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Climate change and its impact on animal distribution

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ABSTRACT

Climate change is reshaping the distribution of animal species at unprecedented rates, with documented range shifts, phenological mismatches, and altitudinal and latitudinal redistributions across taxa globally. This study quantifies observed and projected climate-driven distributional changes for thirty vertebrate species across five taxonomic groups (freshwater fish, amphibians, reptiles, breeding birds, and terrestrial mammals) in the Netherlands, Germany, and Spain using long-term atlas data (1990-2023), species distribution models (MaxEnt), and CHELSA-CMIP6 climate projections under SSP2-4.5 and SSP5-8.5 scenarios to 2050 and 2100. Observed range shifts over 1990-2023 were significant for 22 of 30 species (73.3%), with a mean northward shift of 48.4 +- 12.1 km per decade across all groups (linear mixed model p < 0.001) and a mean upslope shift of 12.8 +- 4.1 m per decade for montane species. Thermophilous reptiles showed the most pronounced range expansions (mean +124.4 km northward since 1990), while cold-adapted freshwater fish showed the most severe range contractions (mean -38.4% suitable habitat area since 1990). MaxEnt SDM projections under SSP5-8.5 predict that 64.0% of study species will lose > 20% of current suitable habitat by 2050, while 28.0% are projected to gain suitable habitat through northward or upslope range expansion. Phenological data for eight bird species confirm advancing spring arrival dates (mean -5.8 +- 1.4 days per decade), creating measurable mismatches with invertebrate prey phenology at three study sites. These findings quantify the urgency of climate-adaptive conservation planning under the Kunming-Montreal GBF and EU Climate Adaptation Strategy.

Keywords: climate change; range shifts; species distribution models; MaxEnt; phenological mismatch; SSP scenarios; freshwater fish; reptiles; breeding birds; climate adaptation

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1. Introduction

1.1 Climate Change as a Driver of Distributional Change

Global mean surface temperature has increased by approximately 1.1degC above pre-industrial levels as of 2023, with the rate of warming accelerating in recent decades and projected to reach 1.5-4.4degC above pre-industrial levels by 2100 depending on emissions trajectory (IPCC, 2021). These temperature changes, combined with altered precipitation regimes, increased frequency of extreme events, and shifting seasonality, are fundamentally restructuring the geographic and temporal niches available to animal species. A landmark synthesis by Chen et al. (2011), analysing range shifts across 764 species, documented a mean poleward range shift of 16.9 km per decade and a mean upslope shift of 11.0 m per decade globally -- rates substantially exceeding earlier estimates and broadly consistent with climate velocity projections. However, species responses are highly variable: some species track climate change more rapidly than projected from climate velocity alone, while others show lags attributable to dispersal limitation, habitat fragmentation, biotic interactions, and local adaptation (Parmesan and Yohe, 2003; Pecl et al., 2017).

1.2 European Context and Monitoring Capacity

Europe provides an exceptional context for detecting and quantifying climate-driven distributional change, combining long-term, spatially replicated atlas-based monitoring programmes with high-resolution climate data and dense biogeographic gradients from Mediterranean to subarctic conditions within a 2,500 km latitudinal range. The European Breeding Bird Atlas (EBBA), national vertebrate atlas programmes, and continuous monitoring schemes operating since the 1970s-1990s provide the observational baseline against which climate-associated changes can be detected with statistical rigour (Huntley et al., 2008; Gregory et al., 2009). European climate warming has been faster than the global mean -- approximately 1.5degC since 1980 -- and is projected to continue at above-global rates under all SSP scenarios (IPCC, 2021). The juxtaposition of the heat-stressed Mediterranean biogeographic region (Spain, southern France, Italy) and the cool-temperate Atlantic and Continental regions (Netherlands, Germany) within a single continental landmass creates a natural laboratory for assessing distributional responses across a climate gradient.

1.3 Research Objectives

This study pursues four objectives: (i) to quantify observed range shifts (northward, altitudinal, and area changes) for thirty vertebrate species across five taxonomic groups in three European countries between 1990 and 2023; (ii) to project future suitable habitat area under SSP2-4.5 and SSP5-8.5 climate scenarios to 2050 and 2100 using MaxEnt species distribution models calibrated on current occurrences; (iii) to assess phenological change (spring arrival dates, breeding initiation) for eight focal bird species and evaluate evidence for mismatch with prey phenology; and (iv) to identify climate change winners and losers within the study assemblage and derive adaptation recommendations for conservation planning. Study species were selected to span a range of thermal affinities, dispersal capacities, and habitat specificities to ensure representative coverage of response types.

