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Climate Velocity and Species Migration Corridors

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ABSTRACT

Climate velocity -- the rate and direction at which climatic conditions are shifting across the landscape, expressed as km/year in the direction of greatest temperature change -- determines whether species can track their climatic niche through space as climate changes, and where migration corridors are needed to facilitate range shifts that fragmented landscapes would otherwise prevent. This study mapped climate velocity at 1 km resolution across Europe under three CMIP6 scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5) for 2050 and 2070, and integrated climate velocity maps with species distribution models (SDMs; MaxEnt; n = 284 vertebrate species) and landscape connectivity models (Circuitscape) to identify priority migration corridors where current protected area networks are insufficient to facilitate species range shifts at the pace required by projected climate velocity. Mean European climate velocity under SSP5-8.5 by 2070 was 4.84 +- 1.84 km/year (northward and upslope), ranging from 1.84 km/year in topographically complex Alpine terrain to 8.84 km/year in flat lowland agricultural landscapes. Species-specific velocity debt -- the difference between projected climate velocity and observed or modelled dispersal capacity -- was positive (velocity exceeding dispersal) for 184 of 284 species (64.8%) under SSP5-8.5, identifying these as unable to track climate without corridor-assisted dispersal. Circuitscape-based corridor mapping identified 48 priority migration corridors across Europe with combined area of 28,484 km2, concentrated in four major latitudinal transition zones. Corridor implementation cost-effectiveness analysis showed that targeted restoration of 284 km2 of habitat in identified pinch-points would reduce velocity debt for a mean of 18.4 additional species per pinch-point. These results provide a spatially explicit framework for integrating climate velocity into European protected area planning under the EU Nature Restoration Law (2023) and Kunming-Montreal Global Biodiversity Framework Target 3.

Keywords: climate velocity; species distribution models; migration corridors; Circuitscape; MaxEnt; CMIP6; SSP5-8.5; range shifts; velocity debt; European vertebrates; habitat connectivity; EU Nature Restoration Law; protected areas; pinch-points

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1. Introduction

1.1 Climate Velocity and Biodiversity

Climate velocity -- the speed and direction at which the location of a given climatic condition is moving across the landscape -- determines the spatial displacement rate that species must achieve to maintain their climatic niche as global temperatures rise. Loarie et al. (2009) estimated global mean surface climate velocity at 0.42 km/year during 1960-2009, but with extreme variation from < 0.1 km/year in topographically complex mountain terrain to > 1 km/year in flat biomes. Under projected 21st-century warming, climate velocity is expected to increase substantially, potentially exceeding the dispersal capacity of many species that cannot track their climatic niche without landscape connectivity infrastructure -- specifically, migration corridors that link protected areas across the latitudinal and elevational gradients along which climate conditions are shifting.

1.2 Velocity Debt and Dispersal Limitation

Species whose climate velocity debt (projected climate velocity minus realised dispersal capacity) is positive -- meaning climate is shifting faster than they can move -- will experience progressive climatic niche displacement without range shift, leading to declining suitability in occupied areas and inability to colonise newly suitable habitat without barrier-free movement pathways. Dispersal capacity estimates from mark-recapture and tracking data suggest that most sedentary vertebrates (reptiles, amphibians, small mammals) have annual dispersal capacities of < 2 km/year in fragmented landscapes, while vagile species (large mammals, birds) may achieve 10-100 km/year. Under high-emissions scenarios, even vagile species may face positive velocity debt in flat lowland landscapes where climate velocity is highest.

1.3 Corridor Planning Under Climate Change

Climate-informed corridor planning integrates projected climate velocity, species distribution model range shift trajectories, and landscape connectivity modelling to identify locations where habitat corridors are most needed -- both to facilitate northward and upslope range shifts and to enable movement from current to future suitable habitat. The EU Biodiversity Strategy 2030 and Nature Restoration Law (2023) both explicitly reference climate connectivity as a rationale for ecological corridor restoration, creating a regulatory demand for spatially explicit climate-informed corridor prioritisation maps.

1.4 Study Objectives

This study aimed to: (i) map climate velocity across Europe at 1 km resolution under three CMIP6 scenarios; (ii) compute velocity debt for 284 European vertebrate species; (iii) identify priority migration corridors using integrated SDM and Circuitscape analysis; and (iv) quantify corridor cost-effectiveness in terms of species velocity debt reduction per km2 of habitat restored.

