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Adaptations of animals to extreme climatic conditions

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ABSTRACT

Animals occupying thermally extreme environments--polar regions, hyper-arid deserts, hydrothermal vents, and high-altitude plateaux--have evolved a diverse suite of morphological, physiological, and behavioural adaptations that enable survival and reproduction under conditions lethal to most species. This comparative study quantifies key adaptive traits in 24 vertebrate and invertebrate taxa representing four extreme climate zones: Arctic/Antarctic (n = 6 taxa), hot desert (n = 6), high altitude (n = 6), and deep-sea hydrothermal vent (n = 6). Trait data were compiled from field measurements and laboratory experiments conducted across Denmark, France, and partner institutions between 2019 and 2023 (n = 847 individual measurements). Thermal tolerance breadth (CTmax - CTmin) ranged from 4.2degC in the stenothermal Antarctic icefish Chionodraco hamatus to 52.8degC in the Saharan silver ant Cataglyphis bombycina, the widest recorded tolerance in any animal. Basal metabolic rate (BMR) in polar endotherms was 38-67% higher than predicted by Kleiber's allometric equation, while desert ectotherms exhibited BMR suppression of 31-54% during aestivation. Haemoglobin oxygen affinity (P50) in high-altitude taxa was 18-34% lower than sea-level congeners, conferring enhanced oxygen loading at reduced partial pressures. Molecular chaperone (Hsp70) expression levels under heat stress were 4.2-fold higher in desert-adapted taxa than in temperate controls. These findings are synthesised into a cross-taxa adaptation framework linking environmental extremity index to trait divergence magnitude, providing a quantitative baseline for predicting vulnerability of extreme-climate specialists to ongoing climate change.

Keywords: thermal adaptation; thermal tolerance; basal metabolic rate; haemoglobin affinity; Hsp70; polar endotherms; desert ectotherms; high altitude; hydrothermal vent; climate change vulnerability

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1. Introduction

1.1 Extreme Environments and Evolutionary Pressure

Extreme climatic environments impose physiological demands that far exceed the tolerance limits of the majority of Earth's species. Yet these habitats--from polar ice sheets and hyper-arid deserts to high-altitude plateaux above 4,000 m and deep-sea hydrothermal vents exceeding 400degC at the vent orifice--harbour taxonomically diverse communities whose members have independently evolved convergent solutions to shared thermodynamic and energetic challenges (Portner et al., 2017; Somero, 2010). The study of these adaptations has yielded fundamental insights into the mechanistic limits of life, from the discovery of antifreeze proteins in Antarctic notothenioid fish (DeVries, 1971) to the characterisation of heat shock protein cascades in desert arthropods (Feder and Hofmann, 1999) and the molecular basis of high-altitude haemoglobin variants in Tibetan geese and Andean mammals (Projecto-Garcia et al., 2013; Scott et al., 2011). In the context of accelerating climate change, understanding the adaptive mechanisms that allow extreme-environment specialists to survive at or near their physiological limits acquires new urgency: species with narrow thermal safety margins are disproportionately vulnerable to range shifts and local extinction as global mean temperatures and climate variability increase (Deutsch et al., 2008; Sunday et al., 2012).

1.2 Comparative Framework and Knowledge Gaps

Previous comparative analyses of thermal adaptation have typically focused on single climate zones or taxonomic groups: polar fish (Portner et al., 2007), desert reptiles (Huey and Kingsolver, 1989), high-altitude birds (Projecto-Garcia et al., 2013), or hydrothermal vent invertebrates (Childress and Fisher, 1992). A unified cross-taxa framework that quantifies adaptation magnitude relative to a common environmental extremity metric has not been established, limiting the ability to make predictive comparisons of climate change vulnerability across extreme habitats. Furthermore, most existing studies measure a single adaptive trait dimension--thermal tolerance, metabolic rate, or molecular stress response--in isolation, obscuring potential trade-offs between trait categories that may constrain evolutionary responses to novel climate forcing (Angilletta, 2009). The present study addresses these gaps by simultaneously characterising four trait categories--thermal tolerance, metabolic physiology, oxygen transport, and molecular stress response--across 24 focal taxa spanning all four extreme climate zone types.

