Trends in
Ecology & Evolution

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Review

Ecological debts induced by heat extremes

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Heat extremes have become the new norm in the Anthropocene. Their potential to trigger major ecological responses is widely acknowledged, but their unprecedented severity hinders our ability to predict the magnitude of such responses, both during and after extreme heat events. To address this challenge we propose a conceptual framework inspired by the core concepts of ecological stability and thermal biology to depict how responses of populations and communities accumulate at three response stages (exposure, resistance, and recovery). Biological mechanisms mitigating responses at a given stage incur associated costs that only become apparent at other response stages; these are known as 'ecological debts'. We outline several scenarios for how ecological responses associate with debts to better understand biodiversity changes caused by heat extremes.

Highlights

Heat extremes are becoming more frequent and severe owing to contemporary climate change, and the observed ecological impacts from past extremes are expected to be exceeded by current and future heat extremes.

Although the vulnerabilities of species to heat extremes are increasingly being investigated, the resulting dynamics of populations and communities, including various response stages during and after heat extremes, are rarely considered.

Several biological mechanisms can buffer ecological responses at different response stages (exposure, resistance, recovery), but also induce debts that become apparent at later stages. These debts amplify and extend ecological responses over longer periods, especially with sequential climatic (or other disturbance) events.

Integrating mechanisms across response stages, with their associated ecological debts, is key to identifying settings where large heat-induced ecological impacts are most likely.

Heat extremes as a major stress in a warming world

Anthropogenic climate change is paving the way for more frequent extreme climatic events [1,2]. The observed ecological impacts of recent climate extremes demonstrate their consequences at large spatial scales, such as forest diebacks and coral bleaching [3–5]. In fact, many present day-climate extremes, including **heat extremes** (see Glossary), have been unprecedented compared with those in recent evolutionary history in terms of intensity and frequency [1,6]. The predicted rate of increase of heat extremes in the next 100 years is much steeper than that of gradual climate change [1], and their extremity is expected to cause stronger ecological effects than by the rise in mean temperatures [7,8]. Therefore, understanding how natural systems will respond to novel heat extremes represents a pressing issue for both fundamental and applied ecological research [9,10].

Our current knowledge of species responses to heat extremes mainly comes from studies on **thermal sensitivity** [11] and **thermal vulnerability** [12] which generally point to greater risks to tropical and mid-latitude organisms from warming compared to high-latitude ones [13–15]. Although these studies have yielded important insights into how organismal fitness responds to warming, as well as which species will shift their ranges or become extinct, we still lack frameworks that consider both the short- and long-term responses of populations and communities to heat extremes [16–18]. Moreover, understanding how short-term responses feedback to long-term responses and how these relationships help to predict population and community stability against heat extremes will be crucial for advancing climate change ecology [19,20].

Short-term responses, such as reductions in population sizes, can indeed persist for the long term (e.g., beyond the end of an extreme heat event) owing to shifts in genetic diversity [21,22], biotic interactions [23,24], and functional traits [17,25]. The immediate impacts of heat extremes can be dampened by **biological mechanisms** emerging at the (sub)organismal level (Table 1), but the derived costs and consequences of such mechanisms for population- and community-level responses have received little attention so far. We review mechanisms operating in the short term that subsequently propagate into population and community dynamics in the long term in response to heat extremes. For this purpose, we integrate key concepts emerging from

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Table 1. Summary of the biological mechanisms and processes modulating the magnitude of ecological responses to heat extremes at different stages of the response (exposure, resistance, recovery), as well as their associated costs/ecological debts[a]

Response stages	Biological mechanisms and processes		Costs/debts
Exposure	Plastic adjustments • Activity patterns: diel narrowing, diapause, seasonal escape (I, P) • Movement: tracking of buffered habitats, postural changes (I, P) • Physiological: evapotranspiration (I) Habitat features • Thermal buffering • Thermal heterogeneity		• Acquisition trade-offs (e.g., between foraging and thermoregulation) [46] • Higher metabolic costs [44] and altered habitat features after seasonal escape [45] • Missed opportunities for reproduction [42]
Resistance	Thermal performance • Plastic changes in the thermal performance curve and energy balance (I) o Reversible acclimation o Developmental plasticity o Hardening • Protective mechanisms against heat damage (I) • Altered demographic structure (P) • Altered resource availability/interacting stressors (I, P) • Biotic interactions (e.g., enemy release, lower mutualist performance) (P, C)		• Allocation trade-offs (between production of heat shock proteins and life-history traits, e.g., growth, fecundity) [55,100] • Long-term reproductive damage [74] • Demographic bottlenecks [65] • Mismatches phenotype-environment caused by previous acclimation [56] • Reduced protection against additional biotic or abiotic pressures [71,80]
Recovery	Redeemed debts (legacies) • Physiological repair of heat damage (I) • Altered fecundity and development (I) • Altered resource availability (I, P) • Biotic interactions (e.g., hindered species re-establishment – "community closure") (P, C)	Compensation and rescue • Life-history strategy (fast vs. slow) (P) • Dispersal (immigration and emigration) (P) • Genetic/species diversity (P, C)	• Incomplete repair of physiological heat damage [54,64] • Increased dominance of fast-living species in communities [62] • Loss of habitat-forming species and ecosystem engineers [38]

