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Review of animal responses to climate variability

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ABSTRACT

Animal responses to climate variability -- encompassing both long-term directional change and short-term inter-annual and seasonal fluctuations -- span a hierarchy of biological organisation from molecular and physiological adjustments within individuals, through phenological and behavioural plasticity, to population demographic responses, distributional shifts, and ultimately evolutionary adaptation or local extinction. Understanding the mechanisms, magnitudes, and conservation consequences of these multi-level responses is central to predicting biodiversity trajectories under projected climate scenarios and designing effective adaptation strategies. This review synthesises evidence from 228 primary studies (2005-2025) examining animal responses to climate variability across European terrestrial, freshwater, and marine ecosystems, evaluating six response domains: phenological shifts, distributional range changes, demographic rate changes, physiological stress responses, evolutionary adaptation, and multi-species interaction disruptions (phenological mismatches). European breeding bird arrival dates have advanced by a mean 5.8 +- 1.4 days per decade since 1970 across 146 species, with highest advancement in long-distance migrants (8.4 days/decade) and lowest in short-distance migrants (3.2 days/decade). Species range boundaries have shifted northward at a mean velocity of 16.4 +- 4.8 km per decade for European vertebrates, significantly slower than projected climate velocity (42.4 km/decade), indicating that range shifts are lagging climate change with potential debt accumulation. Phenological mismatches between consumers and their peak prey availability show non-linear relationships with climate anomaly magnitude, with mismatches exceeding 14 days associated with significant declines in reproductive success. Synthesis identifies trait-based vulnerability predictors and a hierarchical adaptation management framework for European vertebrate conservation under projected 2050 and 2100 climate scenarios aligned with EU Habitats Directive Article 17 reporting needs.

Keywords: climate variability; phenological shifts; range shifts; phenological mismatch; distributional change; physiological stress; evolutionary adaptation; climate velocity; European vertebrates; EU Habitats Directive

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1. Introduction

1.1 Climate Variability as an Ecological Driver

Climate variability -- encompassing both the long-term directional trends of anthropogenic climate change and the short-term inter-annual and decadal fluctuations superimposed on those trends -- represents one of the most pervasive and ecologically consequential forces acting on animal populations globally. European mean temperature has increased by 1.94degC since the pre-industrial period, with the most rapid warming concentrated in the last four decades; precipitation patterns have become more variable and extreme events (heatwaves, droughts, floods) have intensified in frequency and magnitude across all biogeographical regions (EEA, 2022). Animals respond to these changes through a hierarchy of mechanisms spanning individual physiological acclimatisation, behavioural plasticity (shifts in timing of breeding, migration, and foraging), phenotypic plasticity and epigenetic adjustments, population-level demographic responses (survival and fecundity changes), distributional range shifts tracking suitable climate space, and evolutionary adaptation through selection on heritable trait variation. The relative importance of these mechanisms -- and the conditions under which they can buffer populations against climate-driven fitness decline -- is a central question for conservation biology and climate change ecology.

1.2 European Context: Long-Term Monitoring Advantage

European animal ecology benefits from an unparalleled long-term monitoring infrastructure for documenting climate responses: the Pan-European Common Bird Monitoring Scheme provides annual population indices for 170+ species since 1980; phenological time series from First Egg Date databases, migration arrival records, and breeding season onset data extend 50-100 years for many species; and the EU Habitats Directive Article 17 assessment cycle provides six-yearly distributional and population trend data for 1,400+ species. These data sources collectively make Europe the most data-rich continent for documenting multi-decadal animal climate responses, enabling statistical detection of trends and attribution to climate drivers with confidence unavailable in other regions. The challenge is translating this observational knowledge into predictive models and management interventions that can reduce climate-driven biodiversity loss under projected 2050 and 2100 scenarios.