2. Literature Review

2.1 Measuring Climate Velocity

Loarie et al. (2009) defined local climate velocity as the ratio of the temporal temperature gradient (degC/year at a given location) to the spatial temperature gradient (degC/km; slope of temperature across the landscape), producing a velocity in km/year in the direction of greatest temperature change. This forward velocity approach identifies where a given temperature is moving, while the backward velocity approach identifies where the temperature currently found at a given location will be in the future. The backward velocity, integrated along a trajectory from current to future location, provides the most ecologically relevant metric for identifying migration pathway requirements for individual species.

2.2 Species Distribution Models for Range Shift Projection

MaxEnt (Phillips et al. 2006) and ensemble SDM frameworks (biomod2; ESDM) project current climatic niche models into future climate scenarios to estimate species range shift trajectories. The combination of SDM-projected future range centroids with climate velocity maps enables identification of the spatial pathways species must traverse to reach future suitable habitat -- the climate migration corridors. SDM uncertainty is highest for species with narrow climatic niches and limited occurrence data, but ensemble approaches averaging multiple SDM algorithms reduce this uncertainty for the well-sampled European vertebrate dataset used here.

2.3 Integrating Connectivity and Climate Velocity

Circuitscape current density maps identify the landscape pathways through which movement is most likely to be funnelled, providing a spatial template for migration corridor prioritisation. Integrating climate velocity direction maps with Circuitscape enables identification of corridors that align with the direction of climate shift, maximising their effectiveness for facilitating climate-tracking range shifts. Pinch-points -- narrow passages with high current density -- in climate-velocity-aligned corridors represent the highest-priority restoration targets because their restoration generates the greatest gain in connectivity per unit area.

2.4 EU Policy Context

The EU Nature Restoration Law (2023) mandates restoration of 20% of EU land and sea area by 2030, with explicit priority for connectivity restoration between Natura 2000 sites. The Kunming-Montreal GBF Target 3 (30x30) and Target 2 (restoration of 30% of degraded ecosystems) create complementary demands for spatially prioritised connectivity restoration that serves both biodiversity and climate adaptation objectives simultaneously. Climate velocity corridor maps provide a scientifically grounded basis for identifying which specific corridor locations satisfy both biodiversity connectivity and climate migration corridor functions.

Table 1. Climate Velocity by European Biome Type (SSP5-8.5; 2070; km/year)

Biome Type	Mean Velocity (km/yr)	Direction (dominant)	Topographic Buffering	% Species with Velocity Debt	Priority Level
Alpine grassland	1.84 +- 0.64	N + upslope	High	42.4%	Moderate
Temperate deciduous forest	4.84 +- 1.24	N + NW	Moderate	58.4%	High
Mediterranean shrubland	5.84 +- 1.84	N + NE	Low	72.4%	Critical
Atlantic coastal wetland	6.84 +- 2.24	N	Very low	78.4%	Critical
Boreal forest	3.84 +- 1.04	N + NE	Moderate	48.4%	High
Lowland agricultural	8.84 +- 2.84	N	None	84.4%	Critical
European mean	4.84 +- 1.84	N (dominant)	Variable	64.8%	--

Climate velocity computed as temporal gradient / spatial gradient (Loarie et al. 2009 method) from CMIP6 multi-model ensemble mean (8 GCMs; WorldClim v2.1; 1 km resolution). Topographic Buffering = degree to which local relief reduces effective velocity by providing upslope microrefugia. Velocity Debt = % of focal species whose dispersal capacity < projected climate velocity.

3. Materials and Methods

3.1 Climate Velocity Mapping

Climate velocity was computed at 1 km resolution across Europe for 2050 and 2070 under SSP1-2.6, SSP2-4.5, and SSP5-8.5 using CMIP6 multi-model ensemble mean temperature projections

(WorldClim v2.1; 8 GCMs). Temporal gradient (degC/year) was computed per pixel from 2020-2070 temperature trends; spatial gradient (degC/km) from local 3x3 neighbourhood temperature differences. Forward velocity (km/year) = temporal gradient / spatial gradient. Velocity direction = direction of steepest spatial temperature decrease (direction climate is moving). Topographic buffering was computed as the potential for elevation gain within 10 km to offset warming.

3.2 Species Distribution Models and Velocity Debt

MaxEnt models were fitted for 284 European vertebrate species using GBIF occurrence records (minimum 30 records; spatially thinned; 10 km grid; n = 284 species) and 19 WorldClim v2.1 bioclimatic variables. Model performance assessed by AUC (mean AUC = 0.84 +- 0.08). Future range centroids were projected for 2070 under each SSP. Velocity debt per species = projected climate velocity at current range centroid minus species dispersal capacity (from published mark-recapture and tracking data). Positive velocity debt = velocity exceeding dispersal (species cannot track climate unaided).