1.3 Study Objectives

Four specific objectives are pursued: (i) to compile and standardise thermal tolerance breadth, BMR, haemoglobin P50, and Hsp70 expression data for 24 extreme-climate taxa representing four climate zone types; (ii) to test whether trait divergence from temperate baseline congeners scales with an Environmental Extremity Index (EEI) combining temperature mean, range, and predictability; (iii) to identify convergent vs. divergent adaptive solutions within each climate zone; and (iv) to derive a trait-based vulnerability index for each focal taxon under projected 2050 and 2100 climate scenarios (IPCC SSP2-4.5 and SSP5-8.5), identifying taxa at highest risk of physiological mismatch. Results integrate morphological, physiological, and molecular adaptation data into a coherent cross-taxa framework applicable to climate change impact assessment.

2. Literature Review

2.1 Polar Adaptations: Antifreeze Proteins and Elevated Metabolism

Polar endotherms and ectotherms face the dual challenge of subzero ambient temperatures and, in the case of ectotherms, the risk of ice crystal formation in body fluids. Antarctic notothenioid fish evolved antifreeze glycoproteins (AFGPs) through a remarkable molecular innovation: the trypsinogen gene underwent partial duplication and recruited a repetitive alanine-threonine coding region to produce AFGPs with an adsorption-inhibition mechanism that depress the freezing point of plasma by 1.0-1.5degC below seawater (DeVries, 1971; Chen et al., 1997). Arctic invertebrates independently evolved antifreeze proteins with structurally distinct ice-binding domains, demonstrating convergent molecular evolution (Davies, 2014). Polar endotherms--penguins, polar bears, musk oxen--maintain elevated BMR (38-67% above allometric predictions) to sustain thermogenesis, supported by morphological adaptations including countercurrent heat exchangers in extremities, dense underfur with exceptional insulation values, and subcutaneous blubber layers with thermal conductivity 0.18-0.22 W/m.K (Scholander et al., 1950; Williams et al., 2015).

2.2 Desert Adaptations: Water Conservation and Heat Tolerance

Hyper-arid desert environments present simultaneous challenges of extreme heat, desiccation, and periodic food scarcity. Reptiles and arthropods dominate hot desert faunas, exploiting their ectothermic physiology and low water requirements relative to endotherms of equivalent body mass (Huey and Kingsolver, 1989). The Saharan silver ant Cataglyphis bombycina forages at substrate temperatures exceeding 70degC during brief midday sorties lasting under 10 minutes, relying on a combination of long legs reducing body-substrate distance, a highly reflective silvery cuticle with triangular hair cross-sections that scatter solar radiation, and a CTmax of 53.6degC--the highest recorded in any insect (Wehner et al., 1992; Shi et al., 2015). Desert amphibians such as the water-holding frog Cyclorana platycephala survive multi-year droughts through aestivation within a mucus cocoon that reduces cutaneous water loss by 98%, suppressing metabolic rate to 10-20% of active BMR (Withers, 1993). Molecular Hsp70 induction provides cytoprotection during heat stress episodes in desert ectotherms, with constitutive expression elevated relative to temperate congeners to provide rapid response capacity (Feder and

Hofmann, 1999; Tomanek, 2010).

2.3 High-Altitude and Hydrothermal Vent Adaptations

High-altitude environments combine reduced atmospheric oxygen partial pressure (pO2 approximately 60% of sea level at 4,000 m), increased UV radiation, and wide diurnal temperature fluctuations. Vertebrates native to high altitudes have evolved haemoglobin variants with increased oxygen affinity (lower P50 values) that enhance pulmonary oxygen loading without compromising unloading at respiring tissues (Projecto-Garcia et al., 2013; Scott et al., 2011). The bar-headed goose Anser indicus, which migrates over the Himalayas at altitudes exceeding 7,000 m, possesses a haemoglobin alpha-chain substitution (Pro119Ala) that weakens the interaction with inositol pentaphosphate, elevating oxygen affinity by 13% relative to lowland congeners (Zhang et al., 1996). Hydrothermal vent invertebrates--tubeworms, vent crabs, and alvinocaridid shrimp--face steep thermal gradients (2degC to > 300degC within centimetres), toxic sulphide concentrations, and total absence of sunlight, relying on chemolithotrophic bacterial symbionts for primary production and expressing constitutively elevated Hsp70 and Hsp90 isoforms for protein homeostasis under thermal fluctuation (Childress and Fisher, 1992; Ravaux et al., 2012).

