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Predicting responses to marine heatwaves using functional traits

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Marine heatwaves (MHWs), discrete but prolonged periods of anomalously warm seawater, can fundamentally restructure marine communities and ecosystems. Although our understanding of these events has improved in recent years, key knowledge gaps hinder our ability to predict how MHWs will affect patterns of biodiversity. Here, we outline a functional trait approach that enables a better understanding of which species and communities will be most vulnerable to MHWs, and how the distribution of species and composition of communities are likely to shift through time. Our perspective allows progress toward unifying extreme events and longer term environmental trends as co-drivers of ecological change, with the incorporation of species traits into our predictions allowing for a greater capacity to make management decisions.

Integrating marine heatwaves into projected impacts of warming

The oceans of the world absorb much of the excess heat trapped by rising global carbon dioxide emissions, and consequently have warmed by 1.0°C above pre-industrial levels [1]. This heating has already had significant impacts on the survival and distribution of marine species, including range shifts and altered community structure [2]. While we are beginning to understand how gradual warming drives species range shifts over decadal scales [2–4], extreme events driven by climate change have received increased attention as a threat to marine systems globally [5–7]. MHWs are discrete, prolonged, anomalously warm water events [8] that are the result of both local oceanic and atmospheric processes, and can be modulated by large-scale climate variability [7]. Subsequently, some of the most well-known MHWs are associated with major **El Niño-Southern Oscillation** (see Glossary) events [5,7], with recent events causing the complete restructuring of ecosystems across hundreds of kilometers [9–11]. MHWs have become more frequent and more intense over the past century [12], with this trend projected to increase with future climate change [13]. To date, we lack a conceptual framework for incorporating the increased variability associated with MHWs into our predictions for how future ecological patterns and biodiversity will be altered.

The ecological consequences of steady warming trends over many decades are well considered and have been reviewed elsewhere [2]. Broadly speaking, when warmer temperatures begin to compromise fitness or surpass thresholds that would lead to mortality and local extirpation (Figure 1A), responses by individuals and populations include acclimatization or adaptation to higher temperatures (Figure 1B) and/or shifts in geographical location to remain within the preferred **thermal niche** (Figure 1C). A range of marine taxa have already undergone poleward shifts under climate change [2,10,14]. While it appears that marine species are tracking temperature isotherms more closely than terrestrial species [15,16], there is considerable variation in this response [17]. As a result, there has been an emergence of novel communities alongside changes in species interactions that can cause further impacts through their respective marine food webs

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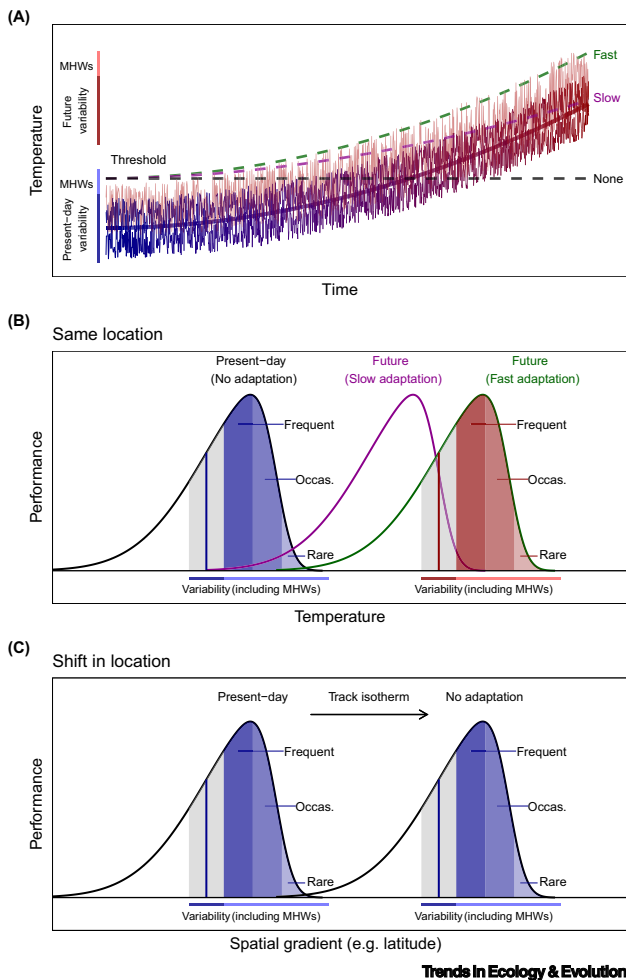brussell@hku.hk (B.D. Russell).