[a]The biological scales of mechanisms and processes are indicated as follows: C, community; I, individual; P, population.

the fields of thermal biology, related to how organisms cope with different thermal environments, and **ecological stability**, that relates to how populations and communities respond to pulse disturbances [26,27]. We extend from previous frameworks for organismal responses to heat extremes [11,28] by depicting how population and community responses to heat extremes (collectively referred to as **ecological responses**) unfold over time. To this end, we suggest that many **biological processes** and mechanisms that buffer immediate responses to heat extremes at the organismal level incur significant costs, but these costs only become apparent in the longer term at population or community levels [18,29] – we refer to such costs as **ecological debts** (Box 1, Figure 1, and Table 1). Ecological debts can therefore alter how thermal responses scale up across levels of organization [30], and how immediate responses are linked to long-term responses to heat extremes [31].

Ecological responses to heat extremes unravel over time: exposure, resistance, and recovery

Ecological responses to heat extremes develop over time in three stages: **exposure**, **resistance**, and **recovery** (Figure 1). The three stages are defined based on how body temperatures of ectotherms oscillate during and after heat extremes, underscoring the main mechanisms involved at each stage (e.g., **thermoregulation** in the exposure stage; Table 1) as well as their associated costs. We stress that such mechanisms are likely to overlap across stages, reflecting the non-independence of each response stage in determining ecological debts (Figure 1 and Table 1). For instance, species frequently exposed to potentially deleterious temperatures (high exposure) often display high heat tolerance and are therefore highly resistant to heat extremes [32]. Likewise,

Glossary

Acclimation: plastic phenotypic changes (e.g., physiological, morphological) that can help to anticipate and provide improved performance (e.g., higher survival or reproductive output) to an ongoing or future exposure to heat extremes. However, acclimation can sometimes be maladaptive, for instance when thermal conditions change across life stages.

Aestivation: a phase of reduced metabolic activity, usually spent in thermal refugia, to minimize exposure to seasonal periods of deleterious hot and dry conditions.

Biological mechanisms: in the context of heat extremes, active biological responses that emerge mainly at the level of organismal traits, with the aim to buffer heat-induced ecological impacts.

Biological processes: in the context of heat extremes, passive biological responses, for instance as a result of thermodynamics (i.e., increased biological rates at higher temperatures) or heat-induced damage.

Demographic bottleneck: in the context of heat extremes, constrained population growth due to a higher (heat-induced) proportion of less energetically efficient life stages.

Ecological debts: delayed costs resulting from the activation of biological mechanisms to buffer the impacts of heat extremes at earlier response stages (akin to the concept of 'resilience debt', whereby a preconditioned state of the system incurs effects that are only apparent after the system is disturbed [18]).

Ecological response: accumulated deviation of a given biological feature (e.g., population size, community composition) from baseline conditions that is induced by exposure to a heat extreme (also known as 'perturbation').

Ecological stability: the study of the dynamics and attributes of biological systems in response to disturbances.

Exposure: the response stage where organisms perceive and avoid conforming to environmental temperatures that potentially cause performance declines.

Heat extremes: periods of extremely high environmental temperatures at daily to weekly timescales, defined in statistical terms (e.g., several consecutive days with temperatures above the 90th percentile for a reference

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Box 1. Inferring ecological debts induced by heat extremes

Inferring ecological responses to heat extremes requires a thorough understanding of the mechanisms involved and ecological debts. However, empirical measures of debts are rare, risking underestimation of the ecological responses when these debts are not taken into account. Theoretically, redeemed ecological debts could be detected as alterations in biological rates or processes (e.g., reduced vital rates, altered connectance in interaction networks) that cannot be explained by, apparently favorable, current environmental or biotic factors (e.g., temperature or competition) and should be attributed to previous exposure to a heat extreme. Ecological debts caused during early response stages (e.g., exposure) can be challenging to measure empirically during a heat extreme event, given that the direct costs of heat can overshadow these accumulated debts. However, ecological debts can be measured more easily in the recovery stage, which is actually the stage where debts are most likely to be redeemed. Shortly after the end of a heat extreme, a measure affecting the response from heat-exposed organisms (e.g., population size) can be compared with naïve organisms at a similar density (orange lines in Figure I), mainly by means of controlled experiments, modeling approaches, or well-replicated observational studies. It must be noted that ecological debts are usually the expression at higher organizational levels of heat-induced costs, but these costs often arise at lower levels (e.g., physiological). For instance, heat-induced damage and repair of the reproductive physiological or morphological machinery can already be measured during a heat extreme (e.g., [61]), but their effects on reproductive output, which is often the measure of ecological relevance (e.g., fitness), cannot be quantified until a time period necessary for gamete production, mating, and embryonic development [74]. It is therefore essential to strengthen the scaling of physiological impacts of heat extremes to more relevant ecological scales by using metrics linked to energy or performance (see Box 2 in the main text).