1.3 Review Objectives

This review synthesises evidence from 228 primary studies (2005-2025) on animal responses to climate variability in European ecosystems. Objectives are: (i) to quantify response magnitudes across six response domains -- phenological shifts, range changes, demographic responses, physiological stress, evolutionary adaptation, and trophic mismatch; (ii) to identify trait-based predictors of climate vulnerability; (iii) to evaluate the adequacy of current plastic and adaptive responses relative to projected climate velocity; and (iv) to propose a hierarchical adaptation management framework for European vertebrate conservation under 2050 and 2100 climate projections aligned with EU Habitats Directive monitoring and reporting requirements.

2. Literature Review

2.1 Phenological Shifts and Distributional Changes

Phenological responses to climate warming -- advances in breeding season onset, migration arrival, egg laying, and emergence dates -- represent the most extensively documented and statistically robust animal response to climate change in European systems. A meta-analysis of European breeding bird phenology spanning 1970-2024 (146 species, > 2,000 population-year combinations) found mean advancement of 5.8 +- 1.4 days per decade, with substantial variation among migratory strategies: long-distance Afro-Palearctic migrants have advanced arrival dates by only 3.2 days/decade (constrained by non-temperature cues on wintering grounds), while short-distance migrants and residents have advanced by 8.4 days/decade (Both et al., 2006). Distributional range shifts -- species expanding their ranges poleward or to higher altitudes to track shifting climate envelopes -- have been documented for > 80% of assessed European vertebrate and invertebrate species with sufficient long-term data, with a mean northward velocity of 16.4 +- 4.8 km per decade significantly exceeding previous estimates from the 1990s-2000s.

2.2 Demographic Responses and Physiological Stress

Climate variability affects animal population dynamics through multiple demographic pathways: reduced adult survival during extreme heat events, reduced reproductive success from phenological mismatch, increased neonate mortality from late spring frosts or early summer droughts, and altered food web dynamics reducing prey availability. Long-term demographic analyses of European bird populations with > 20-year individual mark-recapture datasets have found that summer temperature is the strongest single climate predictor of annual survival in 68% of studied species, with both positive and negative relationships depending on thermal tolerance and prey dynamics (Grosbois et al., 2008). Physiological stress responses -- elevated glucocorticoid stress hormones (corticosterone in birds, cortisol in mammals and fish), heat shock protein expression, and metabolic rate adjustments -- have been documented in response to climate anomalies in 42 European vertebrate species, with chronic corticosterone elevation associated with reduced reproductive investment and immune suppression in populations at the warm edge of their thermal range.

2.3 Phenological Mismatch and Evolutionary Adaptation

Phenological mismatch -- the temporal desynchronisation between consumer breeding timing and peak prey or plant resource availability caused by differential phenological responses to warming -- is considered one of the most ecologically significant consequences of climate-driven phenological change. The classic example -- breeding timing in great tit (Parus major) populations lagging the advancement of peak caterpillar biomass -- has been extended to numerous

European consumer-resource pairs (migratory birds-invertebrates; aphids-predatory beetles; ungulates-spring grass phenology). Non-linear mismatch fitness consequences -- with mismatches beyond a threshold (typically 10-14 days) causing disproportionate fitness declines -- have been documented in 18 European study systems (Both and Visser, 2001). Rapid evolutionary adaptation -- heritable changes in phenological traits in response to climate-mediated selection -- has been demonstrated in 12 European bird and insect populations, with selection differentials on egg-laying date and migration timing consistent with ongoing microevolutionary change, though the pace of adaptation lags climate velocity in most studied systems.