Figure 1. Illustration of changes in temperature and adaptation over time (A), and changes in performance with temperature (B) and spatial gradients (C). (A) Changes in mean temperature (unbroken thick line) and temperature, including variability and marine heatwaves (MHWs; unbroken thin line) over time. Broken lines indicate the physiological thresholds beyond which deleterious impacts will occur, assuming no adaptation (black), slow adaptation (purple), or fast adaptation (green). (B) Changes in performance through increasing temperature with the organism remaining in the same location. Unbroken thick vertical lines indicate present-day (blue) and future (red) mean temperatures with current temperature variability shown either side (light-gray shading), and potential MHWs indicated by shading to the right. MHWs are separated by their extremity and likelihood, either being frequent, occasional (Occas.) or rare. The adaptation potential of the organism [as indicated in (A)] indicates their ability to shift their performance curve to compensate for the higher temperatures, and is shown as no adaptation/present-day (black), slow adaptation (purple), or fast adaptation (green). (C) Changes in performance along a spatial gradient with the organism tracking the isotherm to remain with their thermal niche. The lines and shadings to indicate their performance at different temperatures (mean, variability, and MHWs) are the same as in (B).

[14,18]. Yet, predicting which species will and will not undergo range shifts, the timing of these shifts, and subsequent impacts on local species richness remains problematic (but see [4]).

Currently, attempts to predict species range shifts and changes in local abundance largely focus on latitudinal shifts based on gradual increases in mean temperature over the long term (e.g., [2,16]), alongside consideration of how physical processes currently controlling distribution, such as the role of currents in dispersion, will be altered by climate change (e.g., [18]). Mean temperature increases are clearly important (as described earlier) in determining both lethal limits (e.g., [16]) and will have sublethal implications (e.g., altered energy budgets; [19]) over the coming century. However, individual performance and population dynamics integrate across thermal variation through time, and key failure points (e.g., mortality or local extirpation) are particularly sensitive to thermal extremes [20]. Instead of physiologically determined temperature thresholds only being exceeded toward the end of the century, as is often implicitly assumed when predicting biological changes, the stochastic nature of MHWs means that such thresholds can already be exceeded in the present-day during a MHW event (Figure 1A), thereby adding further uncertainty around predictions. Particularly for those populations close to their upper thermal

limits, regardless of whether marine organisms adapt to novel temperature conditions (Figure 1B) or shift their location to track the isotherm (Figure 1C), they will still be subjected to potentially stressful MHWs before the end of the century, with extreme events becoming increasingly common if the rise in baseline temperature and/or the magnitude of thermal variability outpaces acclimatization and adaptation [6,12]. During individual MHW events, marine organisms have to respond to large changes in temperature over shorter periods (weeks to months) than changes of this magnitude generally occur [21], meaning that the typical response mechanisms used for more gradual warming (adaptation or range shift) may be unfeasible due to the temporal scale of the environmental pressure relative to the life-history patterns of the organism. As a result, acclimatization may have a proportionally much larger role in responses to MHWs; however, significant uncertainties about the potential for adaptive phenotypic plasticity to mitigate climate change effects remain [22]. Therefore, there is a temporal mismatch between most long-term datasets and the realities of the selective forces imposed by MHWs, leaving researchers with relatively few empirical data to guide predictions.