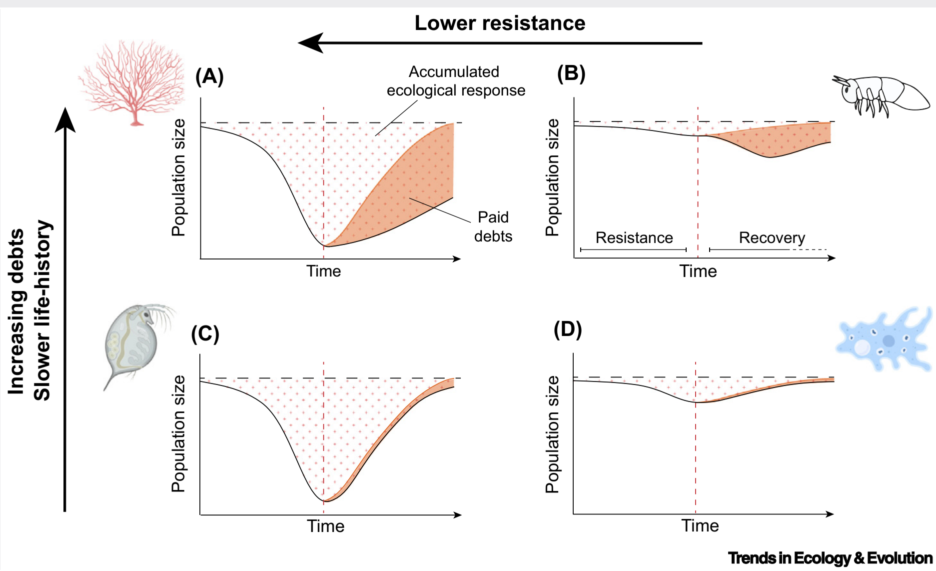

Figure I. Scenarios of ecological responses and debts to heat extremes, using population size as a response variable. A heat extreme takes place over time (horizontal axis) until its end (vertical red broken line). The accumulated ecological response is represented by the spotted area bounded between the baseline population size (i.e., not exposed to the heat extreme; horizontal broken lines) and the temporal dynamics of the ecological response (black curves). The fractions of ecological responses caused by paid debts are shown as orange filled areas. The expected population recovery trajectories in the absence of ecological debts (i.e., only accounting for demographic compensation and rescue after the extreme event) are shown by orange curves. Focal organisms from studies reporting comparable responses after heat extremes are represented next to each scenario, together with their generation times relative to the other organisms shown. (A) Coral, slow-living [97], low resistance, high debt; (B) springtail, slow-living [25], high resistance, high debt; (C) cladoceran, fast-living [98], low resistance, low debt; (D) predatory protist, fast-living [24], high resistance, low debt. Note that ecological debts were not quantified explicitly in these studies, but were suggested as drivers of observed legacies after heat extremes. Images drawn with BioRender.

period) or as absolute temperatures (e.g., related to biologically relevant thresholds), such as CLIMDEX indices (e.g., [2]).
Legacies: redeemed ecological debts.
Recovery: the response stage where body temperatures return to normal after a heat extreme, but ecological responses remain detectable and may even continue to accumulate.
Resistance: the response stage where environmental temperatures induce changes in body temperature, with concomitant and immediate effects on organismal performance.
Thermal performance curve (TPC): the unimodal relationship between body temperature and (performance-related) traits; typically displays an asymmetric shape with a steeper performance drop at high temperatures.
Thermal sensitivity: the physiological or fitness response to a given amount of thermal change.
Thermal vulnerability: a measure of how close key attributes of TPCs (e.g., optimum, upper thermal limits) are to environmental temperatures that organisms experience. The thermal safety margin (i.e., difference between the thermal optimum of a trait and environmental/operative temperature) is one of the main indices of thermal vulnerability.
Thermoregulation: organismal responses via activity patterns, movement, and physiology to keep body temperatures within a temperature range that provide optimal performance.

