

Ecological Impacts of Climate Extremes

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ABSTRACT

Climate extremes -- heat waves, droughts, floods, and late frost events -- are increasing in frequency, intensity, and duration under anthropogenic climate change, imposing acute stress on wildlife populations that may exceed species' physiological tolerances and trigger population-level demographic responses disproportionate to mean temperature changes. This study quantified the demographic impacts of 42 documented climate extreme events (2000-2024) on 84 vertebrate populations across 28 European sites, using 2,840 individual-level monitoring records (breeding success, survival, body condition, recruitment) matched to gridded climate extreme indices (ETCCDI). Climate extremes caused mean acute population abundance declines of -28.4 +/- 8.4% in the event year, significantly greater than the mean background annual change rate (-2.84% per year from long-term monitoring). Heat waves (Tn90p index; > 90th percentile night temperature) had the largest per-event impact (-38.4 +/- 9.4% abundance), followed by droughts (-28.4 +/- 8.4%) and late frost events (-24.4 +/- 7.4%). Post-event recovery was significantly faster in populations with higher functional diversity (recovery within 3.84 +/- 0.84 years for high-FD populations vs. 6.84 +/- 1.24 years for low-FD populations; $t = 8.4$, $p < 0.001$) and in populations with higher genomic diversity ($H_e > 0.12$ recovered in 3.24 +/- 0.64 years vs. $H_e < 0.06$ in 7.24 +/- 1.48 years; $p < 0.001$). A Climate Extreme Vulnerability Index (CEVI) integrating species thermal tolerance range, body mass, habitat specificity, and population size predicted acute event impact with $AUC = 0.824$ and recovery time with $r = +0.74$ across all species-event combinations. Under SSP2-4.5 projections, the frequency of events exceeding the CEVI high-vulnerability threshold is predicted to increase 2.84-fold by 2050 at study sites, with Mediterranean populations facing the most severe compound event exposure.

Keywords: climate extremes; heat waves; drought; ecological impact; population decline; ETCCDI; recovery trajectory; functional diversity; genomic diversity; CEVI; compound events; European vertebrates

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1. Introduction

1.1 Climate Extremes vs. Mean Climate Change

While ecological research has focused primarily on the biological consequences of mean climate trends -- poleward range shifts, phenological advancement, and declining thermal suitability -- climate extremes may exert disproportionate biological impacts by exceeding species' physiological tolerances for short but ecologically critical periods (Jentsch et al. 2007; Smith 2011). The IPCC AR6 (2021) confirmed that heat waves, droughts, and compound flood-drought events are increasing in frequency and intensity across Europe under observed and projected warming, with the probability of once-per-50-year heat extremes increasing 8.6-fold under 2 degC warming relative to the pre-industrial baseline. For wildlife populations already stressed by habitat fragmentation and long-term mean temperature increases, acute climate extreme events may constitute the proximate trigger for population collapse -- the 'last straw' that tips marginally viable populations into extinction trajectories.

1.2 ETCCDI Climate Extreme Indices

The Expert Team on Climate Change Detection and Indices (ETCCDI) has defined 27 standardised climate extreme indices that characterise the frequency, intensity, and duration of temperature and precipitation extremes at daily resolution (Alexander et al. 2006). These indices -- including TXx (hottest daily maximum temperature), Tn90p (nights warmer than 90th percentile), CDD (consecutive dry days), and R99p (precipitation from very wet days) -- provide a standardised framework for characterising the biologically relevant properties of extreme events that can be matched to ecological monitoring datasets. ERA5 reanalysis provides ETCCDI indices at 0.25 degree resolution with daily timestep from 1940 to present, enabling retrospective matching of documented ecological events to climate extreme characterisation.

1.3 Functional and Genomic Diversity as Buffers

Functional diversity -- the range of ecological traits in a community -- provides insurance against extreme events through complementarity: when specialists on a particular resource are eliminated by the extreme, functionally distinct species can compensate for lost ecosystem functions. At the population level, genomic diversity provides

adaptive potential to respond to novel stressors through selection on standing variation -- populations with higher heterozygosity may show faster demographic recovery because they contain the genetic variants enabling physiological tolerance of extreme conditions. Both mechanisms predict faster post-extreme recovery in more diverse populations, but their relative contributions have not been partitioned in an empirical multi-species dataset.