Traits refer to 'any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization' [23]. By using organism traits, rather than the species identity, it is possible to assess differences in the functions performed by organisms, and functionally link individual organisms with community structure and dynamics across spatial or temporal gradients. Although much of the recent work in this area concerns how species traits can predict community structure [24–27], the use of functional traits has been fundamental in the development of a variety of topics, including early considerations of the **r-K selection continuum** [28], the development of **Grime's triangle** [29], attempts to predict which species are most likely to become ecologically important invaders [30], and species and community responses to gradual warming [31,32]. Here, we expand on these ideas as a method to better understand which species and communities will be most vulnerable to MHWs, and how the distribution of species and the composition of communities are likely to shift through time.

How can individual species respond to marine heatwaves?

Although the ecological consequences of MHWs can be felt at any location within the range of a species, its effects are well illustrated by processes occurring at or near the range boundaries (Figure 2). We highlight the relationships between key traits and four such processes: **resistance** during and **re-establishment** following a MHW, as may occur at the warm range edge, and **establishment** and **persistence** beyond the current range, generally at the cool range edge (Figure 2) [33–36].

If a population is to persist at the warm range edge, individuals must either tolerate abnormally warm conditions, move to avoid them, or initiate **resting stages** [37] that can endure until more favorable conditions return. Thus, traits such as critical thermal tolerance (CT_{max}) and whole-organism mobility coupled with thermotaxis will determine whether organisms or their offspring will survive. The magnitude of modulating thermal tolerance through acclimatization [38], **epigenetic inheritance** [39], and **diapause** [40,41] are key uncertainties in this framework, and, since they occur on timescales relevant to MHWs, may have significant roles in resistance. Large and highly mobile species, such as pelagic fish, can sense changes in temperature and move to remain within their preferred thermal environment. The shortest distance to cooler temperatures in marine systems is often 'down' and, thus, **behavioral thermoregulation** by diving has been shown in many species, including whale sharks [42], gray reef sharks [43], and sunfish [44]. Recent work calculating 'thermal displacement' (the shortest distance required to track constant sea surface temperatures) may be another method for capturing the potential for these highly mobile species to survive [45]. At the cool range edge, MHWs alleviate cold stress and

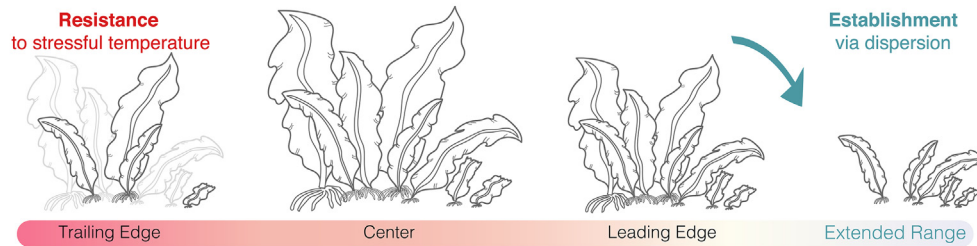activity, allowing the organism to endure otherwise harsh conditions.
Sink populations: populations that reside in poor-quality habitats. Unless individuals are supplied from a source population, then these populations will not be able to support themselves in isolation.
Thermal niche: range of body temperatures maintaining positive population growth.
Translocation: process of changing location or position.

Figure 2. Relevant functional traits during (A) and after (B) a marine heatwave (MHW). Conceptual overview of the functional traits that are relevant (A) during a MHW, resistance (left) and establishment (right), and (B) after a MHW, re-establishment (left) and persistence (right). Relevant traits are described alongside their significance. Note that this is not an exhaustive list of potential traits. See main text for further details. Asterisk denotes functional traits that have the potential to be acted upon by acclimatization or adaptation (e.g., some species could potentially increase CT_{max} in response to MHWs). Note that this potential may not be realized in many species.

can create an opportunity for range expansion (e.g., [46]). The degree to which a species can move into newly thermally suitable habitat will depend on traits related to mobility of adults (sessile vs. mobile or plankton vs. nekton) and dispersal of young (e.g., direct developers vs. species with planktonic propagules or larvae and, for the latter, planktonic larval duration and phenology). Upon arrival, many of the same traits associated with introduced or invasive species come into play (e.g., [47]), including those that allow rapid increases from a small population size during the heatwave itself (e.g., age of maturity, fecundity, or sexual versus asexual reproduction) for species with sufficiently short generation times (e.g., harmful bloom-forming algae [48]).