different organismal traits involved in population resistance and recovery might be subject to trade-offs and, as a consequence, high resistance is likely to come at the expense of reduced ability to recover [33]. Despite the fact that these three stages form the continuum of ecological responses,

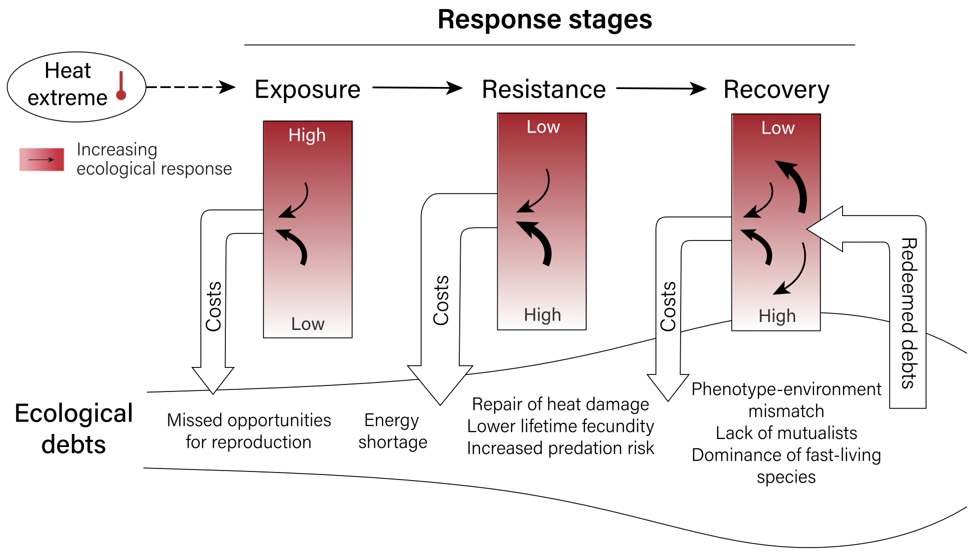

Figure 1. Accumulation of ecological debts along the three stages of the response to heat extremes. Following the onset of a heat extreme (circle), ecological responses unfold over the exposure, resistance, and recovery stages. At each response stage, organisms employ mechanisms to immediately reduce heat-induced impacts, but these mechanisms incur delayed costs that accumulate as ecological debts (see Table 1 in the main text). These are mainly redeemed during recovery, causing larger ecological responses than expected at this stage in the absence of debts. Note that mechanisms favoring recovery also have debts that become apparent when facing a subsequent heat extreme or another disturbance.

decomposing them helps in understanding the underlying mechanisms and processes through which ecological debts arise in populations or communities (Table 1).

Exposure

At the onset of a heat extreme, organisms experience unsuitable external temperatures, and consequently initiate several mechanisms to avoid conforming to such conditions. We refer to this response stage as exposure, and this includes all mechanisms at the individual level that are used to adjust body temperatures in relation to habitat or operative temperatures (thermoregulation). At the population level, such mechanisms can result in fewer active individuals experiencing an extreme event. Since exposure to heat extremes differs across environments and temporal scales (e.g., more variable occurrence of extremes at higher latitude sites, especially at daily to weekly timescales [34]), mechanisms mitigating exposure are expected to have greater fitness consequences in more thermally variable environments. External physical features can significantly modify exposure at the habitat level, thereby affecting the thermal conditions that any population or community will actually experience [35,36] and thus determining costs at the latter response stages (Table 1). For instance, thermal buffering occurs when heat transmission is reduced in a given habitat, and generally takes place by blocking solar radiation and thereby maintaining cooler temperatures with narrower fluctuations (e.g., under the cover of plants or sessile invertebrates [32,37,38]).

Activity changes resulting in reduced exposure can be entirely induced by heat extremes, such as diapause [39,40], or can act upon constituent activity patterns, such as diel narrowing and seasonal escape [41]. In fact, seasonal escape is shaped throughout the evolutionary history of a species to avoid harsh conditions that occur predictably at weekly to seasonal timescales, for instance by means of **aestivation**. As a result, ecological responses after heat extremes could remain small when these events occur during periods of seasonal escape when there is relatively little biological activity [42,43]. However, heat extremes could impact on inactive individuals via increased metabolic costs [44] and altered habitat features [45], causing ecological debts when biological activity resumes (following the extreme heat event) after the seasonal escape. For example, heat extremes accelerate snowmelt in periods when deleterious freeze–thaw cycles occur frequently (e.g., early in the growing season), thereby exposing organisms living in the soil to harmful temperature fluctuations due to the loss of insulating snow cover [45]. Mobile organisms can move to habitat patches with buffered thermal conditions, or can alter their orientation, mainly to reduce incoming solar radiation [11,35]. The occurrence of distinct thermal environments in space and time (i.e., thermal heterogeneity [35]) is crucial to allow tracking of suitable thermal conditions, which could essentially reduce costs at other response stages [46]. By contrast, if activation of mechanisms to reduce exposure becomes exceedingly costly, ecological debts are likely to accumulate and become apparent as **legacies** at later stages (Box 1, Figure 1, and Table 1). For instance, tracking thermally favorable habitats or adopting diel narrowing comes at the expense of lower resource acquisition, leading to high costs of thermoregulation in landscapes with low thermal heterogeneity [46]. The associated energy expenditure could lead to greater detrimental effects during subsequent response stages (e.g., resistance) because energy shortage can lead to reduced thermal tolerance [47,48].