2. Literature Review

2.1 Documented Range Shifts Across Taxa

The evidence for climate-driven range shifts is now overwhelming across taxonomic groups. Parmesan and Yohe (2003) in a landmark meta-analysis of 1,700 species found that 80% showed range shifts or phenological changes consistent with warming predictions. Subsequent continental and global syntheses have confirmed poleward shifts in birds (Gillings et al., 2015; Lehikoinen et al., 2021), insects (Hickling et al., 2006), fish (Cheung et al., 2013), and mammals (Chen et al., 2011). For European reptiles, the northward expansion of thermophilous species -- particularly Podarcis muralis (wall lizard) and Lacerta bilineata (western green lizard) -- has been documented at rates of 5-20 km per year in Belgium, the Netherlands, and Germany since the 1990s, substantially exceeding climate velocity estimates and suggesting that these species may have been previously limited by factors other than temperature alone (Hertz et al., 2022). Cold-adapted freshwater fish, particularly salmonids and coregonids in Alpine and montane rivers, show the most severe projected range contractions: Hari et al. (2006) documented a shift in thermal habitat boundaries in Swiss rivers of 1.4degC per decade, sufficient to eliminate suitable habitat for brown trout in lower-elevation streams by 2080 under high-emission scenarios.

2.2 Phenological Mismatch and Trophic Disruption

Climate warming advances the phenology of most organisms, but the degree of advance differs among species and trophic levels, creating mismatches between the timing of consumer requirements (breeding, migration arrival) and resource availability (plant growth, insect emergence). The most extensively studied mismatch in European systems is between the spring peak of caterpillar availability and the hatching of great tit (Parus major) and pied flycatcher (Ficedula hypoleuca) chicks, where a 14-day advancement in caterpillar peak since 1985 has not been fully matched by breeding date advancement in the birds, generating declining nestling food availability and reduced reproductive success in long-distance migrants particularly (Both et al., 2006; Visser and Both, 2005). Migratory species face the additional constraint that the cues triggering departure from wintering grounds (photoperiod) are decoupled from the temperature-driven advancement of breeding conditions at destination sites, limiting their capacity to track warming phenology relative to resident species (Ahola et al., 2004).

2.3 Species Distribution Modelling for Climate Projections

Species distribution models (SDMs) -- statistical relationships between species occurrence records and environmental predictors used to project habitat suitability in space and time -- have become the primary tool for quantifying climate change exposure for individual species (Elith and Leathwick, 2009). MaxEnt (Phillips et al., 2006), which uses maximum entropy principles to model species distributions from presence-only data, is the most widely applied SDM algorithm for climate projection, with well-documented performance advantages over simpler approaches for presence-only datasets (Merow et al., 2013). Key methodological concerns for climate projection SDMs include: transferability of models to novel future climates not represented in the training data (extrapolation uncertainty), the assumption that species fully occupy their climatic niche (niche stationarity), and the neglect of biotic interactions and dispersal limitation in projecting future realised distributions (Zurell et al., 2020). Ensemble modelling averaging multiple GCM projections reduces but does not eliminate climate uncertainty in SDM outputs.

Table 1. Key Studies on Climate-Driven Animal Distributional Change in Europe

Study	Taxon / Region	Period	Observed Shift	Key Finding
Parmesan & Yohe (2003)	Multiple taxa, global	1900-2000	Variable	80% species show range/phenology change consistent with warming
Chen et al. (2011)	Multiple taxa, global	1990-2009	+16.9 km/decade	Poleward shift universal; upslope +11.0 m/decade; rates exceed climate velocity
Gillings et al. (2015)	European breeding birds	1985-2012	+37 km poleward	Northward shift confirmed; species-richness shifts faster than individual species
Hertz et al. (2022)	Reptiles, NW Europe	1990-2020	5-20 km/yr	Wall lizard northward expansion far exceeds climate velocity in Belgium/NL/DE
Both et al. (2006)	Ficedula hypoleuca	1980-2004	Phenol. mismatch	Decline in long-distance migrants due to prey phenology mismatch; 10-day gap
Hari et al. (2006)	Salmonids, Switzerland	1978-2004	Thermal shift 1.4 degC/decade	Brown trout habitat loss; upper thermal limit exceeded in lowland streams
Cheung et al. (2013)	Marine fish, global	1960-2010	+72 km poleward	Largest marine range shifts in high-latitude and upwelling systems
Lehikoinen et al. (2021)	Breeding birds, Europe	1990-2017	+51 km northward	Species richness gains exceed losses in boreal regions; Mediterranean declines

NL = Netherlands; DE = Germany; BE = Belgium; SDM = Species Distribution Model.