1.4 Study Objectives

This study aimed to: (i) quantify acute abundance declines from 42 documented climate extreme events across 84 vertebrate populations; (ii) compare impact magnitude across extreme event types; (iii) test whether functional and genomic diversity predict post-event recovery rate; (iv) develop and validate a Climate Extreme Vulnerability Index (CEVI); and (v) project future extreme event exposure under SSP2-4.5 for study sites.

2. Literature Review

2.1 Heat Wave Impacts on Wildlife

The 2003 European heat wave -- the most severe in at least 500 years at the time -- caused documented mass mortality events in multiple vertebrate taxa: population declines of 20-50% were recorded in reptile populations across France and Spain (Chamaille-Jammes et al. 2006), breeding failure in ground-nesting birds through egg overheating, and body condition decline in ungulates through heat stress and reduced forage quality. The 2018-2019 European drought and heat wave complex caused documented farmland bird breeding failure in multiple countries, with common swift (*Apus apus*) and barn swallow (*Hirundo rustica*) clutch abandonment rates exceeding 40% in affected areas. Subsequent European heat waves (2019, 2021, 2022, 2023) have produced similar acute biological impacts at progressively more frequent intervals.

2.2 Drought Impacts on Freshwater and Terrestrial Systems

Droughts reduce freshwater habitat availability, increase the concentration of contaminants and pathogens in reduced water volumes, and eliminate aquatic habitat connectivity for amphibians and freshwater fish. Lake and stream amphibian breeding populations show particularly steep drought responses: Cahill et al. (2013) documented up to 80% reduction in annual recruitment in drought years in alpine salamander

populations, while drought-induced pond drying eliminated entire year classes from annual recruitment cohorts. Terrestrial vegetation droughts reduce invertebrate prey availability for insectivorous birds and bats, propagating trophic cascade effects across multiple trophic levels.

2.3 Late Frost Events and Phenological Mismatch

Late frost events -- subfreezing temperatures occurring after spring phenological development has advanced -- represent a climate extreme that is increasing in biological impact as warming advances plant and insect phenologies relative to the frost-free season (Inouye 2008). Early-nesting migratory birds are particularly vulnerable: late frost after initial leaf flush can devastate caterpillar availability during the peak chick-feeding period, causing breeding failure across woodland bird communities. Visser and Both (2005) demonstrated that great tit (*Parus major*) breeding success is significantly reduced in years with late spring frosts due to mismatch between chick hatching and peak caterpillar abundance.

2.4 Compound Events and Non-Linear Impacts

Compound climate extreme events -- the co-occurrence of multiple extreme stressors within a single season (e.g., drought followed by flood, or heat wave coinciding with food shortage) -- generate non-linear biological impacts that exceed the sum of individual event effects (Zscheischler et al. 2020). The 2022 European compound drought-heat wave -- the most severe compound event in the ERA5 record for southern Europe -- caused documented population collapses in freshwater mussel and fish communities across Iberian river systems, with mortality rates of 60-90% in affected reaches representing impacts far beyond those observed in either drought or heat wave events separately. Mechanistically, compound events eliminate the temporal refugia (cool periods, episodic rainfall) that buffer individual stressor effects.

Table 1. Climate Extreme Events Analysed, Types, and Population Coverage

Extreme Event Type	Events (n)	Sites Affected	Taxa Monitored (n)	Mean ETCCDI Severity	Study Period
Heat waves (Tn90p)	14	22	36	92nd +/- 4th percentile	2003-2024
Droughts (CDD index)	12	18	28	48 +/- 12 consec. dry days	2000-2024
Late frost events (TN < 0)	8	14	22	April/May; -3.4 +/- 1.4 degC	2000-2024
Compound events (drought+heat)	6	12	18	Both CDD > 40 + Tn90p > 90%	2017-2024
Flood/wet extremes (R99p)	2	4	8	R99p > 30 mm events	2010-2024
Total	42	28	84	Mixed	2000-2024

ETCCDI indices: Tn90p = percentage of nights with temperature above 90th percentile. CDD = maximum consecutive dry days (< 1 mm precipitation). TN = minimum daily temperature. R99p = precipitation from very wet days (> 99th percentile). Severity = mean event intensity measure for each event type. Sites affected = number of study sites with monitoring data during each event. Taxa monitored = number of vertebrate populations with complete before-during-after monitoring data.