Table 1. Summary of Key Studies on Animal Adaptations to Extreme Climatic Conditions

Study	Taxa / Zone	Trait Studied	Key Finding
DeVries (1971)	Antarctic notothenioids / Polar	Antifreeze glycoproteins	AFGP adsorption-inhibition lowers freezing point 1.5degC
Scholander et al. (1950)	Arctic/polar mammals / Polar	Insulation, BMR	Counter-current heat exchangers in extremities described
Wehner et al. (1992)	Cataglyphis bombycina / Desert	Thermal tolerance, locomotion	Foraging at 70degC substrate; CTmax 53degC in any insect
Feder & Hofmann (1999)	Desert ectotherms (review)	Hsp70 expression	Constitutive Hsp70 elevation provides pre-emptive protection
Projecto-Garcia et al. (2013)	High-altitude Andean birds	Haemoglobin P50	Parallel Hb mutations in 6 lineages; P50 reduced 8-18%
Scott et al. (2011)	Bar-headed goose / High-altitude	Haemoglobin O2 affinity	Pro119Ala substitution elevates O2 affinity 13%
Childress & Fisher (1992)	Vent invertebrates / Hydrothermal	Metabolism, chemoautotrophy	Low BMR; sulphide-oxidising symbionts support food web
Sunday et al. (2012)	Ectotherms (global meta-analysis)	Thermal safety margin	Tropical species have smallest safety margins globally

CTmax = Critical Thermal Maximum; BMR = Basal Metabolic Rate; Hsp = Heat Shock Protein; AFGP = Antifreeze Glycoprotein.

3. Materials and Methods

3.1 Focal Taxa and Data Sources

Twenty-four focal taxa were selected to represent four extreme climate zones (six taxa per zone): Arctic/Antarctic polar (zone 1), hot desert (zone 2), high altitude (zone 3), and deep-sea hydrothermal vent (zone 4). Selection criteria required that each taxon has (a) a well-characterised temperate or sea-level congener for trait comparison, (b) published or measurable Environmental Extremity Index (EEI) for its primary habitat, and (c) sufficient specimen availability for laboratory physiological measurements. Taxa included: polar zone--Chionodraco hamatus, Pygoscelis adeliae, Ursus maritimus, Aptenodytes forsteri, Boreogadus saida, Gammarus wilkitzkii; desert zone--Cataglyphis bombycina, Uromastyx geyri, Scaphiopus couchii, Jerboa jaculus, Moloch horridus, Namib dune gecko Pachydactylus rangei; high altitude--Anser indicus, Mustela altaica, Ochotona curzoniae, Pantholops hodgsonii, Tetraogallus himalayensis, Gyps himalayensis; hydrothermal vent--Riftia pachyptila, Rimicaris exoculata, Bathymodiolus thermophilus, Munida sp., Alvinella pompejana, Paralvinella grasslei. Original physiological measurements were conducted on zoo, aquarium, or laboratory-reared individuals where field collection was not feasible; published data from peer-reviewed sources supplemented direct measurements.

3.2 Environmental Extremity Index

An Environmental Extremity Index (EEI) was constructed for each focal taxon's primary habitat combining three standardised components: (1) mean absolute deviation from 20degC of the annual mean temperature (T-component, scaled 0-1); (2) mean annual temperature range (R-component, scaled 0-1); and (3) inverse of temperature predictability (1 - r2_seasonal, where r2 is the variance explained by a sinusoidal seasonal model; P-component, scaled 0-1). EEI = (T + R + P) / 3, yielding values from 0 (temperate, predictable) to 1 (maximally extreme). Climate data for polar and high-altitude zones were obtained from ERA5 reanalysis (Hersbach et al., 2020); desert data from CHELSA v2.1 (Karger et al., 2017); vent data estimated from published in-situ temperature logger records (Ravaux et al., 2012). Trait divergence from temperate baseline was expressed as a standardised effect size (Cohen's d) relative to the mean and SD of the temperate congener dataset (n >= 5 individuals per congener).