Resistance

Organismal performance in ectotherms is directly linked to body temperature, typically described by a unimodal asymmetric relationship known as the **thermal performance curve (TPC)** [49]. TPCs are widely used to assess organismal and population responses to warming [50], including the immediate effects of heat extremes at a given body temperature (Box 2). In the resistance stage, a widespread strategy to buffer potential heat-induced impacts is the adjustment of key attributes of TPCs (i.e., optimum, breadth, limits, area under the curve), mainly through developmental plasticity, reversible **acclimation**, and hardening [11,39,40,51]. However, under sustained heat stress the mechanisms that actively modulate physiological functions may fail to maintain an optimal fitness of individuals, or may even be maladaptive. In such stress response stages, shifts in morphological and life-history traits are more likely [52], potentially leading to large ecological debts (Figure 1 and Table 1). For example, excessive heat-induced impairment of physiological functions can lead to declines in life-history traits (i.e., growth, survival, reproduction, development) at temperatures beyond their respective thermal optima [5,39,53,54]. Physiological heat damage can thus cause large ecological debts as a result of allocation trade-offs, such as by diverting energy and resources to protective mechanisms that would be otherwise allocated to performance traits (e.g., production of heat-shock proteins at the expense of reduced growth [55]). In addition, ecological debts accumulate when developmental plasticity at higher temperatures produces phenotype–environment mismatches once climatic conditions return to normal, causing reduced performance during recovery [56]. For example, a reduction in body size as a result of warmer conditions during development (a pattern known as the temperature–size rule [57,58]) could incur long-term costs when temperatures return to normal after a heat extreme, since smaller organisms often have lower fecundity and higher predation risks [59]. This phenomenon could be particularly significant for small-bodied organisms with developmental times matching the temporal scales of heat extremes (e.g., several days to weeks).

At the population level, resistance responses to heat extremes further depend on the demographic structure [60]. This is because different life- or size-stages have distinct selective pressures on their thermal tolerance (e.g., [61]) given that each stage is characterized by specific life-history processes (e.g., hatching, development, mating [62]) and particular microhabitat requirements [63]. Consequently, large resistance responses are more likely when heat extremes

Box 2. Can TPCs inform about ecological debts?

TPCs are the gold standard for assessing organismal responses to temperature changes [30,49,50] and have been widely applied to assess the vulnerability of ectotherms to climate warming (e.g., [13,14]). We argue that the use of TPCs can be extended to infer how ecological debts emerging from physiological and organismal processes propagate into population and community levels. TPCs are commonly measured in individuals previously acclimated to benign thermal conditions, but performance can also change substantially as a result of thermal history [49,99]. It is well known that previous exposure to acute heat (hardening) or chronic warming (acclimation) can provide enhanced tolerance/performance to a subsequent heat exposure [51], but the costs associated with such mechanisms (summarized in Table 1 in the main text) have received far less attention in the context of TPCs. The production of heat-shock proteins and other energy-demanding mechanisms is expected to reduce performance traits such as growth, as shown in theoretical models [55]. Therefore, heat-induced costs on performance traits (e.g., fecundity, growth) can be characterized based on TPCs (Figure IA) to inform about ecological debts redeemed at the recovery phase (Figure IB), as well as the resulting performance when facing a subsequent heat extreme (vertical broken lines in Figure IA). Importantly, TPCs could be additionally described as a function of time, either the time of heat exposure (to illustrate how ecological debts may amplify with the buildup of heat stress [95]) or the time of recovery (to depict how ecological debts persist or dampen over time when temperatures return to normal). For instance, TPCs could be measured at different time-steps along the recovery of individuals previously exposed to a heat extreme, to track their deviation in terms of relevant performance metrics from individuals exposed to control temperatures, such as fecundity at the resistance or recovery temperatures (Figure I). However, TPCs have major assumptions and limitations [49], for example, related to the incorporation of realistic variability in thermal regimes [34,99] or the substantial variation in TPCs depending on the trait and life stage under examination, among other methodological aspects [96]. Therefore, the application of TPCs to estimate ecological debts is also subjected to these known limitations, and studies should be carefully designed by considering these caveats. Experimental studies measuring thermal effects across levels of organization (e.g., from organismal to population levels [75]), using species with well-known life histories, can prove highly valuable to assess how ecological debts arise and translate into altered population [25] and community dynamics. Such integrative approaches can be further accompanied by simulations and mechanistic models to obtain more accurate estimates of ecological debts in natural populations and communities (analogous to the methodologies proposed to assess extinction debts [89]).