Once the heatwave has ended, different processes become important. For those species that have their poleward range edge set by temperature, persistence in newly invaded areas depends upon traits related to survival, such as cold thermal tolerance (e.g., overwintering [49]), individual longevity, and production of resting stages, such as algal spore banks [37], which can allow individuals to live until a subsequent heatwave permits growth and reproduction [50–52]. Where MHWs alter the direction or flow of existing currents, poleward range edges set by currents or dispersal limitation may be overcome (e.g., [53]). At the warm end of the range, the speed and degree to which any territory lost to local extirpations can be regained will depend on the same traits that allowed for expansion into new areas during the MHW, as well as the prevailing currents within the region [54].

Finally, the distribution and abundance of any given species is not changing in a vacuum, and resistance, (re-)establishment, and persistence may depend on the presence of key facilitators (e.g., habitat-forming species), mutualists, prey items, or hosts for parasitic species. Regardless of their physiological tolerance and dispersal ability, species with specialist traits, such as nutritional reliance on a specific symbiont, may be lost locally if their partner is lost, and may fail to expand if their partner is not present beyond their pre-MHW range edge [55].

When various functional traits are considered together, we can identify broad generalizations for groups of species about how they are likely to respond to MHWs (see Figure I in Box 1). Whether a population can persist locally in the face of a MHW, species with mobile adults and dispersing larvae may allow at least some individuals to move across larger spatial scales and thereby remain within their thermal niche during a MHW (see Figure IA in Box 1). In many cases, this may take

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Box 1. Using functional traits to predict heatwave-driven biodiversity change

Community responses to ecological perturbations, such as MHWs, reflect the cumulative responses of individual taxa, which depend, in turn, upon the functional traits of those taxa (see Figure 2 in the main text). However, linking trait databases to shifting emergent properties of an ecosystem, such as biodiversity change, is challenging. Here, we suggest a conceptual framework for spanning this gap.

All species ranges span spatial thermal gradients (Figure IAi); we use latitude as a convenient proxy throughout this example. With the onset of a MHW, the thermal isoclines shift poleward, and species ranges will respond (Figure IAii–iv) depending on their traits. Responses will be particularly noticeable at thermally determined range boundaries, which may or may not expand at the cold edge or contract at the warm edge depending on traits related to mobility and/or dispersal ability and tolerance to short-term stress, respectively. When plotted through time (Figure IB; environmental variation includes MHWs along with an underlying warming trend), these range shifts may quickly track the environment (mobile species; Figure IBii) or there may be important lags in expansion–contraction during a MHW or during the post-MHW recovery period. For example, dispersive species with high tolerance to prolonged, suboptimal (cool) temperatures may see their ranges expand (Figure IBiii), albeit with an increase in sink populations. Conversely, species with poor tolerance of hot temperatures, slow adaptation, and poor dispersal will neither be able to persist at their warm range edge nor expand beyond their cool range edge, resulting in a range contraction that may not be recoverable before the next MHW occurs (Figure IBiv). Conversely, species with faster adaptation potential may be able to maintain range-edge populations in the face of MWHs (e.g., Figure IBiii).

The trait-driven range shifts summarized in Figure IBii–iv, when summed across species, produce different patterns of biodiversity change. For communities dominated by mobile or dispersive taxa, the entire community may simply shift temporarily to higher latitudes (Figure ICii), with few lasting MHW effects. For communities dominated by range expanders (Figure I, column iii), local species richness could increase due to increasing range overlap. In the perhaps more likely case of communities dominated by range contractors (Figure I, column iv), local richness will decline as ranges compress and overlap decreases.