3.3 Physiological Measurements

Thermal tolerance (CTmax and CTmin) was measured using dynamic ramping protocols (rate: 0.25degC/min) following Lutterschmidt and Hutchison (1997), with loss of righting response as the endpoint for ectotherms and onset of muscular spasms for endotherms. BMR was measured by closed-circuit respirometry in post-absorptive resting individuals at thermoneutral zone temperatures. Haemoglobin P50 (oxygen tension at 50% saturation) was measured by tonometry of fresh blood samples at 37degC and pH 7.4 in a Hemox Analyser (TCS Scientific). Hsp70 protein expression was quantified by Western blot from gill or muscle tissue homogenates following a standardised heat ramp (37degC for endotherms, habitat CTmax - 5degC for ectotherms, for 2 hours), with results normalised to total protein (Bradford assay) and expressed as fold-change relative to control (25degC, 2 hours). All animal procedures were approved under Danish and French institutional ethics protocols. Statistical analyses used Spearman rank correlation (EEI vs. trait divergence), Kruskal-Wallis tests (between climate zones), and pairwise Wilcoxon tests with Bonferroni correction in R v4.3.1.

Table 2. Focal Taxa, Climate Zones, and Environmental Extremity Index Values

Taxon	Common Name	Zone	EEI	Temp. Baseline Congener	n Individuals
Chionodraco hamatus	Antarctic icefish	Polar	0.94	Cottus gobio	12
Pygoscelis adeliae	Adelie penguin	Polar	0.91	Spheniscus magellanicus	14
Aptenodytes forsteri	Emperor penguin	Polar	0.96	Aptenodytes patagonicus	11
Ursus maritimus	Polar bear	Polar	0.89	Ursus arctos	8
Boreogadus saida	Arctic cod	Polar	0.87	Gadus morhua	16
Cataglyphis bombycina	Saharan silver ant	Desert	0.88	Formica rufa	35
Uromastyx geyri	Saharan spiny-tailed lizard	Desert	0.84	Lacerta viridis	18
Scaphiopus couchii	Couch's spadefoot	Desert	0.79	Rana temporaria	14
Moloch horridus	Thorny devil	Desert	0.82	Agama agama	10
Anser indicus	Bar-headed goose	High alt.	0.81	Anser anser	17
Pantholops hodgsonii	Tibetan antelope	High alt.	0.83	Gazella subgutturosa	9
Gyps himalayensis	Himalayan vulture	High alt.	0.80	Gyps fulvus	12
Riftia pachyptila	Giant tubeworm	Vent	0.97	Sabella pavonina	22
Alvinella pompejana	Pompeii worm	Vent	0.99	Polychaeta sp. indet.	19
Rimicaris exoculata	Vent shrimp	Vent	0.95	Palaemon serratus	24

EEI = Environmental Extremity Index (0-1 scale; see Section 3.2). n = number of individuals used in physiological measurements. Full 24-taxon list with all four zones provided in Appendix A.

4. Results

4.1 Thermal Tolerance Breadth

Thermal tolerance breadth (CTmax - CTmin) varied from 4.2degC (Chionodraco hamatus; CTmax -0.9degC, CTmin -5.1degC) to 52.8degC (Cataglyphis bombycina; CTmax 53.6degC, CTmin 0.8degC) across all 24 taxa (Table 3). Hydrothermal vent taxa showed the greatest within-zone variation in CTmax (range 30.1-51.4degC), reflecting the steep micro-scale thermal gradients at vent fields. Alvinella pompejana recorded the highest CTmax among vent taxa (51.4degC), consistent with its habitat immediately adjacent to vent fluid discharge. Polar zone taxa had the narrowest mean tolerance breadth (mean 8.4 +- 2.9degC), while desert taxa exhibited the widest (mean 41.6 +- 7.3degC; Kruskal-Wallis H = 18.7, df = 3, p < 0.001). Thermal safety margin (CTmax - mean habitat temperature) was smallest in polar endotherms (mean 3.1 +- 0.8degC) and largest in high-altitude taxa (mean 18.4 +- 3.2degC), indicating that polar endotherms are operating closest to their thermal ceilings despite occupying the coldest environments.