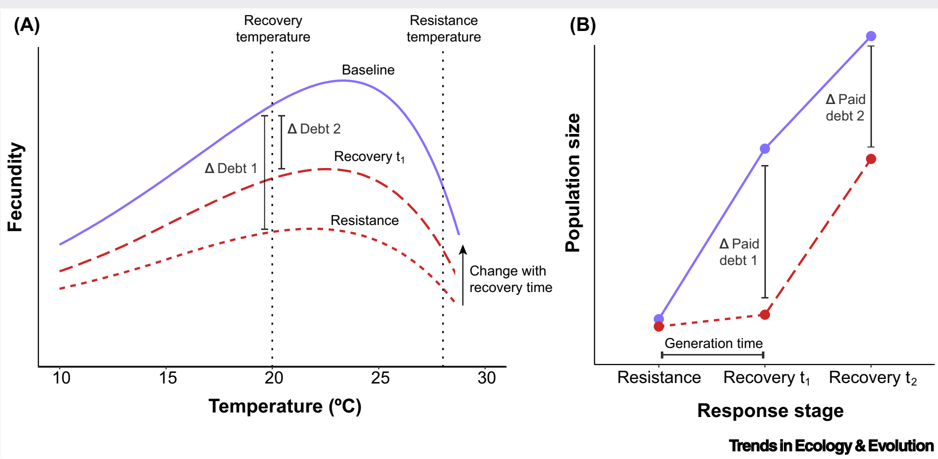

Figure I. Physiological costs induced by heat extremes decrease organismal performance [e.g., thermal performance curves (TPC) of fecundity, panel A], and these effects later scale up to alter population dynamics in the form of paid ecological debts (panel B). TPCs of fecundity and population dynamics are displayed at different response stages: resistance, and recovery at two time intervals (t_1 and t_2). The displayed TPCs and population dynamics are based on [25], where heat exposure (broken red lines) strongly reduced fecundity (but not survival) in a boreal springtail species, resulting in divergent population growth trajectories from the baseline (blue lines) during recovery. Heat-induced costs affect the TPC most strongly at the resistance stage (panel A), which can slowly converge back into the TPC of individuals not exposed to the heat extreme (baseline) as ecological debts are paid over the recovery period (upwards-facing arrow). Ecological debts originating from heat-induced declines in fecundity translate into reduced population growth (panel B) after a time interval necessary for recruitment, such as a period equivalent to the generation time of the species. For example, fecundity debts generated at recovery t_1 are paid at the population level at recovery t_2. Note that emergent properties at the population level (e.g., density-dependent vital rates) and life-history trade-offs (e.g., reduced fecundity but increased offspring viability) can blur how organismal effects propagate to population levels, and should be taken into account to accurately use TPCs in the context of ecological debts.

have disproportionate deleterious effects on thermally sensitive life-stages [42,64]. The resulting altered demographic structure could represent an ecological debt itself if, for example, dominant life-stages after heat extremes constrain population growth through **demographic bottlenecks** [65]. In addition, co-occurring stressors (e.g., heat extremes combined with drought) and low resource availability could bring ecological responses to heat extremes beyond critical thresholds, often as a result of interactive responses [47,66–68], leading to local extinction of populations.

Indirect effects from biotic interactions during the resistance stage can further impact on populations [69]. For example, ectothermic predators are considered to be particularly prone to reducing their population sizes and even becoming locally extinct during heat extremes, given that metabolic costs increase more steeply at higher temperatures than their feeding rates [65,70]. This could release prey species from predation after heat extremes, likely favoring population explosions in heavily top-down controlled communities [62]. Heat extremes can also provide windows of opportunity for the establishment of range-expanding species towards higher latitudes or elevations [71]. This has been shown experimentally in communities composed with several native and a single range-expanding *Drosophila* species, where heatwaves inhibited the fecundity of the native species but promoted the fecundity of the range-expanding species, thereby facilitating the establishment of the latter [72]. A recent global meta-analysis further supports the synergies between heat extremes and range-expanding species, and showed that heat extremes have stronger impacts on native than on non-native species, particularly in freshwater systems [73]. Negative consequences mediated by biotic interactions are also expected for species that are dependent on heat-sensitive mutualists, such as many insect-pollinated plants or habitat-forming marine species [5,38].

