

Thermal Tolerance and Climate Vulnerability of Tropical Ectotherms: A Review of Physiological Limits, Behavioural Buffering, and Conservation Implications

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Article information

Received: 8th June 2026

Received in revised form: 10th July 2026

Accepted: 12th August 2026

Available online: 22nd September 2026

Volume: 1

Issue: 3

DOI: <https://doi.org/10.63090/EJZRS/3139.9215.0009>

Abstract

Ectothermic animals, which make up the great majority of animal diversity, depend on environmental temperature for nearly all physiological functions and are therefore directly exposed to climate warming. This review synthesises published evidence on the thermal physiology of ectotherms to evaluate why tropical species are widely considered disproportionately vulnerable despite the smaller magnitude of warming projected at low latitudes. We examine (1) the conceptual framework of thermal performance curves, critical thermal limits, and thermal safety margins; (2) latitudinal and habitat-related patterns in heat tolerance; (3) the capacity of behavioural thermoregulation, physiological plasticity, and evolutionary adaptation to buffer warming; and (4) observed and projected ecological consequences. The literature shows that upper thermal limits vary little across latitude and are strongly conserved phylogenetically, whereas lower limits are flexible. Tropical ectotherms typically live closer to their thermal optima and possess narrow thermal safety margins. Acclimation of heat tolerance is generally modest, and behavioural buffering depends on the availability of cool microhabitats, linking physiological vulnerability directly to habitat structure. Sublethal effects, including elevated metabolic costs, restricted activity time, and heat-induced fertility loss, may drive population decline well before lethal limits are reached. We identify methodological limitations in current vulnerability assessments and propose conservation priorities centred on microhabitat retention, elevational connectivity, and integration of physiological data into conservation planning.

Keywords:- Thermal Tolerance, Critical Thermal Maximum, Thermal Safety Margin, Ectotherms, Climate Change, Behavioural Thermoregulation, Acclimation, Conservation Physiology.

I. INTRODUCTION

Anthropogenic climate change is altering the distribution, phenology, and abundance of animals worldwide. A globally coherent signal of climate-driven change has been documented across taxa (Parmesan & Yohe, 2003), species' ranges are shifting towards higher latitudes and elevations at accelerating rates (Chen et al., 2011), and syntheses of extinction-risk projections indicate that risk increases with every increment of warming (Thomas et al., 2004; Urban, 2015). Understanding which species are most vulnerable, and why, has therefore become a central task of environmental zoology (Williams et al., 2008; Pacifici et al., 2015).

Ectotherms (insects and other invertebrates, fishes, amphibians, and reptiles) are of particular concern because their body temperature, and hence their metabolism, locomotion, growth, and reproduction, track environmental temperature (Huey & Stevenson, 1979; Angilletta, 2009). Intuitively, the greatest biological impacts would be expected at high latitudes where warming is fastest. However, an influential body of work argues the opposite: tropical ectotherms may be at greatest risk because they are thermal specialists already living close to their physiological optima (Deutsch et al., 2008; Tewksbury et al., 2008). This argument originates in Janzen's (1967) proposal that low seasonal temperature

variation in the tropics selects for narrow thermal tolerance, a hypothesis that has since received considerable empirical support (Ghalambor et al., 2006).

Physiology provides a mechanistic basis for predicting climate impacts that correlative distribution models cannot supply (Pörtner & Farrell, 2008; Somero, 2010). Yet vulnerability is not determined by physiological tolerance alone. It emerges from the interaction of exposure, sensitivity, and the capacity to respond through behaviour, plasticity, and evolution (Williams et al., 2008; Huey et al., 2012).