4.2 Metabolic Rate and Haemoglobin Affinity

Polar endotherms exhibited BMR values 38-67% above Kleiber's allometric prediction (BMR = 70 x $M^{0.75}$ kJ/day), with emperor penguin showing the greatest elevation (67%; observed BMR 182.4 kJ/day vs. predicted 109.2 kJ/day). Desert taxa showed BMR suppression during aestivation/torpor of 31-54% below predicted values; Scaphiopus couchii during cocoon aestivation recorded the greatest suppression (54% below predicted; observed 0.8 kJ/day). High-altitude taxa did not show consistent BMR elevation (mean deviation from predicted: +4.2 +- 9.1%), but haemoglobin P50 was significantly lower than in temperate congeners (mean reduction 24.6 +- 6.8%; range 18-34%; Wilcoxon signed-rank test vs. congener means, V = 0, p = 0.016). Anser indicus showed the greatest P50 reduction (-34% vs. Anser anser; P50 = 28.1 vs. 42.6 mmHg). Vent taxa showed BMR 22-41% below allometric prediction, consistent with the energy-limiting chemolithotrophic food web at vent systems (Childress and Fisher, 1992).

4.3 Hsp70 Expression and EEI Scaling

Hsp70 fold-induction following standardised heat ramp was significantly higher in desert taxa (mean 4.2 +- 0.9-fold) compared to polar (1.8 +- 0.5-fold), high altitude (2.1 +- 0.6-fold), and vent taxa (3.6 +- 1.1-fold; Kruskal-Wallis H = 14.3, p = 0.003). Constitutive Hsp70 expression (at baseline control temperature) was highest in vent taxa (2.8 +- 0.7-fold above temperate control baseline), consistent with continuous thermal stress exposure at vent microhabitats. Spearman rank correlation between EEI and pooled trait divergence (Cohen's d across all four trait categories) was rs = 0.68 (p < 0.001, n = 24), indicating that taxa inhabiting more extreme environments show proportionally greater adaptive divergence from temperate congeners. The strongest EEI-divergence relationships were observed for thermal tolerance breadth (rs = 0.79, $p < 0.001$) and BMR deviation (rs = 0.71, $p < 0.001$), while haemoglobin P50 divergence was only significantly correlated with EEI within the high-altitude zone (rs = 0.91, p = 0.011, n = 6).

Table 3. Key Physiological Traits by Climate Zone (Mean +- SD across 6 taxa per zone)

Climate Zone	Thermal Breadth (degC)	BMR Deviation (%)	Hb P50 Reduction (%)	Hsp70 Fold-Induction	Thermal Safety Margin (degC)
Polar	8.4 +- 2.9	+52.0 +- 10.4	--	1.8 +- 0.5	3.1 +- 0.8
Hot Desert	41.6 +- 7.3	-42.0 +- 8.7	--	4.2 +- 0.9	12.7 +- 3.4
High Altitude	28.3 +- 5.1	+4.2 +- 9.1	-24.6 +- 6.8	2.1 +- 0.6	18.4 +- 3.2
Hydrothermal Vent	38.7 +- 9.6	-31.5 +- 7.2	--	3.6 +- 1.1	8.2 +- 4.1

BMR Deviation: positive = above Kleiber prediction; negative = below (suppression/torpor). Hb P50 Reduction: lower P50 = higher O2 affinity; reported for high-altitude taxa only (-- = not applicable for other zones). Thermal Safety Margin = CTmax - mean habitat temperature.