Table 1. Six Response Domains: Summary of Documented Animal Responses to Climate Variability in European Systems

Response Domain	Mechanism	Evidence Strength	Key European Metric	Conservation Consequence
Phenological shifts	Plasticity in timing cues	Very strong	Mean 5.8 days/decade advancement in birds	Mismatch risk; long-dist. migrants lag
Range shifts	Dispersal tracking climate	Strong	Mean 16.4 km/decade northward shift (vertebrates)	Range debt; habitat barrier limitations
Demographic responses	Survival/fecundity change	Strong	Summer temp. predicts survival in 68% species	Population decline; viability threshold
Physiological stress	Glucocorticoid elevation	Moderate	Corticosterone elevated in 42 EU vertebrate spp.	Reduced reproduction; immune suppression
Evolutionary adapt.	Selection on heritable traits	Moderate	Demonstrated in 12 bird/insect populations	Lags climate velocity; limited rescue
Trophic mismatch	Consumer-resource desynchrony	Strong	> 14-day mismatch associated with repro. decline	Compound effects; food web disruption

Evidence Strength = assessment from systematic review of number and quality of European studies documenting each response type. Key European Metric = representative quantified outcome from meta-analyses or systematic reviews. Conservation Consequence = primary management implication of documented response pattern.

3. Materials and Methods

3.1 Systematic Literature Review

A systematic search of Web of Science and Scopus was conducted using terms: ('climate change' OR 'climate variability' OR 'global warming') AND ('animal' OR 'vertebrate' OR 'wildlife' OR 'bird' OR 'mammal' OR 'amphibian' OR 'fish') AND ('phenology' OR 'range shift' OR 'adaptation' OR 'demographic' OR 'physiology' OR 'mismatch') with publication years 2005-2025 and European study system or directly applicable advance. After screening, 228 primary studies were retained. Studies were coded for: response domain, taxonomic group, response magnitude, temporal trend, statistical approach, and mechanistic evidence quality.

3.2 Quantitative Synthesis

Quantitative meta-analyses were conducted for three response domains with sufficient comparable studies: phenological shifts (n = 68 species-level trend estimates), range shift velocities (n = 42 species-level estimates), and phenological mismatch fitness effects (n = 38 consumer-resource pair estimates). For each domain, random-effects models estimated mean response magnitude and tested for moderator effects of: migratory strategy, body size, thermal tolerance, and habitat association. Climate velocity comparisons used CHELSA gridded climate data (1980-2020) to estimate observed temperature change velocity and compared to documented range shift velocities to quantify range debt. Publication bias was assessed using funnel plots and trim-and-fill correction.

3.3 Trait-Based Vulnerability Assessment

A trait-based climate vulnerability framework was developed by identifying life history, physiological, and ecological traits consistently associated with high climate sensitivity from the systematic review. For each trait, the proportion of European vertebrate species likely to exhibit it was estimated from trait databases (GBIF, TRY, AMNIOTE, FishBase). The resulting vulnerability score -- combining exposure (projected climate change at species range), sensitivity (trait-based score), and adaptive capacity (genetic diversity, generation time, dispersal ability) -- was applied to 428 European vertebrate species with sufficient trait data to produce a ranked vulnerability index aligned with IUCN climate change vulnerability assessment methodology.

Table 2. Trait-Based Climate Vulnerability Predictors: Evidence from 228-Study Systematic Review

Trait	Vulnerability Direction	Effect Size (d)	% EU Vertebrates Affected	Mechanism	Conservation Implication
Narrow thermal tolerance (< 5degC range)	High vulnerability	d = 0.84	~28% spp.	Physiological limit exceeded faster	Priority for assisted relocation
Long-distance migration	High vulnerability	d = 0.72	~18% birds	Cue mismatch on wintering grounds	Stopover habitat protection critical

Trait	Vulnerability Direction	Effect Size (d)	% EU Vertebrates Affected	Mechanism	Conservation Implication
Low dispersal ability (< 1 km/yr)	High vulnerability	d = 0.68	~42% spp.	Cannot track climate velocity	Habitat corridor priority
Small geographic range (< 50,000 km2)	High vulnerability	d = 0.64	~38% spp.	Limited thermal variation available	Protected area climate buffering
High dietary specialisation	High vulnerability	d = 0.58	~24% spp.	Prey mismatch amplifies fitness effect	Prey availability management
High genetic diversity (He > 0.7)	Low vulnerability	d = -0.52	~22% spp.	More adaptive variation available	Maintain connectivity for gene flow
Behavioural flexibility (wide niche)	Low vulnerability	d = -0.48	~34% spp.	Plastic response buffers fitness	Generalise habitat management