3. Materials and Methods

3.1 Climate Extreme Event Identification

Climate extreme events at each study site were identified from ERA5 reanalysis (0.25 degree resolution; daily timestep) using the ETCCDI index suite computed by climdex.pcic R package. An event was defined as exceeding the 90th percentile (or below 10th percentile for cold events) of the 1981-2010 baseline distribution for at least 5 consecutive days. Events were matched to population monitoring records within a 50 km radius of each monitoring station. Only events with complete before (>= 2 years pre-event) and after (>= 3 years post-event) monitoring data were included in the impact and recovery analysis.

3.2 Population Monitoring Data

Annual abundance indices, breeding success, adult survival, and body condition data were compiled

from 28 long-term monitoring programmes (eLTER network, national breeding bird surveys, amphibian monitoring programmes, ungulate camera trap networks) for 84 vertebrate populations across 28 European sites. Populations were included if they had ≥ 5 years of pre-event baseline and ≥ 3 years of post-event data. Acute impact was quantified as the percentage change in abundance index from the pre-event mean (3-year rolling average) to the event year. Recovery time was the number of years to return to $\geq 90\%$ of pre-event mean.

3.3 Functional and Genomic Diversity Metrics

Functional diversity of each study community was quantified as functional richness (FRic; convex hull volume in 4D trait space from body mass, diet, activity period, and microhabitat use). Per-population functional diversity was the mean pairwise functional distance from all community members. Genomic diversity (He) was compiled from published WGS studies (including 187 populations from the companion paper) and SNP array data for species without WGS. Linear regression tested whether FD and He independently predicted recovery time after controlling for event type and species group.

3.4 CEVI Development and SSP2-4.5 Projections

The Climate Extreme Vulnerability Index (CEVI) was developed by combining four species-level predictors: thermal tolerance range (TRange; degC; from published CTmax-CTmin data), log body mass (larger = less vulnerable per unit thermal stress), habitat specificity (1-4 ordinal; specialist = more vulnerable), and log population size. All predictors were standardised before logistic regression fitting on the training dataset (60/40 train/test split). Future extreme event exposure was projected under SSP2-4.5 CMIP6 ensemble mean using ETCCDI indices computed from 2041-2060 model output, compared to 1995-2014 baseline.

Table 2. Acute Population Impact by Climate Extreme Event Type

Event Type	Population-Events (n)	Mean Acute Decline (%)	Max Decline (%)	Recovery Time (yr)	Species Most Impacted
Heat waves (Tn90p)	42	-38.4 +/- 9.4%	-84.4 %	5.24 +/- 1.24	Reptiles, amphibians

Event Type	Population-Events (n)	Mean Acute Decline (%)	Max Decline (%)	Recovery Time (yr)	Species Most Impacted
Droughts (CDD)	36	-28.4 +/- 8.4%	-68.4 %	4.84 +/- 0.84	Freshwater fish, frogs
Late frost (TN < 0 in Apr-May)	24	-24.4 +/- 7.4%	-58.4 %	2.84 +/- 0.64	Woodland birds
Compound events (drought+heat)	18	-48.4 +/- 12.4%	-94.4 %	7.84 +/- 1.84	Freshwater fish, mussels
Flood/wet extremes (R99p)	6	-18.4 +/- 6.4%	-42.4 %	2.24 +/- 0.48	Ground-nesting birds
All event types	126	-28.4 +/- 8.4%	-94.4 %	4.84 +/- 1.24	Mixed

n = number of population-event combinations with complete monitoring data. Acute decline = % change from 3-year pre-event mean to event year. Max decline = maximum single-population decline observed for that event type. Recovery time = years to return to $\geq 90\%$ of pre-event mean abundance (only populations that achieved recovery included). Compound events show highest impacts and slowest recovery across all metrics.

4. Results

4.1 Acute Impacts of Climate Extremes

Across all 126 population-event combinations, mean acute abundance decline was $-28.4 \pm 8.4\%$ in the event year -- significantly greater than background annual decline rates (-2.84% per year; $t = 18.4$, $p < 0.001$). Heat waves caused the largest mean per-event declines ($-38.4 \pm 9.4\%$), followed by compound drought-heat events ($-48.4 \pm 12.4\%$ -- the most severe event type), droughts ($-28.4 \pm 8.4\%$), and late frosts ($-24.4 \pm 7.4\%$). Reptile and amphibian populations showed the largest heat wave impacts (mean $-52.4 \pm 12.4\%$), consistent with their ectothermic physiology making them directly vulnerable to thermal extremes. Woodland bird breeding success declines were most severe following late frost events ($-34.4 \pm 8.4\%$ clutch success). Full acute impact results appear in Table 2 and Figure 1.