Obviously, no community will be dominated entirely by species with a single suite of traits that corresponds to columns ii, iii, or iv in Figure I. Furthermore, change in some communities will be driven disproportionately by some species, and range shifts may not occur independently among taxa. Nevertheless, the summation of trait information across multiple, ecologically relevant taxa represents a promising way of forecasting ecological change in a system of interest, and for predicting which types of system may be especially vulnerable to MHWs (e.g., coral reefs with thermally intolerant habitat-formers with limited dispersal).
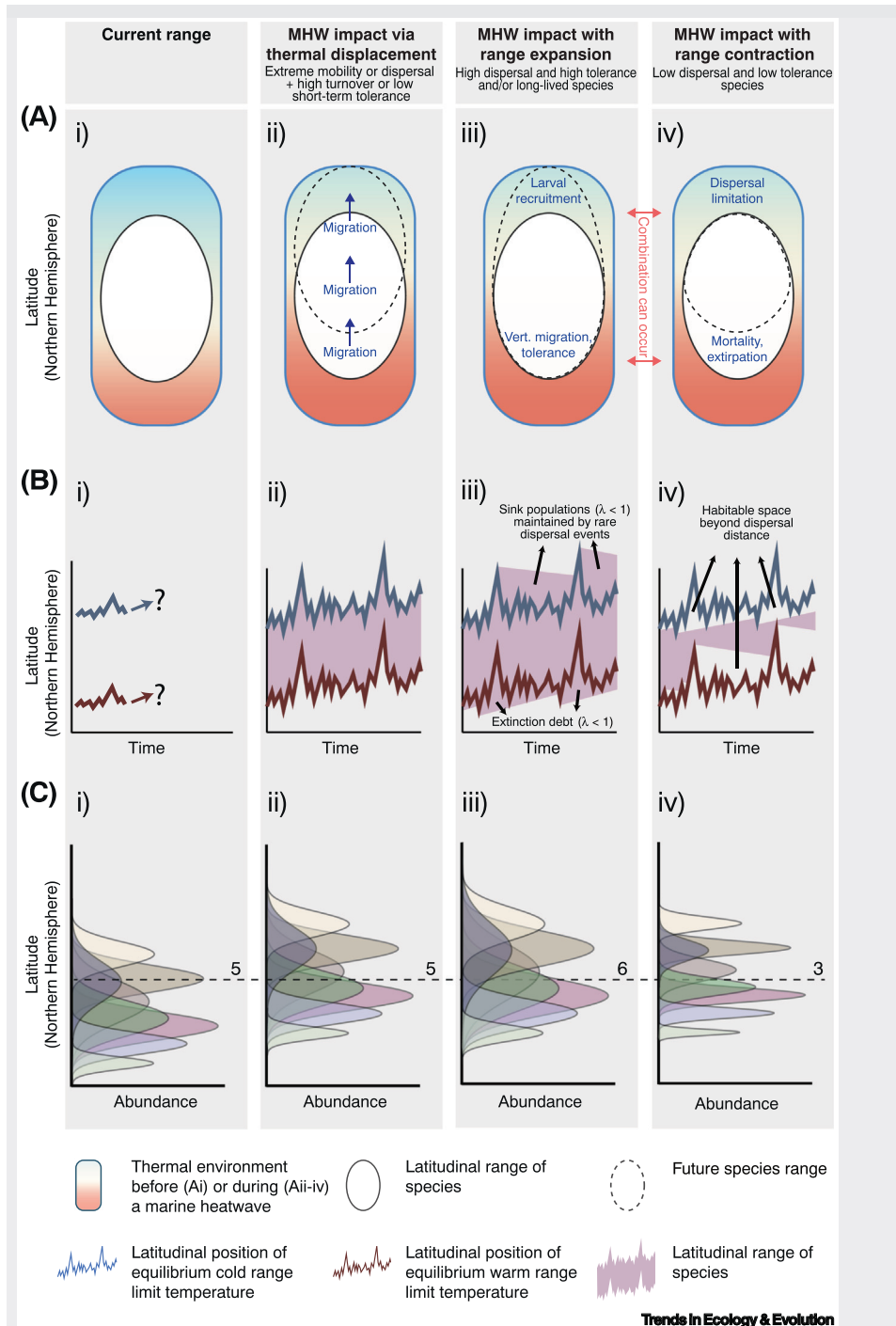
Figure I. Illustration outlining the effects of marine heatwaves on the distribution of species (A), trajectories of the distribution of species over time (B), and the consequences for local diversity (C) for species with different trait distributions. Ecological responses to marine heat waves (MHWs) can be considered as deviations from steady-state conditions (left-hand column) that are dependent upon the types of trait that are present (examples in the remaining three columns). Biodiversity responses (bottom row) can be predicted from the summation of individual species responses (top row) and temporal scales of MHW-driven range expansion or contraction (middle row); see box text for details.