The objectives of this review are to:

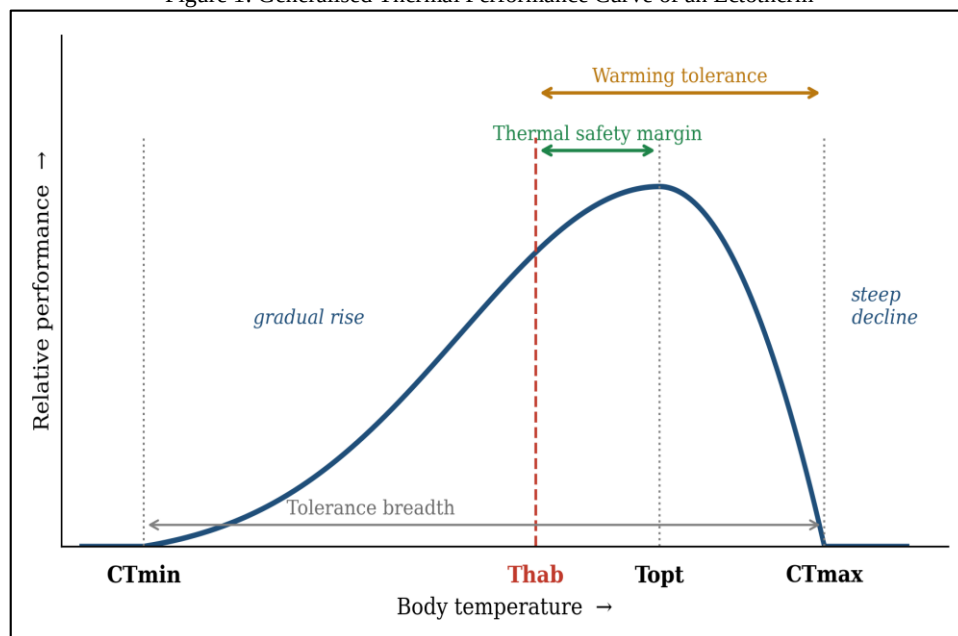
- Outline the conceptual framework and principal metrics used to quantify thermal vulnerability in ectotherms
- Summarise global patterns in thermal tolerance across latitude, elevation, and habitat
- Evaluate the potential of behavioural thermoregulation, acclimation, and evolutionary adaptation to buffer warming
- Examine sublethal and population-level consequences of warming
- Identify methodological limitations and derive conservation implications, with emphasis on tropical faunas.

II. CONCEPTUAL FRAMEWORK

2.1. Thermal Performance Curves and Critical Limits

The relationship between body temperature and physiological performance in ectotherms is described by the thermal performance curve (Figure 1). Performance rises gradually from a critical thermal minimum (CT_{min}) to an optimum temperature (T_{opt}), then declines steeply to the critical thermal maximum (CT_{max}) (Huey & Stevenson, 1979; Angilletta, 2009). The asymmetry of the curve has an important consequence. A given increase in body temperature above T_{opt} reduces performance far more than an equivalent decrease below it. Species living near their optimum are therefore highly sensitive to further warming. CT_{max} is conventionally measured as the temperature at which an animal loses coordinated locomotor function during experimental heating (Lutterschmidt & Hutchison, 1997).

Figure 1: Generalised Thermal Performance Curve of an Ectotherm



Source: Author's schematic based on Huey and Stevenson (1979) and Deutsch et al. (2008); axes unscaled, no empirical data plotted

Schematic thermal performance curve showing the critical thermal minimum (CT_{min}), thermal optimum (T_{opt}), critical thermal maximum (CT_{max}), and habitat temperature (Thab). The thermal safety margin and warming tolerance are the distances from Thab to T_{opt} and to CT_{max} respectively.

2.2. Indices of Vulnerability

Deutsch et al. (2008) formalised two widely used indices: warming tolerance, the difference between CT_{max} and mean habitat temperature, and the thermal safety margin, the difference between T_{opt} and habitat temperature (Figure 1). Subsequent work refined these indices by replacing mean air temperature with the operative body temperatures that animals actually experience in exposed and shaded microhabitats (Sunday et al., 2014). The principal metrics are summarised in Table 1.