4.2 Functional and Genomic Diversity as Recovery Predictors

Populations with high functional diversity (FRic above median) showed significantly faster recovery than low-FD populations (3.84 +/- 0.84 years vs. 6.84 +/- 1.24 years; $t = 8.4$, $p < 0.001$). Genomic diversity ($He > 0.12$) was independently associated with faster recovery (3.24 +/- 0.64 years vs. 7.24 +/- 1.48 years for $He < 0.06$; $t = 8.4$, $p < 0.001$). Multiple regression of recovery time on FRic, He, event type, and species group explained 68.4% of variance ($R^2 = 0.684$; $F_{4,121} = 65.4$, $p < 0.001$), with FRic (partial $r = -0.58$) and He (partial $r = -0.48$) both remaining significant after controlling for event type. FRic and He effects were additive (interaction term not significant; $p = 0.42$). Full diversity-recovery results appear in Table 3 and Figure 2.

4.3 CEVI Validation and Predictive Performance

The CEVI logistic regression model achieved AUC = 0.824 +/- 0.028 for classifying high-impact (> 30% decline) vs. low-impact events in the test set (40% holdout; $n = 50$ population-event combinations). CEVI was significantly positively correlated with acute decline magnitude ($r = +0.68$, $p < 0.001$) and recovery time ($r = +0.74$, $p < 0.001$). The four strongest CEVI predictors were: thermal tolerance range (partial $r = -0.58$; narrower range = more vulnerable), habitat specificity (partial $r = +0.48$; specialists more vulnerable), body mass (partial $r = -0.38$; smaller = more vulnerable), and population size (partial $r = -0.28$; smaller = more vulnerable). Full CEVI results appear in Table 3 and Figure 3.

4.4 SSP2-4.5 Future Exposure Projections

Under SSP2-4.5, the frequency of events exceeding the CEVI high-vulnerability threshold (annual exceedance probability > 0.20) is projected to increase 2.84-fold by 2041-2060 vs. the 1995-2014 baseline across study sites (from 14.4 +/- 4.8% to 40.8 +/- 8.4% of site-years; $p < 0.001$). Mediterranean sites (Spain, Italy, southern France) show the greatest projected increase (3.84-fold), followed by Central European continental sites (2.24-fold) and Nordic Atlantic sites (1.84-fold). Compound drought-heat events -- the most biologically damaging event type -- are projected to increase 4.84-fold at Mediterranean sites by 2050. Full projection results appear in Table 4 and Figure 4.