Recovery

Ecological responses after an extreme heat event, when body temperatures return to normal following elevated environmental temperatures, belong to the recovery stage. Although ecological responses can persist in the long term after the occurrence of heat extremes, the mechanisms underlying recovery remain poorly understood and, more importantly, are only loosely linked to the mechanisms that buffer immediate responses to heat extremes [17]. Essentially, heat-induced ecological debts accumulated in earlier stages are often redeemed and manifested as legacies at the recovery stage when (abiotic) stressful conditions are reduced (Figure 1 and Table 1). Ecological debts affecting long-term fecundity may be common in the face of heat extremes, given that reproductive thermal limits are often much lower than those of survival, thus causing legacies at the population level after a time-period necessary for recruitment (Boxes 1 and 2) [74–76]. The overlap between key life-history processes and the timing of heat extremes is crucial for recovery responses [42] given that skipped reproductive events due to heat extremes can represent missed opportunities in seasonal environments [77]. For instance, a heat extreme during mating can dramatically reduce reproductive success in beetles, but have only minor effects shortly before or after mating [78]. Interestingly, physiological recovery of reproductive traits after heat stress may be decoupled from heat tolerance [79], suggesting weak relationships between population resistance and recovery from heat extremes.

Debts caused by biotic interactions are expected to affect recovery in populations and communities in compound ways that require a thorough understanding of the trait responses and life histories of the species involved. Among the possible factors at play, we put emphasis on the timing of heat extremes relative of the phenology of the interacting species [80], as well as on the differences in thermal tolerance and recruitment among species [17,53,62]. Furthermore, at the community level, compositional recovery after pulse disturbances often mediates functional recovery [27,31], but this relationship could be altered in the context of heat extremes because of temperature effects on metabolism. For instance, in an outdoor experiment with freshwater communities exposed to experimental heatwaves [81], complete functional recovery (biomass production) was observed despite low compositional recovery, possibly as a result of warming-induced increases in metabolic rates. Invasive species, owing to their high propagule pressure and fast resource acquisition, could also recover better than native species after heat extremes [71,73], potentially leading to long-term changes in community composition [82]. Assessing whether such compositional changes are transient or persistent, especially with the expected increase in the frequency of heat extremes, warrants further research. In addition, altered resources after heat extremes can slow down the rate of recovery, such as when long-living predators experience a delayed scarcity of short-living prey because of time-lags in the propagation of disturbance effects across trophic levels [23,29,67].

Mechanisms involving compensation and rescue, mostly at the population level, depend more strongly on the intrinsic features of species than on previous heat-induced debts, and can largely explain the differences in recovery responses between species [83]. Life-history strategies explain how long-lived and low-reproductive animal species often display high resistance but low recovery after pulse disturbances, whereas the opposite is found in short-lived and highly reproductive species [33,84]. Dispersal (i.e., immigration and emigration) is crucial for accelerating recovery after heat extremes [85,86]; for instance, large responses may persist over time in heavily fragmented and dispersal-limited landscapes [20]. A high degree of thermal heterogeneity, denoting spatial asynchrony in thermal exposure, can promote the arrival of heat-tolerant and fast-colonizing species in focal patches [82], thus fueling community and ecosystem recovery [87]. However, despite their ability to disperse from source habitats, locally extinct species may fail to reestablish in the recovery phase if the biotic environment has shifted during heat extremes. For example, rotifers returning to heat-exposed microcosms after becoming extinct either did not manage to re-establish ('community closure') or resulted in greatly divergent trajectories of community reassembly during recovery [88].

Sequential heat extremes

Recovery mechanisms reduce ecological responses (thus lowering ecological debts) to a single extreme heat event. This is true when populations and communities are not immediately exposed to another sequential extreme event, including heat extremes. However, an increased frequency of heat extremes can substantially reduce the potential of a population to shrink its ecological debt from the previous heat extreme event [64,89]. Accumulated ecological debts from the previous heat extreme could even lead to local extinction or migration of species, particularly when they are exposed to another heat extreme event (or a stress of similar severity, such as extreme drought). As such, the buildup of small effects of heat stress on survival (e.g., accumulation of ecological debts) can cause population crashes following multiple heat extremes [90]. This could override the benefits of priming effects – the mechanisms that provide enhanced performance in the face of sequential stressors, mostly over the lifespan of an individual [91]. At the community level, priming effects can also occur through increased dominance of heat-resistant or fast-growing genotypes after heat extremes, such as in the case of the Great Barrier Reef, where coral reefs surviving a single extreme heat event were more resistant to exposure to another heat event in the following year [92]. In general, we suggest that the accumulation of ecological debts will make responses to heat extremes more likely to be amplified, rather than buffered, by the occurrence of sequential events (Box 2). In the earlier example, recruitment in the coral reefs was severely compromised after two consecutive heat extremes due to earlier adult mortality, perhaps hindering complete recovery of coral populations before subsequent heat extremes [93]. Indeed, considering how the frequency of sequential events relates to the species generation times is key to predict these consequences [67], as short-lived species are expected to recover better before the onset of a subsequent heat extreme [23,84] (see Figure I in Box 1).