Table 1. Principal Metrics Used in Assessing Thermal Vulnerability of Ectotherms

Metric	Definition	Key source
Critical thermal maximum (CT _{max})	Upper temperature at which coordinated locomotion is lost	Lutterschmidt & Hutchison (1997)
Thermal optimum (T _{opt})	Body temperature at which performance is maximal	Huey & Stevenson (1979)
Warming tolerance	CT _{max} minus habitat temperature	Deutsch et al. (2008)
Thermal safety margin	T _{opt} (or CT _{max}) minus habitat or operative temperature	Deutsch et al. (2008); Sunday et al. (2014)
Acclimation response ratio	Change in thermal limit per degree change in acclimation temperature	Gunderson & Stillman (2015)
Hours of restriction	Daily time during which operative temperature exceeds the preferred range and activity is curtailed	Sinervo et al. (2010)

Notes: Definitions follow the cited sources; operational details vary among studies.

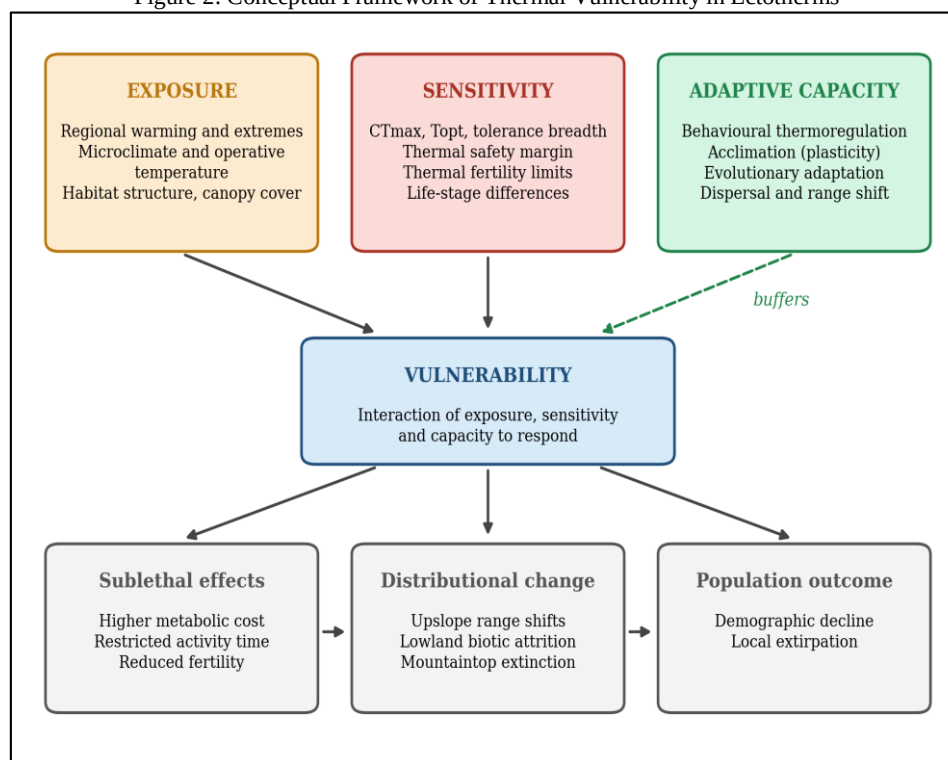
2.3. Oxygen Limitation and Mechanistic Bases of Heat Tolerance

For aquatic ectotherms, the concept of oxygen- and capacity-limited thermal tolerance proposes that the upper limit is set by a mismatch between rising oxygen demand and the limited capacity of circulatory and ventilatory systems to supply it (Pörtner & Farrell, 2008). Field evidence from marine fish links warm-season declines in abundance to this mechanism (Pörtner & Knust, 2007). At the cellular level, heat tolerance is constrained by protein stability, membrane integrity, and the cost of the heat-shock response. This helps explain why upper limits appear difficult to shift (Somero, 2010).

2.4. An Integrated View of Vulnerability

Following Williams et al. (2008), vulnerability can be treated as the outcome of three components: exposure to climatic change at the scale the organism experiences it, intrinsic sensitivity determined by thermal physiology, and adaptive capacity provided by behaviour, plasticity, evolution, and dispersal. Figure 2 summarises how these components combine and the ecological outcomes to which they lead. This framework organises the synthesis that follows.

