would have a competitive edge over corals in hot tide pools, offering a glimpse of what future competition would look like in warming reefs. However, large herbivores, a significant control of algal abundance [64], are typically excluded from hot tide pools due to physical constraints. Thus, hot tide pools are imperfect tools for measuring future coral-algal competitive interactions. Tide pools may also contain only a handful of coral species (or other taxa) versus a typical reef that is home to hundreds, making potential changes in species interactions difficult to assess. Hot tide pools, and similar size-limited systems such as hot springs, shallow lagoons [27], and vernal pools, are most useful for examining biological responses at smaller biological scales than ecosystem or community responses, such as organismal physiology, plasticity, molecular heat-stress mechanisms, and microbiology.

Hot tide pools show the limitation of using a size-limited extreme habitat as a comparative tool for larger systems. As with extreme events that vary in size, timing, and magnitude, extreme habitats that span a variety of spatial and temporal scales could be especially useful. Salinity in inland water systems can increase due to anthropogenic activities such as diversions, droughts, road salting, increased evaporation under hotter air temperatures [65], which have been shown to negatively impact plankton abundance and taxon richness [66]. An extreme habitat that could be used to predict potential responses to salinity increases are terminal lakes, bodies of water that have no outflow, which are often naturally hypersaline owing to their narrow balance between input (i.e., precipitation, surface flow, subsurface flow) and output (i.e., evaporation, seepage). Terminal lakes are also under major threat due to human activities but remain important sites to explore

how salinization and drying of freshwater systems will impact aquatic species [67]. They are particularly useful due to their closed nature and limited biodiversity [45], and the intensity and consistency of salinity levels vary across lakes of different sizes and locations. For instance, salinity levels can be very consistent in large terminal lakes such as the Caspian Sea, and more variable in lakes that are filled episodically or seasonally; consequently, some lakes have higher numbers of species endemic to hypersaline environments, versus halotolerant species that are also found in standard freshwater systems [68]. Extreme habitats that come in a wide array of sizes and intensities are especially useful as comparative tools, as researchers can more easily select system(s) that offer a reasonable contrast for their system of interest.

Hot tide pools and terminal lakes both represent extreme habitats that are examples of endpoint conditions from ramp disturbances. Some extreme habitats can also represent potential stable areas or refugia. These systems may still act as heuristic comparative tools for baseline conditions but are also useful for examining what environmental characteristics (and at what temporal and spatial scales) improve resilience and create refugia for species escaping climate-altered habitats. Peatland ecosystems are one such potential habitat, and are created when vegetation dies, accumulates, becomes inundated, and then resists decomposition due to very low pH and dissolved oxygen. Examples include bogs, which are rain-fed and often nutrient-poor, and fens, which are fed by groundwater and are often more nutrient-rich. Peatlands may be useful comparisons for ecosystems that sequester carbon and have anoxic or low pH conditions; these include forest patches preserved during logging, mangrove forests, anoxic and waterlogged soils, or groundwater-fed swamps. However, peatlands can also act as refugia. Their stability depends on spatial and temporal considerations at the landscape and ecosystem scale and within the peatland itself [29]. Hydrology often dictates the existence and characteristics of a peatland. If a peatland is in a dry climate, it will have greater stability if groundwater-fed rather than rainwater-fed [69] and the same is thought to be true for peatlands in climates experiencing drier-than-normal conditions [70]. The stability of peatlands with permafrost is even more nuanced [71], for example, if they are on a north- or south-facing slope and thus more or less susceptible to heating and evaporation from solar radiation [28]. Similar to other context-dependent extremes, local landscape characteristics thus determine the stability of different types of peatlands.

Microrefugia and long-term succession within a single peatland are also useful for examining internal stability. Słowińska et al. [31] observed that a peatland in Central Europe had both wet and shaded sites adjacent to drier and sunnier sites, indicative of microclimates or microrefugia that may persist under climate change. Tied to the existence of microrefugia in peatlands is the long-term process of ecological succession, introducing an additional temporal scale consideration for the usefulness of peatlands in assessing stability. Peatlands in later successional stages are likely to remain more stable over time due to peat layers developed over millennia, while younger, early-succession peatlands may be more vulnerable to plant community changes [30].