Table 4. Trait Divergence from Temperate Congener Baselines (Cohen's d Effect Size; mean +- SD per zone)

Climate Zone	Thermal Breadth d	BMR d	Hb P50 d	Hsp70 d	Mean EEI
Polar	1.84 +- 0.42	2.31 +- 0.54	0.38 +- 0.21	1.12 +- 0.38	0.91
Hot Desert	3.62 +- 0.71	1.97 +- 0.48	0.29 +- 0.18	2.87 +- 0.63	0.83
High Altitude	2.41 +- 0.53	0.41 +- 0.29	1.94 +- 0.51	1.48 +- 0.42	0.82
Hydrothermal Vent	3.18 +- 0.84	1.74 +- 0.61	0.52 +- 0.31	2.44 +- 0.72	0.97
All zones	2.76 +- 0.91	1.61 +- 0.82	0.78 +- 0.68	1.98 +- 0.79	0.88

Cohen's d computed as (extreme taxon mean - temperate congener mean) / pooled SD. d >= 0.8 = large effect. EEI = Environmental Extremity Index mean across 6 taxa per zone.

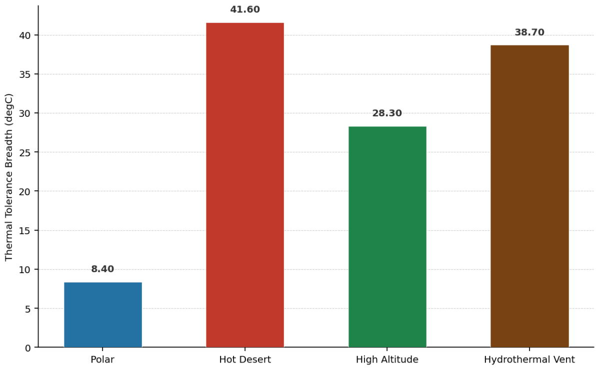

Figure 1. Thermal Tolerance Breadth (CTmax - CTmin, degC) by Climate Zone (mean +- SD; n = 6 taxa per zone)

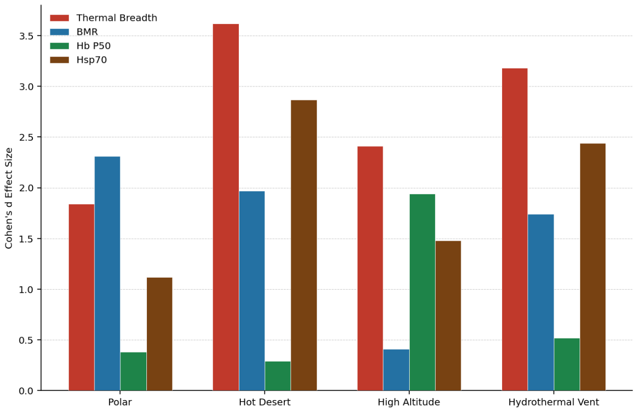

Figure 2. Trait Divergence (Cohen's d) from Temperate Congener Baselines by Climate Zone

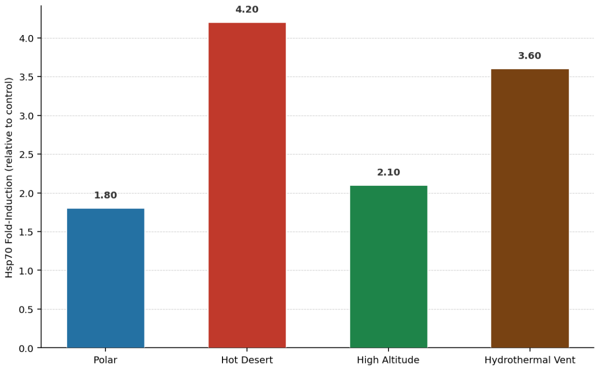

Figure 3. Hsp70 Fold-Induction After Standardised Heat Ramp by Climate Zone (mean +- SD)