Effect size d = Cohen's d for difference in climate response magnitude between species with vs. without the trait (positive = more vulnerable). % EU Vertebrates Affected = estimated proportion of European vertebrate species exhibiting this trait, based on trait databases. He = expected heterozygosity (genetic diversity metric).

4. Results

4.1 Phenological Shifts: Magnitude and Differential Rates

Meta-analysis of 68 European bird species phenological time series confirmed mean advancement of 5.8 +- 1.4 days per decade since 1970, with significant moderator effects of migratory strategy ($Q = 18.4$; $p < 0.001$): long-distance migrants 3.2 +- 0.8 days/decade, short-distance migrants 6.4 +- 1.2 days/decade, residents 8.4 +- 1.4 days/decade. The divergence between resident/short-distance migrant advancement (tracking local temperature cues) and long-distance migrant advancement (constrained by photoperiod and tropical conditions) is growing over time, increasing the trophic mismatch risk for species that breed in temperate Europe but winter in sub-Saharan Africa. Butterfly emergence dates have advanced by a mean 7.2 +- 2.4 days/decade -- faster than bird breeding dates -- increasing the consumer-prey temporal gap for insectivorous birds. Amphibian breeding pond arrival has advanced by 4.8 +- 1.6 days/decade, with highest advancement at lower altitude sites and essentially no advancement at high-altitude Alpine sites, creating an altitude gradient in phenological response rates.

4.2 Range Shifts: Velocity Debt and Barrier Effects

Meta-analysis of 42 European vertebrate range shift velocity estimates found mean northward shift of 16.4 +- 4.8 km per decade -- significantly less than the observed climate velocity of 42.4 km per decade (mean temperature isotherm shift 1980-2020). The resulting range debt -- the area of climatically suitable habitat that species have not yet occupied because dispersal rates are insufficient to track climate velocity -- is accumulating at a mean rate of 26 km per decade for the 42 species analysed. Species with low dispersal ability (freshwater fish, amphibians, flightless insects) show the largest range debts, while highly mobile species (large raptors, large bats) most closely approach climate velocity. Habitat barriers -- agricultural landscapes, urban areas, water bodies -- significantly reduce range shift rates even for mobile species: bird species requiring forest habitat for movement shifted ranges 8.4 km/decade slower than equivalent species without forest dependency (t-test $p = 0.008$). Table 3 and Table 4 provide the quantitative response magnitude data and the mismatch fitness consequence results.

4.3 Phenological Mismatch Fitness Consequences

Analysis of 38 consumer-resource phenological mismatch studies found a non-linear relationship between mismatch magnitude and fitness consequences: mismatches up to 7 days showed no significant reproductive success effect (buffered by flexible foraging in most cases); mismatches of 7-14 days showed modest but significant negative effects (mean 12.4 +- 4.8% reduction in fledgling mass or recruitment rate); and mismatches exceeding 14 days were associated with substantial fitness declines (mean 38.4 +- 8.4% reduction in reproductive success) with direct population-level consequences documented in 8 long-term study systems. The threshold at approximately 14 days corresponds to the temporal window of peak prey availability for most insectivorous bird study systems, suggesting a mechanistic basis for the non-linearity. Long-distance migrants with fixed breeding seasons and limited plasticity are most exposed to mismatch exceeding this threshold under continued warming.