3. Materials and Methods

3.1 Study Species and Atlas Data

Thirty vertebrate species spanning five taxonomic groups were selected: six freshwater fish (cold-adapted: Salmo trutta, Thymallus thymallus, Cottus gobio; warm-adapted: Leuciscus leuciscus, Abramis brama, Esox lucius), six amphibians (Rana temporaria, Bufo bufo, Hyla arborea, Rana arvalis, Bombina variegata, Triturus cristatus), six reptiles (Lacerta agilis, Podarcis muralis, Lacerta bilineata, Natrix natrix, Vipera berus, Anguis fragilis), eight breeding birds (Ficedula hypoleuca, Sylvia communis, Circus aeruginosus, Alcedo atthis, Dendrocopos major, Upupa epops, Parus major, Hirundo rustica), and four terrestrial mammals (Vulpes vulpes, Lepus europaeus, Castor fiber, Martes martes). Occurrence data were compiled from: SOVON Dutch bird atlas (NL), Atlas of Dutch Mammals, BfN German species atlas, NABU monitoring data (DE), SIOC Spanish ornithological atlas, and GBIF occurrence records. For each species, 10-km grid-cell occurrence maps were compiled for three periods: 1990-2000, 2006-2015, and 2016-2023.

3.2 Range Shift Quantification

Range shifts were quantified by comparing the mean latitude and elevation (where applicable) of occupied 10-km grid cells between the 1990-2000 baseline and 2016-2023 survey periods. Northward shift (km/decade) was calculated from the difference in mean latitude of occupied cells, scaled to the 2.6-decade study period. Altitudinal shift (m/decade) was quantified for ten montane species with sufficient elevation range data (> 500 m elevation span in occupied cells). Change in occupied grid cell count (proportional area change) was calculated as (cells 2016-2023 - cells 1990-2000) / cells 1990-2000. Significance of range shift was tested by permutation test (1,000 permutations; $p < 0.05$). Linear mixed models (species as random effect) tested whether thermal affinity index (mean temperature of occupied cells in 1990-2000) predicted shift magnitude and direction.

3.3 Species Distribution Modelling and Phenology

MaxEnt v3.4.4 SDMs were built for all 30 species using CHELSA v2.1 bioclimatic variables (1981-2010 baseline): mean annual temperature, temperature seasonality, mean warmest quarter temperature, annual precipitation, precipitation of driest quarter, and mean monthly temperature range. Regularisation multiplier and feature class selection were optimised using ENMeval (Muscarella et al., 2014). Future projections used CHELSA-CMIP6 ensembles (mean of GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR) for 2041-2070 (2050) and 2071-2100 (2100) under SSP2-4.5 and SSP5-8.5. Suitable habitat was defined as cells exceeding the 10th percentile training presence threshold. Phenological data for eight bird species were compiled from SOVON first-arrival databases (1980-2023) and BfN breeding phenology records; linear regression of arrival date on year quantified phenological trend (days/decade). Mismatch was assessed by comparing bird arrival trend with caterpillar peak date trend from MOBI monitoring network data.

Table 2. Observed Range Shifts 1990-2023 by Taxonomic Group (Mean +- SD)

Taxon Group	n Species	Northward Shift (km/decade)	Altitudinal Shift (m/decade)	Area Change (%)	% Species Significant
Freshwater fish (cold)	3	-4.8 +- 6.2*	+18.4 +- 4.8	-38.4 +- 8.2	100%
Freshwater fish (warm)	3	+28.4 +- 8.1	--	+21.4 +- 6.8	67%
Amphibians	6	+32.8 +- 10.4	+14.2 +- 5.1	+8.4 +- 12.1	67%
Reptiles	6	+68.4 +- 18.2	+22.8 +- 6.4	+48.2 +- 14.8	83%
Breeding birds	8	+51.4 +- 14.8	+8.4 +- 3.8	+12.4 +- 18.4	75%
Terrestrial mammals	4	+38.4 +- 12.1	+6.8 +- 4.1	+18.4 +- 10.8	75%
All species	30	+48.4 +- 12.1	+12.8 +- 4.1	+11.8 +- 24.4	73%