Box 2. Species traits determine community structure following MHWs

While the contraction or shift in species ranges due to long-term ocean heating are becoming commonplace, examples of persistent change following MHWs have received less attention, potentially because of the ephemeral nature of the heatwaves themselves. Changes to the structure of biological communities following MHWs are the culmination of the ecological traits of multiple key species that undergo shifts in abundance or geographical distribution (Figure I). A prominent case study is the large-scale MHW that increased seawater temperatures to >2°C above normal summer conditions along 2000 km of the coast of Western Australia for over 10 weeks in 2011 [9]. While water temperatures have since reverted to the long-term climatological baseline, the equatorward 100 km of this system have now been 'tropicalized', with the MHW conditions having exceeded the thermal limit of the dominant habitat-forming kelp (*Ecklonia radiata*), causing a range contraction at the equatorward edge (traits: sessile + thermally sensitive). As is consistent with this system, algal turfs that are naturally a minor component of the system rapidly took advantage of the altered environmental conditions [75,76] and expanded to reinforce the shift from algal forest to a turf-dominated environment [9]. This simplified community structure has persisted for the decade following the MHW because of the combination of traits of the key species involved. Kelps are sessile and have limited dispersal, which is exacerbated by the prevailing southerly Leeuwin Current running counter to the dispersal direction required for re-expansion into the former range. Concomitant with the contraction of the kelp forests was the expansion of the poleward range edge of tropical herbivorous fishes under the MHW due to the increased flow of the Leeuwin current, which increased the likelihood of tropical fish larvae reaching the warm temperate zones (trait: dispersion) and may have allowed the adults to track the warmer thermal conditions (trait: mobile migration) [53]. These species then did not contract their range once cooler conditions were restored (trait: thermally broad/persistent), establishing populations that have been sustained for over a decade [77]. While cryptic remnant kelp populations provide a localized source of propagules [77], these novel herbivores have further suppressed the expansion of kelps into their former range by consuming any individuals (trait: trophically broad) that manage to overcome space competition with algal turfs [77], potentially facilitating the increased settlement and persistence of a local species of coral that was previously not abundant [78].
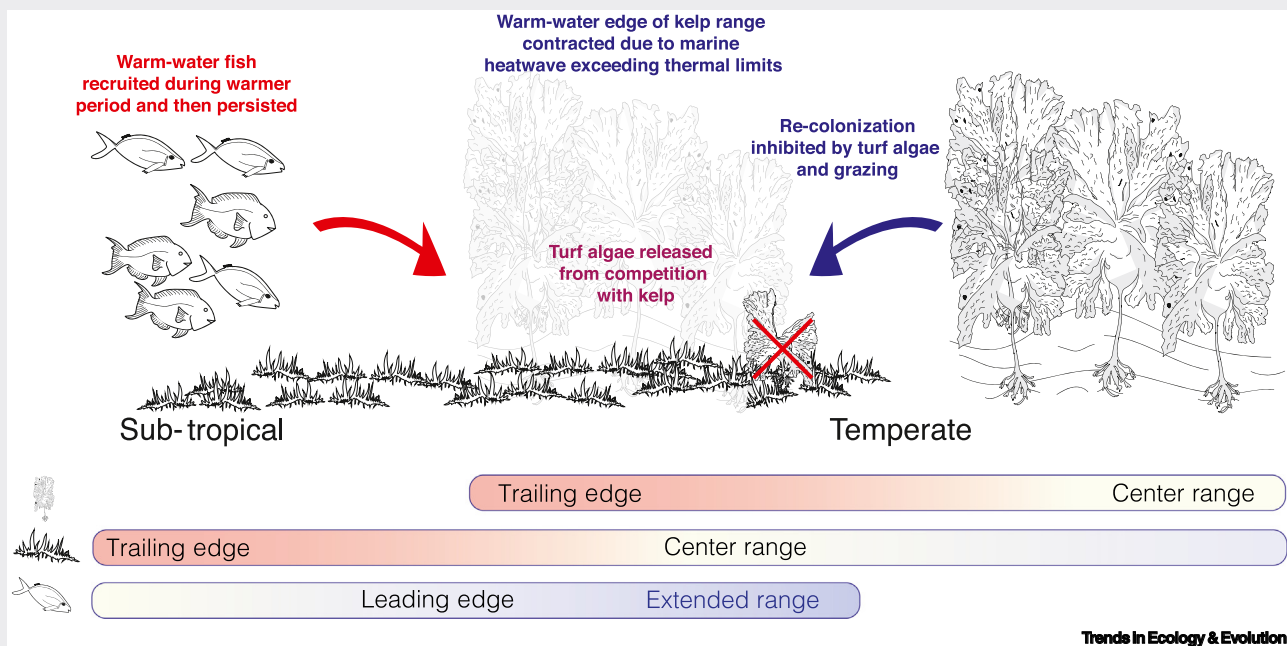
Figure I. Summary of the ecosystem consequences of the 2011 extreme marine heatwave in Western Australia. Conceptual figure demonstrating the ecological processes involved in the altered community structure at the tropical–temperate biogeographic boundary following the 2011 extreme marine heatwave off the western coast of Australia. See box text for more details.