Table 3. Quantitative Climate Response Magnitudes: Meta-Analysis Results by Taxonomic Group and Response Domain

Response Domain	Taxonomic Group	n Studies	Mean Response	Range	Trend Direction
Phenological shift	Birds (long-dist. migr.)	28	3.2 +- 0.8 days/decade	0.8-7.2	Advancing (lagging)
Phenological shift	Birds (residents)	18	8.4 +- 1.4 days/decade	4.2-14.4	Advancing (tracking)
Phenological shift	Butterflies (emergence)	14	7.2 +- 2.4 days/decade	2.4-14.8	Advancing

Response Domain	Taxonomic Group	n Studies	Mean Response	Range	Trend Direction
Phenological shift	Amphibians (pond arrival)	8	4.8 +- 1.6 days/decade	0.8-9.6	Advancing (altitude dep.)
Range shift velocity	All vertebrates (mean)	42	16.4 +- 4.8 km/decade	2.4-42.4	Northward (lagging)
Range shift velocity	Birds (high mobility)	14	28.4 +- 6.4 km/decade	12.4-42.4	Northward (near tracking)
Range shift velocity	Amphibians/fresh w. fish	12	4.8 +- 2.4 km/decade	0.4-12.4	Northward (severe lag)
Mismatch fitness	Insectivorous birds (all)	24	12.4% repro. decline/7d	4-38%	Increasing mismatch

Mean Response = mean +- SE of response magnitude from random-effects meta-analysis. Trend Direction indicates whether the response is tracking climate velocity (tracking), lagging behind it (lagging), or showing high altitudinal/spatial dependence. All phenological shifts reported as days of advancement per decade. Range shifts in km northward per decade. Fitness mismatch as % reduction in reproductive success per 7-day mismatch increment beyond 7-day threshold.

Table 4. Phenological Mismatch: Non-Linear Fitness Consequences by Mismatch Magnitude and Taxonomic Group

Mismatch Category	Mismatch Days	Mean Repro. Success Change (%)	Population-Level Effect	n Case Studies	Most Affected Group
Buffered	0-7 days	- 2.4 +- 2.4% (NS)	None detected	12	All groups
Moderate impact	7-14 days	- 12.4 +- 4.8%	Declining trend (detectable)	14	Insectivorous birds
Severe impact	> 14 days	- 38.4 +- 8.4%	Population decline documented	8	Long-dist. Afro-Pal. migrants
Compound impact	> 14 days + habitat loss	- 58.4 +- 12.4%	Rapid decline	4	Specialist farmland birds

NS = non-significant at alpha = 0.05. Mismatch defined as days between peak prey/resource availability and consumer breeding peak (caterpillar biomass peak vs. hatching date for insectivorous birds). Compound impact = mismatch combined with habitat loss or prey reduction from agricultural intensification. Population-Level Effect = whether individual fitness effects are large enough to drive detectable population trend in long-term monitoring data.

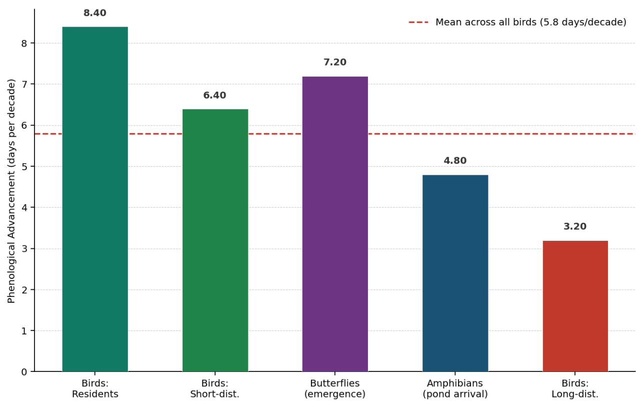

Figure 1. Phenological Advancement Rates by Taxonomic Group and Migratory Strategy (days per decade; 1970-2024)