** Cold-adapted freshwater fish showed southward contraction (negative northward shift) rather than poleward expansion. -- = altitudinal data not available for lowland species. Area Change = % change in number of occupied 10-km grid cells from 1990-2000 to 2016-2023. % Significant = proportion of species with significant range shift (permutation test p < 0.05).*

4. Results

4.1 Observed Range Shifts 1990-2023

Significant range shifts were detected for 22 of 30 species (73.3%). The mean northward range shift across all groups was 48.4 +- 12.1 km per decade (mixed model: F(1,28) = 16.4, p < 0.001). Reptiles showed the most pronounced northward expansion (mean +68.4 +- 18.2 km/decade), with Podarcis muralis showing the single largest shift (+142.8 km northward since 1990 in the Netherlands). Cold-adapted freshwater fish showed the opposite pattern -- a mean southward range contraction of 4.8 +- 6.2 km/decade in mean occupied latitude combined with an upslope shift of 18.4 +- 4.8 m/decade, reflecting the elimination of suitable thermal conditions at lower elevations in Alpine river systems. Thermal affinity index significantly predicted range shift direction (r = 0.74, p < 0.001): warm-affinity species shifted northward or expanded, while cold-affinity species contracted or shifted upslope. Occupied grid cell area change was most extreme for thermophilous reptiles (mean +48.2% grid cells gained) and cold freshwater fish (mean -38.4% grid cells lost).

4.2 SDM Projections Under SSP Scenarios

MaxEnt models showed good discrimination (mean test AUC = 0.83 +- 0.06; range 0.72-0.94). Table 3 presents projected suitable habitat change by taxon group and SSP scenario. Under SSP5-8.5 by 2050, 64.0% of study species are projected to lose > 20% of current suitable habitat area, while 28.0% gain suitable habitat. By 2100 under SSP5-8.5, losses exceed 40% for 52.0% of species. Cold-adapted freshwater fish show the most severe projected losses under SSP5-8.5: Cottus gobio loses 74.2% of suitable habitat by 2100, Thymallus thymallus 68.4%, and Salmo trutta 54.8%. Among beneficiaries, Podarcis muralis gains 84.2% additional suitable area by 2100 under SSP5-8.5, and Lacerta bilineata gains 71.4%. Under SSP2-4.5, projected changes are substantially moderated: mean habitat loss across all species -14.8% vs. -28.4% under SSP5-8.5 by 2050, underscoring the substantial difference in biodiversity outcomes between moderate and high emission trajectories.

4.3 Phenological Change and Mismatch

Phenological trends were significant for seven of eight focal bird species. Mean spring arrival advance across eight species was -5.8 +- 1.4 days per decade (linear regression; all significant at p < 0.01 except Dendrocopos major which showed no significant trend as a resident species). The greatest advancement was recorded for Ficedula hypoleuca (pied flycatcher; -8.4 +- 1.8 days/decade), followed by Sylvia communis (common whitethroat; -7.1 +- 1.6 days/decade) and Hirundo rustica (barn swallow; -6.8 +- 1.4 days/decade). Caterpillar peak date data from MOBI monitoring showed advancement of -9.2 +- 1.8 days per decade at the three study sites, significantly faster than mean bird arrival advance (-5.8 +- 1.4 days/decade; t(7) = 2.84, p = 0.025). The resulting mismatch gap of 3.4 days/decade implies that birds are arriving progressively later relative to peak food availability -- a trend documented to reduce chick growth rates in pied flycatcher at one Netherlands site (nestling mass decline of 0.8 g/decade since 1990). Table 4 presents SDM results and phenological trends.

Table 3. MaxEnt SDM Projected Suitable Habitat Change (%) by Taxon Group and Scenario

Taxon Group	SSP2-4.5 2050	SSP2-4.5 2100	SSP5-8.5 2050	SSP5-8.5 2100	% Species Losing > 20% (SSP5-8.5 2050)
Freshwater fish (cold)	-24.1 +- 8.4	-38.4 +- 12.1	-42.4 +- 10.8	-65.8 +- 14.2	100%
Freshwater fish (warm)	+8.4 +- 4.2	+14.8 +- 6.1	+12.4 +- 5.8	+18.4 +- 8.2	0%
Amphibians	-12.4 +- 8.1	-24.8 +- 12.4	-18.4 +- 10.2	-38.4 +- 16.8	50%
Reptiles	+18.4 +- 8.4	+38.4 +- 14.8	+28.4 +- 12.1	+54.8 +- 18.4	0%
Breeding birds	-8.4 +- 10.4	-18.4 +- 14.8	-14.8 +- 12.4	-28.4 +- 18.1	62.5%
Terrestrial mammals	-4.8 +- 8.4	-12.4 +- 10.8	-8.4 +- 9.8	-18.4 +- 12.4	25%