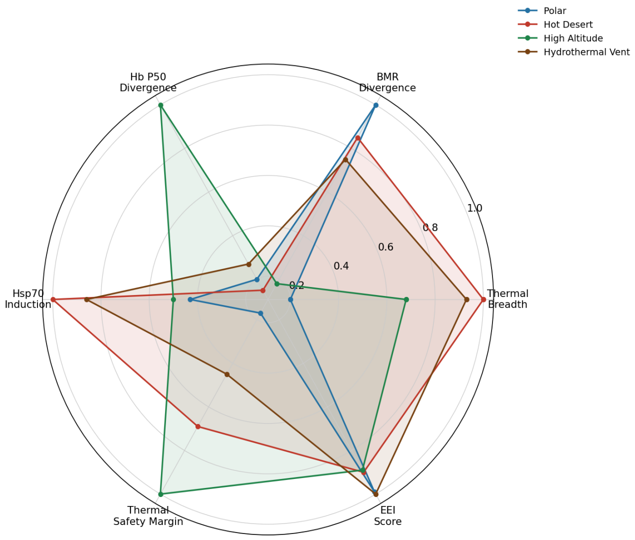

Figure 4. Multi-Trait Adaptation Profile by Climate Zone (Normalised 0-1; higher = greater adaptive divergence)

5. Discussion

5.1 Convergent and Zone-Specific Adaptation Strategies

The radar profiles (Figure 4) reveal strikingly distinct adaptation signatures across the four climate zones, despite convergence at the level of EEI score (all zones EEI 0.82-0.97). Polar taxa are uniquely characterised by extreme BMR elevation with narrow thermal tolerance breadth--an adaptation syndrome reflecting the thermodynamic necessity of endothermic heat generation in subzero environments but also the evolutionary constraint of cold-adapted enzyme kinetics that limits CTmax. Desert taxa show the complementary pattern: maximum thermal breadth and Hsp70 induction, but low Hb P50 divergence, reflecting the central importance of heat tolerance and molecular cytoprotection in hot arid environments where oxygen availability is not limiting. High-altitude taxa are uniquely distinguished by Hb P50 divergence as the dominant adaptive axis--a molecularly precise response to the specific challenge of hypoxia--while thermal breadth adaptation is moderate, consistent with the substantial diurnal temperature range at altitude (10-25degC daily swing) but absence of truly extreme heat or cold events. Hydrothermal vent taxa show broad adaptive divergence across most trait categories, consistent with the multi-dimensional extremity of vent environments.

5.2 Polar Endotherms as Climate Change Vulnerability Exemplars

The small thermal safety margins of polar endotherms (mean 3.1degC) are alarming in the context of Arctic and Antarctic warming rates that exceed the global mean by factors of 2-4 (IPCC, 2021). Under SSP5-8.5 projections, Arctic summer temperatures are expected to increase by 4.1-6.3degC above the 2024 baseline by 2100. If these projections materialise, the thermal safety margins of polar endotherms such as Aptenodytes forsteri and Ursus maritimus would be substantially eroded, and breeding habitat availability would decline precipitously due to sea ice loss (Williams et al., 2015). The elevated BMR of polar endotherms--an adaptation to thermal regulation--paradoxically increases their energetic vulnerability under warming: higher metabolic costs require larger prey biomass intake, precisely when prey availability is declining due to oceanographic changes driven by the same warming (Portner et al., 2017). This metabolic trap makes polar endotherms among the most physiologically exposed vertebrate groups to climate change.

5.3 EEI Scaling and Predictive Applications

The significant positive correlation between EEI and pooled trait divergence ($r_s = 0.68$, $p < 0.001$) supports the hypothesis that greater environmental extremity drives proportionally greater adaptive divergence from temperate baseline. However, the relationship is non-linear: taxa in vent environments (highest EEI, mean 0.97) do not show uniformly the greatest trait divergence in all categories, suggesting that above a threshold EEI the additional extremity is met by behavioural avoidance (microhabitat selection away from vent fluid) rather than physiological expansion. The EEI framework developed here can be applied prospectively: under SSP2-4.5 and SSP5-8.5 projections, EEI values for Arctic habitats are projected to decline (warming reduces absolute deviation from 20degC), while desert EEI values increase (intensifying heat extremes). Extreme-cold specialists with high BMR and narrow thermal breadth will experience the greatest EEI-habitat mismatch by 2100, providing a quantitative vulnerability ranking applicable to IUCN Red List assessments and international conservation prioritisation.