Figure 2: Conceptual Framework of Thermal Vulnerability in Ectotherms



Source: Author's schematic adapted from the frameworks of Williams et al. (2008) and Huey et al. (2012)

Exposure and sensitivity jointly determine potential impact, which adaptive capacity may buffer (dashed arrow). The resulting vulnerability is expressed first as sublethal effects and distributional change and ultimately as population decline.

III. APPROACH AND SCOPE OF THE REVIEW

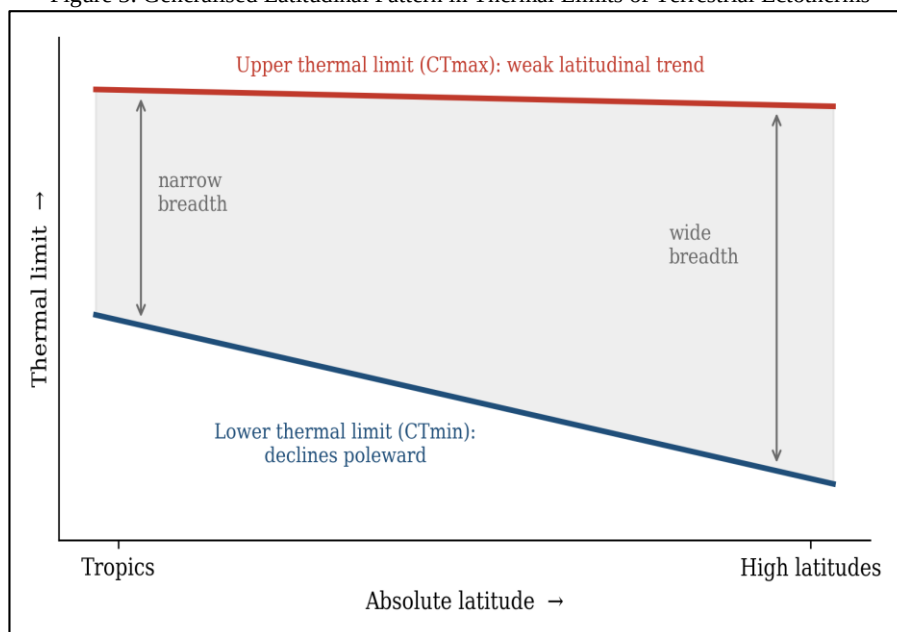
This article is a narrative synthesis of peer-reviewed literature on ectotherm thermal physiology and climate vulnerability. We drew principally on global comparative analyses, meta-analyses, and landmark empirical and modelling studies, and supplemented these with foundational theoretical works. We emphasised studies that (a) compared thermal traits across latitude, elevation, or realm, (b) quantified plasticity or evolutionary potential of thermal limits, or (c) linked thermal physiology to demographic or distributional outcomes. No new empirical data are presented, and all figures are conceptual schematics that illustrate published ideas without plotting data. Because the review is narrative rather than systematic, it does not claim exhaustive coverage, and the conclusions should be read as an integration of the dominant lines of evidence rather than a quantitative meta-analysis. Openly available compilations such as the GlobTherm database (Bennett et al., 2018) offer a basis for future quantitative work.

IV. SYNTHESIS OF EVIDENCE

4.1. Global Patterns in Thermal Tolerance

Comparative analyses consistently reveal an asymmetry between upper and lower thermal limits (Figure 3). In insects, lower limits decline markedly towards the poles whereas upper limits show little geographic variation (Addo-Bediako et al., 2000). A global analysis across ectotherm groups confirmed this pattern and showed that in terrestrial species heat tolerance varies only weakly with latitude (Sunday et al., 2011). Heat tolerance is also strongly conserved across lineages, while cold tolerance is evolutionarily labile (Araújo et al., 2013). In *Drosophila*, upper limits are tightly constrained phylogenetically and are linked to species' distributions (Kellermann et al., 2012). Tolerance breadth consequently increases with latitude, in keeping with the climatic variability hypothesis (Stevens, 1989) and with Janzen's (1967) prediction of narrow tolerance in thermally stable tropical environments (Ghalambor et al., 2006).