individuals beyond their current distributional limits and allow for the temporary extension of the geographical range (see Figure IB in Box 1). The degree to which such an extension may occur depends on the mobility of the species in the required direction, and the dispersal ability of off-spring [46], which may be with or against prevailing currents [54,56]. Once the MHW ends, it may be possible for these extralimital populations to persist as **sink populations** for many years, perhaps even long enough to be replenished by new immigrants or local reproduction during subsequent MHWs [57] (see Figure IB in Box 1). For less mobile species, or those with low dispersal and low thermal tolerance, MHWs will lead to range contractions if expansion is limited and adaptive capacity is low (see Figure IA,B in Box 1). The traits of these species will mean that habitable space will exist within their **fundamental niche**, but beyond their dispersal

potential (see Figure IB in Box 1). In all cases, the degree to which any given species can resist MHW-related thermal stress in its present range and establish and perhaps persist beyond its current range depends on the functional traits that relate to processes such as dispersal, survival, and adaptation in variable conditions.

How do marine heatwaves affect communities?

The impact of MHWs on communities will filter through individual species-level traits to drive changes in local diversity (Box 1). The fact that species will respond differently to complex warming patterns will drive important changes in community structure and diversity beyond that of only decadal-scale warming. In a world with more frequent and more intense MHWs, thermally resistant species and highly dispersive, weedy, or highly invasive species will make up increasingly large fractions of local communities, tipping Grime's triangle [29] away from K-selected competitive dominants. For communities dominated (numerically or ecologically) by thermally sensitive but highly mobile or dispersive taxa, such as pelagic fish, community changes may be large but transient, with limited lasting impacts since species are able to displace from the stressor. By contrast, in communities such as coral reefs, which are dominated by taxa that are thermally sensitive but poor dispersers, local extirpations may persist well beyond the duration of the MHW, resulting in declines in local diversity [58]. Communities are often then restructured by the rise of competitively inferior but thermally tolerant taxa (e.g., turf algae replacing kelp forests [11,53]), along with immigrating warm-water species into the higher latitude regions (see Box 2 for a case study). The distribution of traits among species within a community can also predict changes in diversity on localized scales even in situations in which range shifts do not occur. In coral reef systems, it is often expected that protected reefs (e.g., marine protected areas) will have greater resilience to disturbance than will heavily exploited areas because herbivorous fish will trophically control any shifts toward algal domination [59]. However, biodiversity *per se* does not protect reefs from the effects of climate change [60]. While these protected communities are still more diverse and productive than are their unprotected counterparts, the incorporation of species traits into predictions of community structure following MHWs may lead to fewer surprises and allow for a greater capacity to make management decisions. Identification of the traits of key species that maintain system structure or function (e.g., habitat-forming species, herbivores on coral reefs, or predators in temperate systems) would allow for more targeted management, such as more spatially connected networks of protected areas for highly dispersive species or larger protected areas for species with restricted dispersal.