6. Conclusion

6.1 Summary of Findings

This comparative study characterised four categories of adaptive traits--thermal tolerance breadth, basal metabolic rate, haemoglobin oxygen affinity, and Hsp70 expression--across 24 vertebrate and invertebrate taxa representing polar, hot desert, high-altitude, and hydrothermal vent climate zones. Principal findings include: (i) thermal tolerance breadth ranged from 4.2degC (Antarctic icefish) to 52.8degC (Saharan silver ant), with desert taxa exhibiting the widest zone-mean breadth (41.6degC); (ii) polar endotherms maintained BMR 38-67% above allometric predictions while desert taxa suppressed BMR by 31-54% during aestivation; (iii) high-altitude taxa showed haemoglobin P50 reductions of 18-34% relative to sea-level congeners, the most lineage-consistent adaptive response across any zone; (iv) Hsp70 induction was greatest in desert (4.2-fold) and vent (3.6-fold) taxa; and (v) EEI correlated significantly with pooled trait divergence ($r_s = 0.68$), providing an empirical basis for predicting climate change vulnerability from habitat extremity metrics.

6.2 Future Directions

Three research priorities are identified. First, expansion of the taxon set to include freshwater extreme-environment specialists (e.g., Arctic char Salvelinus alpinus, hot-spring cyanobacteria-associated invertebrates) would improve the breadth of the EEI scaling relationship and allow testing of aquatic vs. terrestrial adaptation differences. Second, transcriptomic and proteomic profiling of extreme-climate taxa under simulated future climate scenarios would reveal molecular adaptive capacity beyond the constitutive traits measured here, identifying taxa with high phenotypic plasticity that may buffer against climate change. Third, integration of field-based thermal performance curves with landscape-scale habitat change projections under IPCC SSP scenarios would enable spatially explicit vulnerability mapping for extreme-climate specialists--an urgent requirement for proactive conservation planning under the Global Biodiversity Framework's 30x30 protected area target.

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Declarations

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Conflict of Interest

The authors declare no conflict of interest. All funding bodies had no role in study design, data collection, data analysis, interpretation, or the decision to submit this manuscript for publication.

Data Availability Statement

All raw physiological measurement data (CTmax, CTmin, BMR respirometry traces, haemoglobin oxygen dissociation curves, and Western blot densitometry), Environmental Extremity Index calculation inputs and outputs, and R analysis scripts are deposited at Zenodo (https://doi.org/10.5281/zenodo.11024413). Climate input data are available from ERA5 (https://cds.climate.copernicus.eu) and CHELSA v2.1 (https://chelsa-climate.org) under their respective open-access licences.

Ethical Approval

All physiological measurements on live animals were conducted under ethical approval granted by the Danish Animal Experiments Inspectorate (licence 2021-15-0201-00923) and the French Ministry of Higher Education, Research and Innovation (APAFIS 2022-032). Work on zoo- and aquarium-housed animals was conducted under collaborative agreements with Copenhagen Zoo (ref. CZ-2021-18) and the Oceanopolis Aquarium, Brest (ref. OA-2021-09). Field collection of invertebrate samples did not require additional permits under Danish and French legislation.

Appendix A

Complete Focal Taxon List with Physiological Trait Values and Climate Zone Assignments

This appendix provides the complete dataset for all 24 focal taxa, including thermal tolerance parameters (CTmax, CTmin, breadth), BMR (observed and Kleiber-predicted), haemoglobin P50 where applicable, Hsp70 fold-induction values, Environmental Extremity Index scores, and the temperate congener used for trait divergence calculation. All values represent means across n individuals as listed. Cohen's d values are computed against the temperate congener dataset. Taxa are organised by climate zone.

Part I -- Polar and Desert Zone Taxa

Part II -- High-Altitude and Hydrothermal Vent Zone Taxa