Figure 3: Generalised Latitudinal Pattern in Thermal Limits of Terrestrial Ectotherms



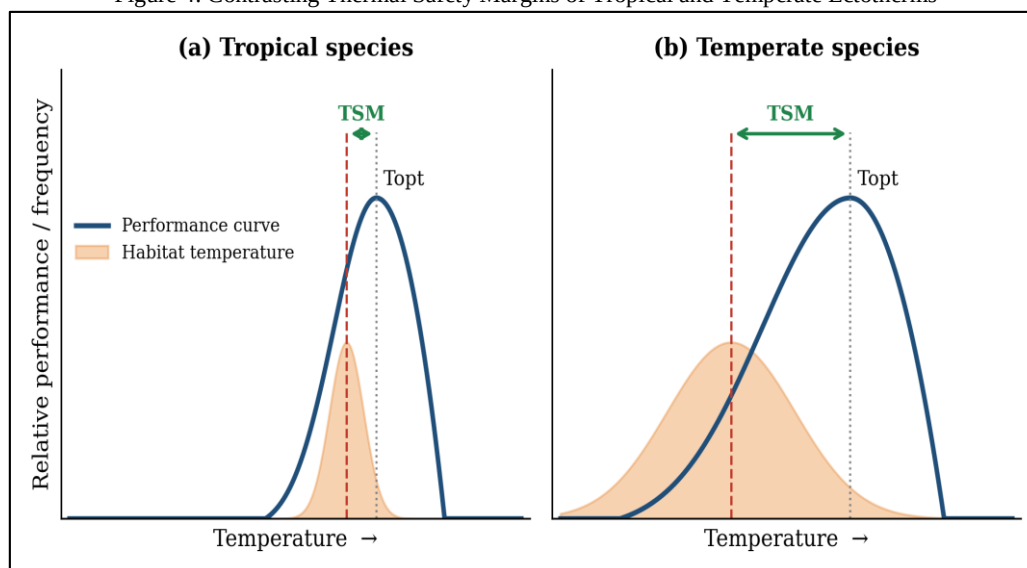
Source: Author's schematic of the qualitative pattern reported by Addo-Bediako et al. (2000) and Sunday et al. (2011); axes unscaled, no empirical data plotted

Upper thermal limits change little with latitude whereas lower limits decline towards the poles, so that tolerance breadth (shaded) widens with latitude.

4.2. Narrow Safety Margins in the Tropics

Because upper limits are relatively invariant while environmental temperatures are higher at low latitudes, tropical ectotherms have little thermal headroom (Figure 4). Deutsch et al. (2008) showed that tropical insects live close to their optimum, so that even modest warming is predicted to reduce fitness, whereas many temperate species may initially benefit. Comparable results have been reported for tropical forest lizards, which are often thermoconformers with low body temperatures and are poorly equipped to cope with warming of the forest interior (Huey et al., 2009). They have also been reported for ants, in which warming tolerance is lowest in the tropics (Diamond et al., 2012), and for larval amphibians, in which subtropical communities from warm ponds showed the smallest margins (Duarte et al., 2012). Metabolic considerations reinforce this concern. Because metabolic rate rises exponentially with temperature, the small absolute warming recorded in the tropics has produced large increases in the estimated metabolic rates of ectotherms there (Dillon et al., 2010).

Figure 4: Contrasting Thermal Safety Margins of Tropical and Temperate Ectotherms



Source: Author's schematic after Deutsch et al. (2008) and Tewksbury et al. (2008); axes unscaled, no empirical data plotted

Panel (a) shows a tropical species with a narrow performance curve occupying a thermally stable habitat close to its optimum, giving a small thermal safety margin (TSM). Panel (b) shows a temperate species with a broad performance curve in a variable habitat whose mean lies well below the optimum, giving a large margin.

4.3. Terrestrial Versus Aquatic Realms

Realm strongly modifies vulnerability. The latitudinal ranges of marine ectotherms conform closely to their thermal tolerance limits, whereas terrestrial species are often absent from the warm portions of their potential range (Sunday et al., 2012). After accounting for access to thermal refugia, marine ectotherms have narrower safety margins than terrestrial species, and local extirpations associated with warming have been approximately twice as frequent in the ocean as on land (Pinsky et al., 2019). Among fishes, climatic vulnerability is geographically uneven, and tropical marine and northern freshwater assemblages have been identified as areas of particular concern (Comte & Olden, 2017). Aquatic species cannot easily escape ambient temperature, since water offers limited fine-scale thermal heterogeneity compared with terrestrial landscapes.