Thus far, we have discussed traits as though they are fixed characteristics of species; however, both sessile and mobile species are often both phenotypically plastic and can evolve. For example, many marine species are able to shift their CT_{max} and CT_{min} in response to long-term, seasonal, and short-term temperature shifts [61–63], although there is extensive geographical and temporal variation in acclimatory capacity among species [22,64] and even among populations [65,66]. Similarly, there is also the possibility of **evolutionary rescue** in response to climate warming since both basal and plastic responses to temperature can evolve on the same timescale as warming [67,68] and MHWs themselves may be agents of selection [69]. Evidence gathered so far in marine systems suggests that evolutionary rescue can occur [70,71]; however, there are limits to its extent, and species with complex life cycles or in tropical habitats may be unable to adapt at a sufficient pace to match either long-term heating or discrete MHWs [72]. Finally, rapid evolution of traits linked to dispersal and intrinsic growth rate can affect colonization and range expansion at the leading range edge [73,74]. Fundamentally, a trait-based approach to predicting the effects of rapid environmental change relies on a solid understanding of how much those traits can change over space and time (see Outstanding questions).

Concluding remarks

Organisms do not respond to abiotic change on the decadal scale; instead, they respond in a matter of hours (behavioral responses) to months (acclimatization responses). As a result, MHWs have the potential to restructure populations and communities on shorter timescales than currently being widely considered and, thus, represent an urgent knowledge gap. An understanding of species functional traits represents a useful first step in predicting which species will respond to MHWs, and whether responses are likely to include increases or decreases in local abundance and/or expansion or contraction of geographic range boundaries (see Outstanding questions). The summation of changes across individual taxa, modified by important interspecific relationships, can lead to dramatic shifts in the structure and diversity of marine communities on timescales well beyond the duration of individual MHWs. By better understanding the links between the environment and relevant biological traits, and how those traits are distributed within and among species, it may be possible to begin unifying short-term extreme events and longer term environmental trends as co-drivers of ecological change.

Declaration of interests

No interests are declared.

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Outstanding questions

MHWs differ in peak intensity, duration, and seasonal timing. Biological processes may be disproportionately influenced by thermal extremes, cumulative exposure, thermal time history, and so on. How would different biological traits be affected by different types of heatwave?

MHWs are generally defined as temperature deviations from a fixed baseline climatology for specific locations. Yet, different species, and traits within species, show physiological variation across seasons and populations, and adaptation among generations, and so may change at different rates relative to these climatological baselines. How plastic and readily evolvable are these traits, does this vary among species or biogeographical regions, and how will different rates of adaptation affect community responses to MHWs?

Species ranges, and the distribution of genotypes and phenotypes within those ranges, can shift at rates determined by mobility and dispersal traits. Given that some traits will provide differential resistance to MHWs within a range-shifting population, how will traits interact with geographical position within populations to either slow or accelerate range shifts?

The community-level effect of MHWs will depend on not only trait-driven patterns of range expansion and contraction, but also local community dynamics, tropicalization, and other processes. What will the ultimate impact of MHWs be on local or regional diversity?

Species do not experience MHWs in isolation, but in tandem with other species in their community, including mutualists, competitors, predators, and prey. Therefore, some species may be indirectly affected by MHWs. How will ecological interactions alter the role of functional traits in determining species persistence and what affect will this have on our ability to predict community redistributions under MHWs?

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