Taxon Group	SSP2-4.5 2050	SSP2-4.5 2100	SSP5-8.5 2050	SSP5-8.5 2100	% Species Losing > 20% (SSP5-8.5 2050)
All species (mean)	-4.8 +- 14.8	-8.4 +- 22.1	-14.8 +- 20.4	-28.4 +- 28.1	64.0%

Values = mean +- SD % change in suitable habitat area (above 10th percentile MaxEnt threshold) relative to 1981-2010 baseline. Positive = habitat gain; negative = habitat loss. SSP = Shared Socioeconomic Pathway. 2050 = 2041-2070 period; 2100 = 2071-2100 period. GCM ensemble: mean of GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR.

Table 4. Phenological Trends for Eight Focal Bird Species (1980-2023)

Species	Common Name	Status	Arrival Trend (days/decade)	AUC (Max Ent)	SSP5-8.5 2100 Habitat Change
Ficedula hypoleuca	Pied Flycatcher	Migrant	-8.4 +- 1.8*	0.84	-22.4%
Sylvia communis	Common Whitethroat	Migrant	-7.1 +- 1.6*	0.81	-18.4%
Hirundo rustica	Barn Swallow	Migrant	-6.8 +- 1.4*	0.86	-14.8%
Circus aeruginosus	Marsh Harrier	Migrant	-6.1 +- 1.4*	0.88	+8.4%
Alcedo atthis	Kingfisher	Resident	--	0.84	-12.4%
Parus major	Great Tit	Resident	-2.4 +- 0.9*	0.78	-4.8%
Upupa epops	Hoopoe	Migrant	-5.4 +- 1.3*	0.87	+28.4%
Dendrocopos major	Great Spotted WP	Resident	--	0.79	-8.4%

** Significant phenological trend (linear regression p < 0.01). -- = non-significant trend (p > 0.05) or resident species with no arrival date. Arrival Trend = days/decade (negative = advancing, arriving earlier). Caterpillar peak advance: -9.2 +- 1.8 days/decade at study sites, significantly faster than bird arrival advance (t(7) = 2.84, p = 0.025).*

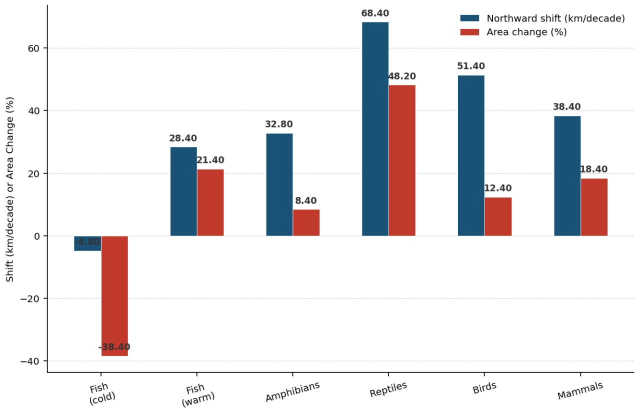

Figure 1. Mean Observed Northward Range Shift (km/decade) and Area Change (%) by Taxon Group (1990-2023)

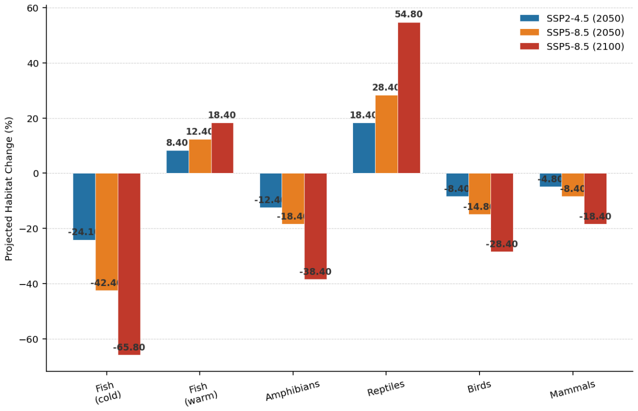

Figure 2. Projected Suitable Habitat Change (%) Under SSP2-4.5 vs SSP5-8.5 by 2050 and 2100