4.4. Behavioural Buffering and the Role of Microhabitat

Since Bogert (1949), behavioural thermoregulation has been recognised as a primary means by which ectotherms decouple body temperature from ambient conditions. Biophysical modelling indicates that under warming, thermoregulation at low latitudes shifts from the problem of gaining heat to that of avoiding it, which makes access to shade essential (Kearney et al., 2009). A global analysis of operative temperatures found that body temperatures of fully exposed animals in the warmest months would exceed CTmax across most latitudes. Survival therefore already depends on retreating to shade, burrows, or other refugia (Sunday et al., 2014). Field measurements in tropical forest confirm that microhabitats such as tree holes, epiphytes, and soil substantially dampen temperature extremes relative to ambient air (Scheffers et al., 2014).

Two caveats follow. First, time spent in refugia is time lost to foraging and reproduction. Sinervo et al. (2010) linked the extinction of 12% of surveyed local populations of Mexican *Sceloporus* lizards since 1975 to increasing hours of activity restriction during the breeding season, and their global model projected substantial further losses by 2080. Second, behavioural buffering depends on habitat structure. Deforestation, canopy opening, and fragmentation remove the cool microhabitats on which buffering depends, so that land-use change and climate warming act together.

4.5. Physiological Plasticity

Acclimation offers a second line of defence, but its scope for heat tolerance appears limited. A broad analysis of acclimation response ratios found that ectotherms generally shift CTmax by only a small fraction of a degree per degree of acclimation temperature. This is insufficient to offset projected warming, and the capacity does not vary strongly with latitude (Gunderson & Stillman, 2015). Plasticity of physiological rates more generally is greater in aquatic than in terrestrial ectotherms and can meaningfully increase resilience in some groups (Seebacher et al., 2015). The contrast between these conclusions reflects the traits examined (rates versus limits), and it underlines that upper tolerance limits are among the least plastic components of thermal physiology (Hoffmann et al., 2013).

4.6. Evolutionary Potential

Whether heat tolerance can evolve rapidly enough remains uncertain. The phylogenetic conservatism of upper limits (Araújo et al., 2013; Kellermann et al., 2012) and generally low evolutionary potential reported in laboratory studies

(Hoffmann et al., 2013) suggest constraint. Among Caribbean *Anolis* lizards, cold tolerance has diverged readily among environments while heat tolerance has remained comparatively static, a pattern attributed partly to effective behavioural thermoregulation shielding populations from selection during the day (Muñoz et al., 2014). On the other hand, measurable natural selection on thermal performance was detected when lizards were transplanted to a warmer, more variable site (Logan et al., 2014), indicating that adaptive responses are possible when selection is strong. For long-lived vertebrates with long generation times, however, evolutionary rescue within the timeframe of projected warming appears unlikely. The potential and constraints of each buffering mechanism are compared in Table 2.

Table 2. Buffering Mechanisms Available to Ectotherms Under Climate Warming

Mechanism	Evidence of buffering potential	Principal constraints	Key sources
Behavioural thermoregulation	Most effective short-term buffer; refuge use is already necessary in the warmest months across most latitudes	Reduces time for foraging and breeding; requires shade and refugia; limited in forest thermoconformers	Kearney et al. (2009); Sinervo et al. (2010); Sunday et al. (2014)
Acclimation (plasticity)	Physiological rates adjust appreciably, particularly in aquatic species	CTmax shifts by only a small fraction of a degree per degree of acclimation	Gunderson & Stillman (2015); Seebacher et al. (2015)
Evolutionary adaptation	Selection on thermal performance is detectable in wild populations	Upper limits phylogenetically conserved; low evolutionary potential; long generation times; behaviour shields populations from selection	Hoffmann et al. (2013); Muñoz et al. (2014); Logan et al. (2014)
Dispersal and range shift	Poleward and upslope shifts widely documented	Shallow latitudinal gradient in the tropics; requires habitat connectivity; no refuge beyond mountaintops	Chen et al. (2011); Colwell et al. (2008)

Notes: Assessments are qualitative summaries of the cited sources.