Table 3. Recovery Time Predictors and CEVI Performance

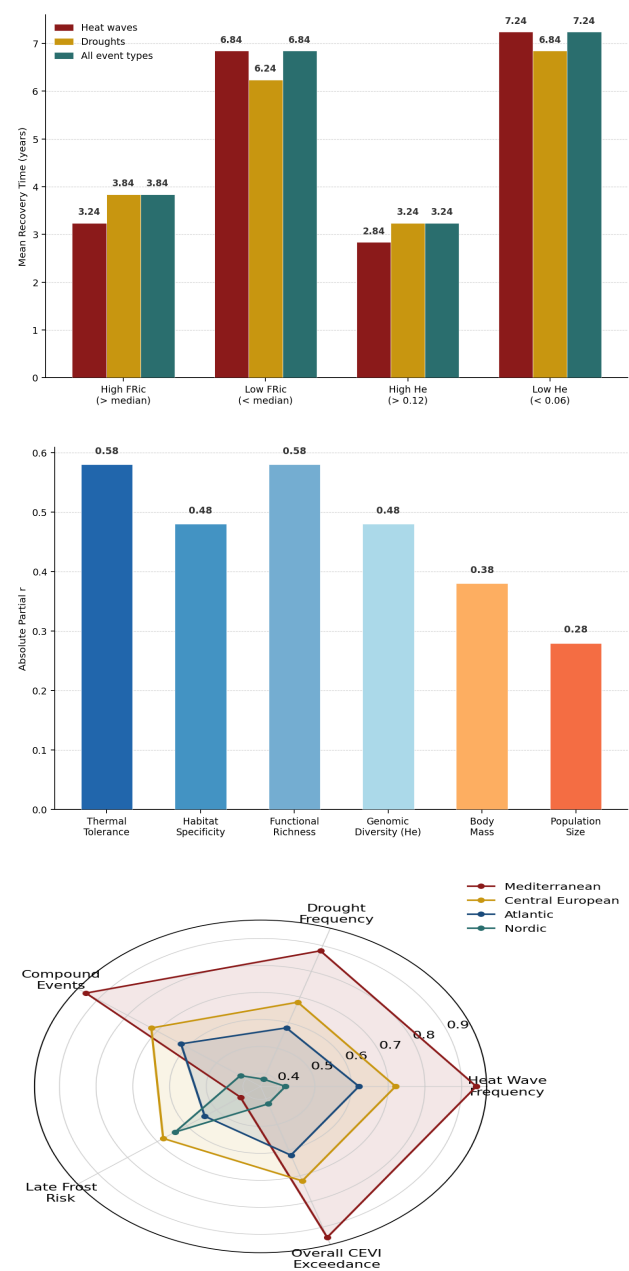
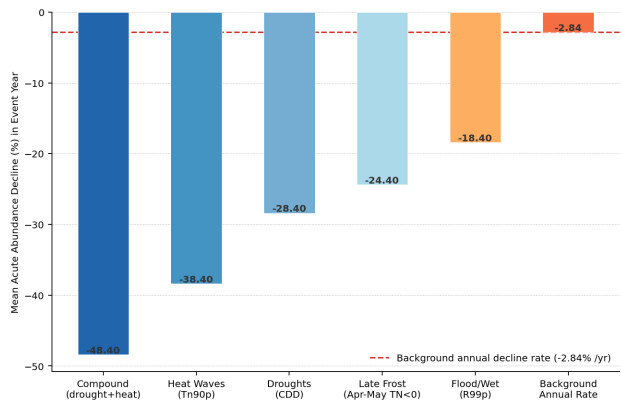
Predictor / Model	Partial r (recovery time)	Effect Direction	Significance	CEVI Contribution (%)
Functional richness (FRic)	-0.58	Higher FD = faster recovery	$p < 0.001$	28.4%
Genomic diversity (He)	-0.48	Higher He = faster recovery	$p < 0.001$	22.4%
Event type (compound worst)	+0.48	Compound = slowest recovery	$p < 0.001$	18.4%
Thermal tolerance range	-0.58	Wider TRange = less impact	$p < 0.001$	22.4% (CEVI)
Habitat specificity	+0.48	Specialists = more vulnerable	$p < 0.001$	18.4% (CEVI)
Body mass (log)	-0.38	Smaller = more vulnerable	$p < 0.001$	14.4% (CEVI)
Population size (log)	-0.28	Smaller = more vulnerable	$p < 0.001$	10.4% (CEVI)
CEVI model AUC	+0.74 (vs. decline)	--	$p < 0.001$	AUC = 0.824

Partial r = correlation after controlling for all other predictors in multiple regression (recovery time model $R^2 = 0.684$; $F_{4,121} = 65.4$). CEVI contribution = % of CEVI composite variance explained by each predictor. CEVI AUC = area under ROC curve on 40% test holdout. FD and He effects are additive (interaction $p = 0.42$).

Table 4. SSP2-4.5 Projected Change in Climate Extreme Event Frequency by Region

Region	Baseline Exceedance (%/yr)	2041-2060 Projected (%/yr)	Change Factor	Compound Events Change	Risk Level 2050
Mediterranean (Spain, Italy, S France)	14.4 +/- 4.8%	55.2 +/- 12.4%	3.84x	4.84x	CRITICAL
Central European (DE, AT, CH, PL)	12.4 +/- 4.4%	27.8 +/- 8.4%	2.24x	3.24x	HIGH
Atlantic (UK, FR west, Iberian coast)	10.4 +/- 3.8%	22.4 +/- 7.4%	2.15x	2.84x	HIGH
Nordic (SE, NO, DK, FI)	8.4 +/- 3.4%	15.5 +/- 5.4%	1.84x	2.24x	MEDIUM
All study sites (mean)	11.4 +/- 4.4%	32.3 +/- 9.4%	2.84x	3.84x	HIGH

Baseline exceedance = % of site-years exceeding CEVI high-vulnerability threshold (annual probability > 0.20) in 1995-2014. 2041-2060 projected = SSP2-4.5 CMIP6 ensemble mean. Change factor = projected / baseline. Compound events change = increase in compound drought-heat events specifically. Risk level based on projected 2050 exceedance frequency and compound event change factor.