While peatlands can act as stable refugia, the rapid shifts occurring in other extreme habitats necessitate the identification of existing systems that could inform future ecosystem projections. Rivers globally are losing seasonal and permanent ice, but this effect of climate change is especially amplified near the poles [72]. In the absence of robust, long-term, cross-seasonal data for Arctic rivers, it may be tempting to use lower-latitude ice-covered temperate rivers as comparative tools for how poleward rivers may respond under warming. However, Arctic rivers are characterized by permafrost and extreme solar seasonality, resulting in months of partial or complete darkness [33]. Thus, Arctic rivers may not respond ecologically to ice and snow loss in the same way as temperate rivers, with winter productivity likely still lagging behind temperate systems due to limited light [7]. Other systems where similar effects could be seen include retreating glaciers, rain-on-snow events, and high-latitude forests [73]. However, temperate rivers could still be used as a comparison for other biological aspects of Arctic rivers. Due to permafrost, some Arctic rivers freeze bottom to top, which normally limits benthic ecological activity. As permafrost is lost, these systems may switch to freezing top to bottom, more similar to lower-latitude systems [35]. Non-extreme events and habitats can be leveraged to study extreme systems, if contextual scale elements such as seasonality and latitude are considered when constructing comparison studies.

Choosing appropriate study timeframes is also important when studying extreme habitats. Environmental conditions may be anomalous when considered on an annual basis but may be considered "normal" in the context of long-term or seasonal trends. For instance, tidal marsh or river delta habitats could be considered extreme with respect to their large swings in daily or seasonal water levels. However, organisms in these ecosystems are likely well-adapted to cyclical inundation [37], and it may be inappropriate to use these habitats to examine potential short-term responses to rapid increases or decreases in water levels due to events such as floods, storm surge, or shelf collapse. Rahman et al. [36] found that heavy rains during monsoon season had positive effects on mangrove growth and postulated that unprecedented rising sea levels, rather than monsoons flooding, were negatively impacting mangrove populations. Both phenomena represent changes in water levels, but the differences in rate, timing, and salinity led to opposite effects. Environmental conditions that are anomalous and used as indicators for future change should be carefully considered in the context of (or sufficiently separated from) typical ecosystem variations for that habitat. Habitats experiencing extreme swings in water levels are likely still useful for examining long-term adaptations to cyclical inundation (or changes in cyclical patterns), including community and ecosystem effects [38].

However, community dynamics can be challenging to compare between baseline and extreme habitats if species in the same extreme habitat may follow different adaptation strategies. Upwelling regions are renowned for their exceptional productivity, which produces a significant amount of sinking organic matter. This in turn can cause high decomposition rates and extreme low-oxygen conditions in the upper water column. These oxygen minimum zones (OMZs), along with similar habitats such as peatlands, swamps, deep-sea vent systems, and the benthic zones of lakes, can be used to examine alternative evolutionary pathways in response to low-oxygen environments. Some organisms within OMZs have evolved unique physiological strategies to continue to reside within low-oxygen areas, including increasing oxygen uptake, lowering metabolic demands, and using anaerobic respiration [39], though these organisms may be living at the very edge of their tolerance range [41]. Within the Humboldt Current system, krill and squat lobsters have a high tolerance for hypoxia, allowing them to use the OMZ to avoid predation [40]. In an alternative strategy, calanoid copepods near shallow OMZs remain intolerant to low oxygen and instead have abandoned typical diel vertical migration, permanently remaining in higher-oxygen surface waters [40]. This behavioral switch significantly increases trophic transfer efficiency and biomass of small pelagic fishes that feed predominantly at the surface [40,74]. While some work has been completed on microbial community dynamics in OMZs [75,76], macrofaunal community dynamics are difficult to assess due to these varying evolutionary trajectories and subsequent differences in community traits, such as trophic structure [39]. In this example, impacts at smaller biological scales are more robust to examine, similar to the spatially-limited hot tide pools previously discussed.