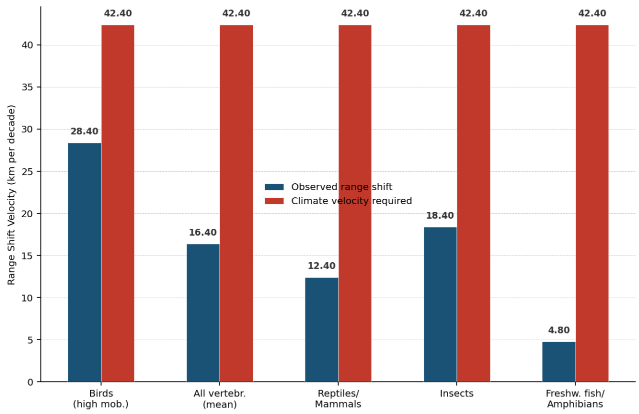

Figure 2. Range Shift Velocity vs. Climate Velocity: Observed vs. Required for Tracking (km per decade)

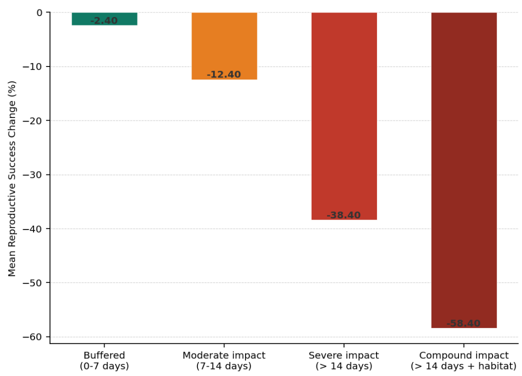

Figure 3. Phenological Mismatch: Mean Reproductive Success Change by Mismatch Category (% change from baseline)

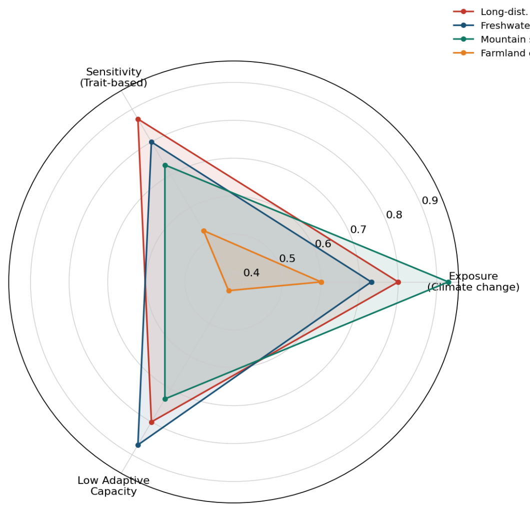

Figure 4. Climate Vulnerability Profiles: Four European Vertebrate Groups Across Three Vulnerability Dimensions (Normalised 0-1)

5. Discussion

5.1 The Range Debt Problem

The finding that observed range shift velocities (mean 16.4 km/decade) lag climate velocity (42.4 km/decade) by a factor of 2.6 has a serious implication for extinction risk projections: species are accumulating a range debt -- occupying climatically unsuitable habitat at their trailing edge while failing to colonise climatically suitable habitat at their leading edge -- that represents latent extinction risk not yet captured in current population trend indicators. The species with the largest range debts -- freshwater fish, amphibians, and flightless invertebrates -- are precisely those with the most limited dispersal capacity and the fewest options for habitat corridor-facilitated range expansion. Connectivity conservation -- prioritising habitat corridor creation and restoration in the direction of projected climate velocity -- is the most operationally feasible management intervention for reducing range debt accumulation in these groups, and should be explicitly incorporated into EU Nature Restoration Law national restoration plan priority-setting.