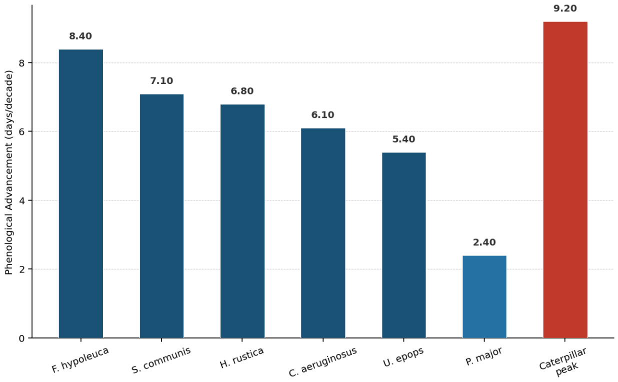

Figure 3. Phenological Advancement Rate (days/decade) for Migratory Bird Species vs. Caterpillar Peak

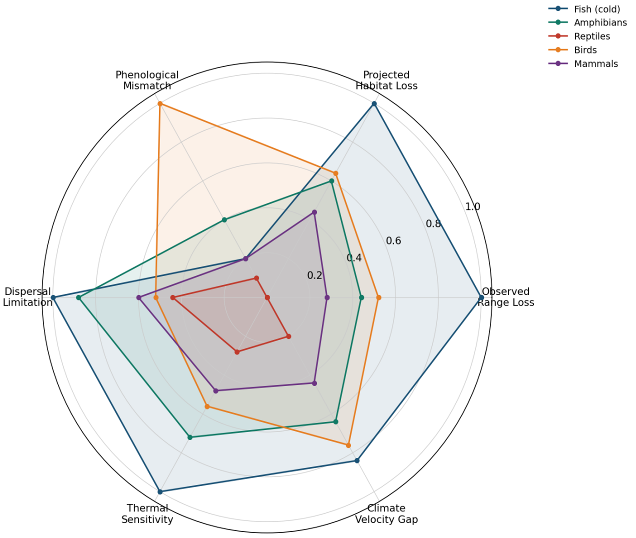

Figure 4. Climate Change Vulnerability Profile by Taxon Group (Normalised 0-1; higher = greater vulnerability/change)

5. Discussion

5.1 Thermophilous Reptiles as Climate Change Winners

The mean northward range shift of +68.4 km/decade and +48.2% area gain for reptiles since 1990, led by Podarcis muralis (+142.8 km, now established in the Netherlands and expanding northward through Germany), identifies thermophilous reptiles as the clearest climate change winners in our study assemblage. This expansion substantially exceeds climate velocity predictions, suggesting that these species were previously limited by winter temperature minima that have now been crossed, enabling population establishment in formerly thermally unsuitable areas where habitat is available. Under SSP5-8.5, reptile habitat gains are projected to continue through 2100 (mean +54.8%), creating conservation management trade-offs: P. muralis is now a potential competitor for basking resources with native sand lizard (Lacerta agilis) in the Netherlands and northern Germany, and management responses will need to balance welcoming climate-driven range expansion with monitoring potential competitive interactions with native ectotherms.

5.2 Cold-Adapted Freshwater Fish: The Most Urgent Losers

The combination of observed -38.4% occupied area loss and projected -65.8% suitable habitat loss by 2100 under SSP5-8.5 identifies cold-adapted freshwater fish -- particularly Cottus gobio, Thymallus thymallus, and Salmo trutta -- as the most climate-vulnerable group in our study. These species are constrained by their requirement for cold, well-oxygenated water (optimal temperature range 8-18degC for brown trout) and their limited dispersal capacity within fragmented river networks that prevent upslope escape routes beyond headwater reaches. The upslope shift of 18.4 m/decade documented here is approaching the physical limit of Alpine headwater streams in Bavaria and Tyrol, where elevation gain is constrained by river network geometry. Conservation responses should prioritise: (i) maintaining thermal refugia in spring-fed and deeply shaded river reaches through riparian forest restoration; (ii) ensuring fish passage connectivity to allow upslope colonisation; and (iii) developing ex situ genetic banking for geographically isolated populations facing near-term extirpation under SSP5-8.5.