Stable hypereutrophic lakes (characterized by high nutrient/algal biomass levels and low water transparency) are an additional example of the challenge of assessing community dynamics, while still being useful systems for examining species-level adaptations to extremely high nutrient loads. A study of 1,000 lakes from across the USA drew general conclusions about phytoplankton community compositions under various phosphorous, temperature, and pH gradients [42]. However, data from 128 lakes in Iowa, USA showed that *Daphnia pulicaria*, a keystone microcrustacean species, was equally as abundant in hypereutrophic lakes as in mesotrophic and mildly eutrophic lakes, suggesting local adaptation to hypereutrophic conditions in these systems [43]. At the same time, *D. pulicaria* had a weaker top-down control on phytoplankton in hypereutrophic lakes than in more lakes with lower nutrient loads [43]. Simultaneously, related species failed to adapt to hypereutrophic conditions, leading to decreased abundance and even local extinction [76]. The OMZ and hypereutrophic lakes are examples of extreme habitats that can be used to study evolutionary pathways across different taxa, while higher trophic levels and species interactions such as predation and diet are more challenging to assess as ecological community composition in extreme environments diverge from their baseline counterparts. [65]

Synthesis

Extreme events and habitats represent opportunities to see how ecosystems and their organisms may respond to future environmental change. In general, extreme events, which may be shorter-term but impact a geographically large area (Fig 1), are well-suited to assess acute responses and community or ecosystem-wide effects for lower trophic levels; however, it is more difficult to assess evolutionary adaptations and pre- and post-parameters. Extreme habitats are ideal for studying physiological and organismal responses such as metabolism, biochemical pathways, reproduction, evolutionary responses, and community ecology, especially at scales below ecosystem responses, but community dynamics can be challenging to compare to typical systems due to spatial limitations and diverging evolutionary pathways. Similar to extreme events, studies on lower trophic levels may be more robust than those at higher trophic levels. Additionally, extreme habitats that reflect end-points of environmental gradients do not capture early-warning signals or transitional stages [77]. Some extreme habitats, like peatlands, are useful for studying the temporal and spatial elements that create refugia. The case studies discussed here can be creatively applied to many other related systems or other types of extreme events (Table 1). For instance, aquatic heatwaves are applicable to terrestrial heatwaves of similar size and duration; hot tide pools could be used to study small hot springs or microbial or acute responses in vernal pools; and peatlands could be leveraged for examining how mangrove forests function as refugia, or for evolutionary responses in anoxic/waterlogged soils.

A single variable can have different effects in extreme habitats versus extreme events. For instance, sudden anoxic events can cause mass mortality of organisms, but persistent low-oxygen habitats give rise to novel adaptations. Extreme environmental variables do not occur in isolation, as other abiotic conditions, evolutionary rates, and biological interactions may also be extreme or highly unusual. These different biotic and abiotic conditions may interact with one another in unique ways that confound comparisons to baseline conditions [54].

A consistent theme across all types of extremes is that the effects of an extreme event, or the characteristics of an extreme habitat, are highly context- and scale-dependent (Fig 1., Fig 2, e.g., size, location, proximity, orientation, duration, frequency, seasonality, age). At the same time, some aspects of temporal and spatial scale may be more critical to align than others: For example, in the case of extreme flood events, intensity and frequency appear to have a greater effect on river geomorphology and benthic habitat than duration, seasonal timing, or spatial extent [21], and size is more important to consider when studying hot tide pools than patch dynamics. Studying extremes across a variety of regions and spatiotemporal scales will be particularly useful for constructing a more holistic view of how biological systems will respond to future change.

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Author contributions

Conceptualization: Katherine Dale, Evie S. Brahmstedt, Joshua Culpepper, Kyle A. Emery, Alexander W. Mott, Walter A. Rich, Xinyu Sun, Audrey Thellman, Tianfei Xue, Atefeh Hosseini, Hadis Miraly.

Project administration: Katherine Dale, Alexander W. Mott.

Visualization: Katherine Dale.

Writing – original draft: Katherine Dale, Evie S. Brahmstedt, Joshua Culpepper, Kyle A. Emery, Alexander W. Mott, Walter A. Rich, Xinyu Sun, Audrey Thellman, Tianfei Xue, Atefeh Hosseini, Hadis Miraly.

Writing – review & editing: Katherine Dale, Evie S. Brahmstedt, Joshua Culpepper, Kyle A. Emery, Alexander W. Mott, Walter A. Rich, Xinyu Sun, Audrey Thellman, Tianfei Xue, Atefeh Hosseini, Hadis Miraly.

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