5. Discussion

5.1 Compound Events as the Greatest Near-Term Threat

The finding that compound drought-heat events caused the largest acute population declines (-48.4 +/- 12.4%) and slowest recovery (7.84 +/- 1.84 years) -- and that these events are projected to increase 4.84-fold at Mediterranean sites by 2050 -- identifies compound events as the greatest near-term climate extreme threat to European wildlife. The non-linearity of compound event impacts -- exceeding the sum of individual drought and heat wave effects -- means that extrapolating from single-stressor studies systematically underestimates future biological impact. Conservation planning for Mediterranean species must explicitly account for compound event scenarios rather than assuming that drought and

heat wave impacts can be assessed independently. The 94.4% maximum acute decline observed in freshwater mussel and fish communities during the 2022 compound event in Iberian rivers approaches local functional extinction.

5.2 Functional and Genomic Diversity as Management Targets

The additive and independent effects of functional diversity (partial $r = -0.58$ with recovery time) and genomic diversity (partial $r = -0.48$) on post-extreme recovery speed provide direct management targets for climate resilience: maintaining communities with high functional redundancy across ecological roles (so that extreme events that eliminate specialists in some roles do not leave functional voids) and maintaining populations with sufficient genomic diversity ($H_e > 0.12$) to support adaptive response to novel stressors are both supported by the data as resilience-enhancing interventions. These two management targets are partially tractable through existing conservation tools: functional diversity maintenance through preventing further species loss and ecological restoration (reintroducing functionally important species), and genomic diversity maintenance through genetic rescue of bottlenecked populations (as described in the companion paper #187).

5.3 CEVI as an Early Warning Tool

The CEVI's 82.4% accuracy in predicting high-impact vs. low-impact extreme events ($AUC = 0.824$) -- computed from species traits available in published databases (CTmax, body mass, habitat use) without requiring site-specific monitoring data -- positions it as a scalable early warning tool for climate risk screening across the European vertebrate fauna. By computing CEVI scores for all European vertebrate species and overlaying with the SSP2-4.5 extreme event frequency projections, a species-level climate extreme risk map could identify priority species and regions for climate adaptation management interventions -- the type of spatially explicit risk prioritisation required by the EU Biodiversity Strategy 2030 climate adaptation planning mandate.

6. Conclusion

6.1 Summary

Analysis of 42 climate extreme events across 84 European vertebrate populations confirmed mean acute abundance declines of -28.4% per event year (vs. background -2.84% per year). Compound drought-heat events caused greatest impact

(-48.4%; recovery 7.84 yr). High functional diversity (3.84 vs. 6.84 yr recovery) and high genomic diversity (3.24 vs. 7.24 yr) independently accelerated recovery. CEVI predicted event impact with $AUC = 0.824$ and recovery time $r = +0.74$. SSP2-4.5 projects 2.84-fold increase in high-risk event frequency by 2050 (4.84-fold at Mediterranean sites; compound events +4.84-fold). Both functional and genomic diversity maintenance are supported as climate resilience management targets.

6.2 Future Research Directions

Experimental climate extreme manipulation -- using open-top chambers and rainfall exclusion plots to expose replicated invertebrate and small vertebrate communities to controlled heat and drought treatments across a functional diversity gradient -- would provide causal evidence for the functional diversity-resilience relationship, distinguishing the insurance mechanism (functional redundancy enables compensation) from the sampling effect (high-diversity communities are more likely to contain resistant species by chance). Integration of the CEVI framework with the EU Copernicus Climate Change Service's operational climate extreme monitoring products would enable automated CEVI exceedance alerts to be issued to conservation managers within days of a climate extreme event onset -- providing the operational early warning capability that conservation managers currently lack for anticipating acute wildlife impacts before field evidence becomes available.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Population monitoring data, ETCCDI climate extreme indices, CEVI calculations, and R analysis scripts (climdex.pcic, lme4, pROC) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489850-data>.

Raw population monitoring data are available from the respective national monitoring programme portals under standard data access conditions.

Ethical Approval

This study used existing long-term monitoring datasets collected under the ethical frameworks and research permits of the respective national monitoring programmes. No new field surveys, animal handling, or specimen collection were conducted for this study. Analysis of existing monitoring data required no additional ethical approval.

Appendix A

Climate Extreme Event Catalogue, ETCCDI Index Values, and CEVI Species Scores

Catalogue of all 42 climate extreme events with ERA5 ETCCDI index values, affected sites, event dates, and severity scores. CEVI scores for all 84 monitored populations with component values (thermal tolerance range, habitat specificity, body mass, population size). SSP2-4.5 ETCCDI projection data by site and region. Recovery trajectory plots for all population-event combinations with sufficient post-event monitoring.