4.7. Sublethal Effects, Variability, and Range Shifts

Populations may decline long before CTmax is approached. Heat stress reduces fitness through cumulative sublethal damage, and models that include the variability and extremes of temperature predict greater fitness losses than those based on mean warming, including for temperate species (Kingsolver et al., 2013; Vasseur et al., 2014). Reproduction is especially sensitive. Fertility is frequently lost at temperatures well below lethal limits, which implies that vulnerability estimates based on CTmax are systematically optimistic (Walsh et al., 2019).

Range shifts offer an escape, but one that is geographically constrained in the tropics. The shallow latitudinal temperature gradient at low latitudes means that upslope movement is the principal option. Colwell et al. (2008) predicted that lowland tropical biotas face net attrition because no warmer-adapted source pool exists to replace species that move upslope, while montane species face shrinking ranges and mountaintop extinction. Landmark studies underpinning these conclusions are summarised in Table 3.

Table 3. Selected Landmark Studies on Thermal Vulnerability of Ectotherms

Study	Taxa / scope	Principal conclusion
Janzen (1967)	Conceptual	Low thermal seasonality in the tropics selects for narrow tolerance, making elevational gradients stronger barriers
Deutsch et al. (2008)	Insects, global	Tropical species live near T _{opt} , so warming reduces fitness most at low latitudes
Huey et al. (2009)	Tropical forest lizards	Forest thermoconformers have low heat tolerance and limited behavioural options
Sinervo et al. (2010)	Lizards, global	Activity restriction linked to observed local extinctions, with large projected losses by 2080
Sunday et al. (2011)	Ectotherms, global	Upper limits vary little with latitude, whereas lower limits decline poleward
Araújo et al. (2013)	Ectotherms, endotherms, plants	Heat tolerance phylogenetically conserved, cold tolerance labile
Sunday et al. (2014)	Terrestrial ectotherms	Exposed operative temperatures exceed CTmax widely, so behavioural refuge use is essential
Gunderson & Stillman (2015)	Ectotherms, global	Plasticity of CTmax too limited to offset projected warming
Pinsky et al. (2019)	Marine vs terrestrial	Marine ectotherms have narrower safety margins and more frequent extirpations

Notes: Conclusions are paraphrased from the cited sources.

V. DISCUSSION

5.1. Integration of Evidence

The literature converges on a coherent picture. Upper thermal limits are conserved across latitude and phylogeny (Addo-Bediako et al., 2000; Sunday et al., 2011; Araújo et al., 2013), so ectotherms in hot environments operate with little margin. Tropical species, adapted to stable climates, combine narrow performance breadth with proximity to their optima (Janzen, 1967; Deutsch et al., 2008). Neither plasticity (Gunderson & Stillman, 2015) nor rapid evolution (Hoffmann et al., 2013) can be relied upon to raise upper limits substantially. Behaviour is the most effective short-term buffer (Kearney et al., 2009; Sunday et al., 2014), but it carries opportunity costs (Sinervo et al., 2010) and depends on habitat structure (Scheffers et al., 2014). Vulnerability is therefore best understood as an interaction between physiology and landscape, not as a fixed property of species (Huey et al., 2012), as summarised in Figure 2.

5.2. Methodological Limitations of Current Assessments

Several limitations warrant caution. Estimates of CT_{max} depend on methodological context, including starting temperature and heating rate, which complicates comparison among studies (Terblanche et al., 2007). Thermal tolerance is a function of both the intensity and the duration of exposure. The tolerance landscape approach shows that a single CT_{max} value cannot capture this relationship (Rezende et al., 2014). Many analyses rely on coarse air-temperature data and do not use the operative temperatures experienced in occupied microhabitats, which may over- or underestimate exposure (Sunday et al., 2014). Most data derive from adult stages, whereas eggs, larvae, and reproductive functions may be more sensitive (Walsh et al., 2019). Finally, geographic and taxonomic coverage is strongly uneven. Tropical Asia, Africa, and most invertebrate groups remain poorly represented in global databases (Bennett et al., 2018), which limits inference for precisely those faunas considered most at risk.