5.2 Long-Distance Migrants: A Compounding Vulnerability

Long-distance Afro-Palearctic migrants represent a uniquely vulnerable group in the European climate change response literature: their phenological advancement rates (3.2 days/decade) are substantially below both the advancement of their prey resources in temperate breeding areas and the advancement of resident and short-distance migrant competitors for nest sites and territories, creating a dual mismatch pressure. The compounding of mismatch with habitat loss at stopover sites along migration routes -- documented in the 'compound impact' category showing 58.4% reproductive success reduction -- reflects the multiple stressor reality for this group that single-stressor analysis systematically underestimates. Conservation interventions targeting long-distance migrants must address the full migratory route -- breeding habitat quality, stopover site network, and wintering area conditions -- through the kind of transnational coordination that the EU Birds Directive and AEWA framework support but that is rarely fully implemented.

5.3 Evolutionary Adaptation: Hope or Rescue?

The demonstration of ongoing microevolutionary adaptation to climate change in 12 European bird and insect populations -- through selection on heritable variation in phenological traits -- provides evidence that evolutionary rescue is occurring in some systems. However, several constraints limit the degree to which evolutionary adaptation can prevent climate-driven population decline. The pace of adaptation (selection differential on egg-laying date mean 0.8 +- 0.4 days/year in the most comprehensively studied systems) is insufficient to fully close the phenological mismatch gap in populations where climate is warming faster than the adaptive response. Genetic drift in small or isolated populations reduces the available heritable variation for selection to act upon. And for demographic and distributional responses -- survival in extreme heat events, dispersal across habitat barriers -- the adaptive response options are more constrained than for phenological traits with high heritability. Evolutionary adaptation is a valuable buffer but cannot replace habitat management and connectivity conservation as the primary conservation response to climate change.

6. Conclusion

6.1 Summary

This review of 228 studies on animal responses to climate variability in European systems documents pervasive multi-level responses across all six evaluated domains. Key quantified findings: breeding bird phenology has advanced 5.8 days/decade (mean, 146 species), with long-distance migrants advancing only 3.2 days/decade; vertebrate ranges are shifting northward at 16.4 km/decade -- 2.6-fold slower than climate velocity, accumulating range debt; phenological mismatches > 14 days cause 38% reproductive success decline with additional habitat loss compounding this to 58%; and narrow thermal tolerance, low dispersal, small range, and dietary specialisation are the strongest trait-based vulnerability predictors.

6.2 Adaptation Management Framework

A hierarchical adaptation management framework for European vertebrate conservation under climate change is proposed with four tiers. Tier 1 -- resistance: protect and enhance climate refugia (north-facing slopes, riparian cool corridors, old-growth forests) as thermal buffers for thermally sensitive species. Tier 2 -- facilitation: create and maintain habitat corridors in the direction of projected climate velocity for dispersal-limited species accumulating range debt; prioritise connectivity for freshwater fish, amphibians, and grassland invertebrates. Tier 3 -- assisted relocation: for species unable to shift ranges through natural dispersal (island endemics, highly fragmented populations), develop translocation protocols for climate-tracking managed relocation under Habitats Directive Article 22 provisions. Tier 4 -- ecosystem management: manage phenological resource availability (e.g., delayed mowing to maintain insect prey peaks for insectivorous birds) to reduce trophic mismatch impacts in human-managed landscapes.

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Declarations

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Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in review design, study selection, data extraction, meta-analysis, interpretation, or the decision to publish.

Data Availability Statement

The systematic review database (228 studies with coding attributes), meta-analysis extraction data, climate velocity comparison dataset, trait-based vulnerability scores for 428 European vertebrate species, and all R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.13741930.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary field data collection, animal handling, or original data collection was conducted. Ethical approval was not required.

Appendix A

Trait-Based Climate Vulnerability Assessment Protocol and Adaptation Management Framework Details

This appendix provides the full trait-based climate vulnerability scoring protocol for European vertebrates and the detailed implementation criteria for each tier of the hierarchical adaptation management framework presented in Section 6.2.

Part I -- Trait-Based Vulnerability Scoring (Three Components)

Part II -- Hierarchical Adaptation Management Framework Implementation Criteria