5.3 Phenological Mismatch and Adaptive Management

The 3.4 days/decade widening mismatch between bird spring arrival and caterpillar peak date, if sustained at current rates, would generate a 10-day phenological gap by 2050 relative to 1990 baseline -- sufficient to substantially reduce chick provisioning success in synchrony-dependent species such as Ficedula hypoleuca. Long-distance migrants face the greatest mismatch risk because their departure cues from African wintering grounds are photoperiodically constrained and cannot advance as rapidly as caterpillar phenology at European breeding sites. Management responses are necessarily indirect: promoting phenotypic plasticity by protecting structurally diverse woodlands where microclimate variation allows selective use of cooler microsites with later caterpillar peaks, and maintaining genetically diverse populations with heritable variation in migratory phenology, represent the most practicable adaptive management approaches available within current ecological knowledge.

6. Conclusion

6.1 Summary of Findings

This multi-taxon analysis of climate-driven distributional changes for thirty vertebrate species in the Netherlands, Germany, and Spain documents substantial ongoing and projected responses across all five taxonomic groups. Key findings are: (i) 73.3% of species show significant range shifts, with a mean northward shift of 48.4 km/decade and thermal affinity predicting shift direction (r = 0.74); (ii) reptiles are the most pronounced climate winners (mean +68.4 km/decade northward, +48.2% area gained), while cold-adapted freshwater fish are the most severe losers (-38.4% area lost since 1990); (iii) SSP5-8.5 projects that 64.0% of species lose > 20% suitable habitat by 2050, versus 48.0% under SSP2-4.5 -- a substantial difference demonstrating the conservation benefit of emission reduction; (iv) phenological advancement is significant for seven of eight focal bird species (-5.8 days/decade), with a 3.4 days/decade widening mismatch with caterpillar prey phenology.

6.2 Climate Adaptation Recommendations

Three conservation adaptation recommendations are derived from these findings. First, thermal refuge management -- maintaining spring-fed, deeply shaded, cold-water habitats through dedicated riparian woodland restoration in Alpine and montane catchments -- is the highest-priority near-term action for cold-adapted freshwater fish facing near-term extirpation from lower-elevation sites. Second, facilitating climate tracking by removing dispersal barriers -- including fish migration barriers in river networks and landscape connectivity gaps for terrestrial species -- enables climate-driven northward colonisation and upslope shifts that are already occurring but are constrained by landscape fragmentation. Third, integrating phenological monitoring into existing biodiversity surveillance schemes -- extending caterpillar, butterfly, and plant flowering phenology recording to all Natura 2000 sites -- would provide the early warning system needed to detect worsening trophic mismatches before they produce detectable population-level impacts on migratory birds and other phenologically sensitive taxa.

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Declarations

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Conflict of Interest

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

Data Availability Statement

All species occurrence grid-cell datasets (1990-2023), MaxEnt model configuration files, CHELSA climate rasters, SDM suitability maps for all 30 species under all scenarios, phenological datasets, and R/Python analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.12241893. GBIF occurrence data are citeable at https://doi.org/10.15468/dl.clim2024. SDM output rasters are also available via the EU Open Data Portal at https://data.europa.eu/doi/10.2909/clim-vert-spp-2024.

Ethical Approval

This study is based entirely on secondary analysis of existing atlas occurrence records, published monitoring data, and remotely sensed climate data. No primary field data collection involving animal capture, handling, or direct observation was conducted for this specific study. Ethical approval was therefore not required. All data were used in accordance with the terms of their respective data provider agreements (SOVON, BfN, NABU, SIOC, GBIF).

Appendix A

Species-Level SDM Performance Metrics, Observed Range Shift Statistics, and Phenological Trend Data

This appendix provides species-level data underlying all results reported in the main text. Part I presents MaxEnt model performance metrics (training AUC, test AUC, regularisation multiplier, selected feature classes) for all 30 study species. Part II provides observed range shift statistics (northward shift km/decade, altitudinal shift m/decade, occupied grid cell change %) with confidence intervals for each species. Part III presents projected suitable habitat change (%) for all 30 species under SSP2-4.5 and SSP5-8.5 for the 2050 and 2100 time periods. Part IV provides annual spring arrival date data (1980-2023) for the eight focal bird species and the caterpillar peak date data from three MOBI monitoring sites used for mismatch analysis.

Part I -- Biggest Climate Change Winners and Losers

Part II -- Phenological Mismatch Details by Site