5.3. Conservation Implications and Management Recommendations

The evidence reviewed supports several practical priorities, summarised in Table 4. First, retention of structurally complex habitat (closed canopy, large trees, epiphytes, deep leaf litter, and riparian shade) maintains the thermal refugia on which behavioural buffering depends (Scheffers et al., 2014). Habitat protection is therefore itself a climate-adaptation measure. Second, maintaining continuous habitat along elevational gradients allows upslope range shifts. This is especially important in tropical mountain systems where lowland attrition and mountaintop extinction are anticipated (Colwell et al., 2008). Third, vulnerability assessments for threatened ectotherms should incorporate physiological sensitivity and adaptive capacity alongside exposure; assessments should not rely on distribution models alone (Williams et al., 2008; Pacifici et al., 2015). Fourth, monitoring programmes should track sublethal indicators such as activity time, body condition, and reproductive output, which are likely to signal decline earlier than mortality events (Kingsolver et al., 2013). For aquatic systems, the protection of cold-water inflows, deep pools, and riparian vegetation offers analogous thermal refugia.

Table 4. Conservation Priorities Derived from the Reviewed Evidence

Priority	Recommended action	Supporting evidence
Retain thermal refugia	Protect canopy cover, large trees, epiphytes, leaf litter, and riparian shade	Microhabitats dampen temperature extremes (Scheffers et al., 2014); refuge use is essential (Sunday et al., 2014)
Maintain elevational connectivity	Secure continuous habitat from lowlands to montane zones	Upslope shift is the main escape route in the tropics (Colwell et al., 2008)
Integrate physiology into assessments	Combine exposure, sensitivity, and adaptive capacity in vulnerability assessments	Williams et al. (2008); Pacifici et al. (2015)
Monitor sublethal indicators	Track activity time, body condition, and reproductive output	Fitness declines precede mortality (Kingsolver et al., 2013; Walsh et al., 2019)
Protect aquatic thermal refugia	Conserve cold-water inflows, deep pools, and shaded stream reaches	Aquatic ectotherms have narrow margins and few refugia (Pinsky et al., 2019)

Notes: Recommendations are the authors' synthesis of the cited literature.

5.4. Research Priorities

Future work should prioritise:

- Measurement of thermal limits for under-sampled tropical taxa, including endemic amphibians, reptiles, freshwater fishes, and insects of biodiversity hotspots such as the Western Ghats.
- Thermal fertility limits and early life-stage tolerance.
- Fine-scale mapping of operative temperatures in intact versus degraded habitats.
- Quantification of heritable variation in heat tolerance in wild populations.
- Integration of physiological data with demographic models to predict population-level outcomes.

VI. CONCLUSION

This review integrates evidence on the thermal physiology of ectotherms to evaluate their vulnerability to climate warming.

Key conclusions include:

- Upper thermal limits are strongly conserved across latitude and lineage, whereas lower limits are variable, so that species in warm environments have limited thermal headroom
- Tropical ectotherms are thermal specialists living close to their physiological optima, and even modest warming is predicted to reduce their fitness
- Acclimation and evolutionary adaptation appear insufficient, in most groups, to raise heat tolerance at the pace of projected warming
- Behavioural thermoregulation is the principal buffer, but it restricts activity time and depends on the availability of cool microhabitats, so habitat degradation and warming act synergistically
- Sublethal effects on metabolism, activity, and fertility are likely to drive declines before lethal limits are reached, meaning CT_{max}-based assessments underestimate risk
- Marine and freshwater ectotherms, with limited access to thermal refugia, may be more vulnerable than terrestrial species.

These findings indicate that conserving ectotherm diversity under climate change requires protecting the structural complexity and elevational connectivity of habitats as well as their extent. Incorporating physiological data into conservation planning, and closing the large geographic gaps in thermal-tolerance data for tropical faunas, are urgent priorities for zoological research.

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