Concluding remarks and future directions

Ecological responses to heat extremes are determined by both distinct and overlapping mechanisms across different response stages, mainly to overcome thermal stress. We advocate that a more temporally explicit view of ecological responses to heat extremes could yield insights into biodiversity conservation in a world with increasing extreme climatic events. By considering how exposure, resistance, and recovery affect the dynamics of populations and communities, as proposed in our conceptual framework (Figure 1), we can better identify vulnerable species and ecosystems, and accordingly devise management and mitigation strategies against the impacts of heat extremes on ecological systems. For example, restoration programs can enhance the availability of cooler microhabitats by promoting ecosystem engineers, thereby already reducing ecological impacts at early response stages [36,94]. Faster recovery could be promoted by enabling the flow of individuals across thermally heterogeneous landscapes, by enhancing access to decimated resources (e.g., natural vegetation cover, water availability), and by preventing the establishment of invasive species after heat extremes [71]. Implementing such strategies can potentially shorten the timeframes for reducing ecological debt, especially as the intervals between heat extremes are shrinking [1]. Nevertheless, to achieve this we need to overcome current knowledge gaps in our understanding of responses to heat extremes (see Outstanding questions). For instance, mechanisms promoting recovery after heat extremes are largely understudied (e.g., rates of repair of physiological heat damage [95]), despite their strong contribution to the overall ecological response. We recommend that measurements assessing recovery should capture delayed effects on heat-sensitive biological processes that are otherwise overlooked (e.g., dispersal, recruitment) [25,85], which will require careful consideration of the life history (e.g., generation time) of the study species [84]. In addition, mechanisms modulating responses at earlier response stages often have associated debts, but we still ignore the importance of these debts in driving long-term ecological responses. Notably, a greater focus is needed on evolutionary changes that can promote recovery after heat extremes, and should build on our current understanding of how gradual warming and extremes drive the evolution of thermal performance and tolerance (e.g., [43,54,76,96]). Possible trade-offs in the evolutionary potential of mechanisms conferring resistance and recovery could be explored, as well as how these relationships differ with heat extremes of varying severity. Finally, even though sequential heat extremes are more likely to occur as the climate becomes warmer, we are only starting to depict their potential impacts in relation to single extreme heat events. Our ability to anticipate and act upon the ecological consequences of heat extremes will only improve by acknowledging the response continuum during and after heat extremes, and the mechanisms underlying variation in responses that contribute to ecological debts. Our conceptual framework is a step towards achieving this, although we also maintain that its application is more likely to be successful in experimental studies, and is more likely to be exclusive to ectotherms. Integrative approaches combining experiments and theory can help to infer ecological debts in real-world settings, a necessary step towards understanding biodiversity dynamics in response to climate extremes.

Outstanding questions

How can variation in ecological responses to heat extremes be predicted?

What are the relative contributions of different mechanisms (across different ecological scales) at the various stages of the response to heat extremes?

Can heat extremes induce evolutionary changes that reduce ecological responses? If so, are trade-offs in evolutionary changes of mechanisms involved at different response stages? For instance, could the evolution of higher heat tolerance (i.e., related to resistance) come at the expense of reduced repair of heat damage and/or compensatory mechanisms (i.e., related to recovery)?

Can we identify environmental settings where biotic interactions are particularly important in determining ecological responses to heat extremes?

How do ecological debts change with more severe heat extremes and with the occurrence of sequential extreme events?

How will heat extremes trigger gradual ecological responses over yearly to decadal timescales as a result of the accumulation of ecological debts?

Acknowledgments

We are thankful to four anonymous reviewers for their suggestions on previous versions of our manuscript. We are grateful to the members of Terrestrial Ecology Group for their insights on the topic covered in this review. We thank Philipe Piccardi for drawing illustrations for Figure I in Box 1. M.P.T. acknowledges the support from the Swiss State Secretariat for Education, Research, and Innovation (SERI) under contract M822.00029 and from the Swiss National Science Foundation (grant 310030_212550).

Declaration of interests

The authors declare no conflicts of interests.

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