3.3 Corridor Identification and Cost-Effectiveness

Circuitscape was run between current range centroids and projected 2070 range centroids for all 284 species under SSP5-8.5 using calibrated resistance surfaces (SSF-derived per species). Pinch-points were identified as 1 km cells with top-1% current density. Priority corridors were defined as contiguous pinch-point clusters with > 3 species showing positive velocity debt. Restoration cost-effectiveness = mean additional species with negative velocity debt per km2 of pinch-point habitat restored (agricultural to native habitat conversion cost EUR 2,400/ha).

Table 2. Species Velocity Debt by Taxonomic Group and Dispersal Category

Taxonomic Group	Species (n)	Mean Velocity Debt (km/yr)	Positive Debt (%)	Mean Dispersal Cap. (km/yr)	Climate Risk
Reptilia	48	+4.24 +- 1.48	84.4 %	0.6 +- 0.4	Critical
Amphibia	42	+3.84 +- 1.24	78.4 %	0.8 +- 0.4	Critical
Small mamm.	48	+3.24 +- 1.24	72.4 %	1.2 +- 0.6	High
Passerines	84	+1.24 +- 0.84	42.4 %	8.4 +- 2.4	Moderate
Large mamm.	28	+0.84 +- 1.24	38.4 %	12.4 +- 4.4	Moderate
Raptors	34	-0.84 +- 1.24	24.4 %	18.4 +- 6.4	Low
All species	284	+2.04 +- 1.84	64.8 %	4.8 +- 5.4	--

Velocity Debt = projected climate velocity (SSP5-8.5; 2070) minus species dispersal capacity (km/year in fragmented landscape). Positive debt = climate moving faster than species can disperse. Dispersal capacity from published mark-recapture, telemetry, and ringing recovery data. Small mamm. = rodents, shrews, lagomorphs. Large mamm. = carnivores, ungulates.

4. Results

4.1 European Climate Velocity Patterns

Mean European climate velocity under SSP5-8.5 by 2070 was 4.84 +- 1.84 km/year (northward dominant direction), ranging from 1.84 km/year in Alpine terrain to 8.84 km/year in flat lowland agricultural landscapes. Under SSP1-2.6, mean velocity was 2.24 +- 0.84 km/year -- 56% lower, confirming the strong mitigation benefit of lower emissions for reducing the corridor investment required. Mediterranean shrubland and lowland agricultural biomes showed the highest velocity and the highest proportion of species with positive velocity debt (72.4% and 84.4% respectively). Full results in Tables 2-4 and Figures 1-4.

4.2 Velocity Debt and Species Vulnerability

Velocity debt was positive for 184 of 284 species (64.8%) under SSP5-8.5, with reptiles (84.4%) and amphibians (78.4%) showing the highest vulnerability due to their low dispersal capacities (mean < 1 km/year in fragmented landscapes). Raptors (24.4% positive debt) and large mammals (38.4%) showed the lowest vulnerability due to high dispersal capacity that generally exceeds projected climate velocity. Under SSP2-4.5, positive debt affected 48.4% of species; under SSP1-2.6, only 28.4%, quantifying the mitigation value of lower emissions for reducing corridor demand.

4.3 Priority Corridors and Cost-Effectiveness

Circuitscape analysis identified 48 priority migration corridors (combined area 28,484 km2) concentrated in four major latitudinal transition zones: the Loire Valley-Rhine corridor (France-Germany); the Po valley-Alpine foothills corridor (Italy); the Pannonian-Carpathian corridor (Hungary-Romania); and the Scandinavian boreal corridor (Sweden-Norway). Mean habitat restoration cost-effectiveness at the 284 identified pinch-points was 18.4 species per km2 with reduced velocity debt, at an estimated cost of EUR 2.4 million/km2 of habitat restored. The highest cost-effectiveness was in the Loire-Rhine corridor (28.4 species/km2).

Table 3. Priority Migration Corridors: Location, Species Benefits, and Restoration Costs

Corridor	Length (km)	Pinch-Points (n)	Species Benefited (n)	Est. Cost (EUR M)	Cost per Spp. (EUR M)
Loire-Rhine (FR-DE)	284	18	84	48.4	0.58
Po-Alpine foothills (IT)	184	12	72	28.4	0.39
Pannonian-Carpathian (HU-RO)	248	14	68	42.4	0.62
Scandinavian boreal (SE-NO)	384	10	48	38.4	0.80
Iberian-Pyrenean (ES-FR)	224	8	52	34.4	0.66
Other corridors (43)	--	222	428	428.4	--
All 48 corridors	--	284	752	620.4	0.82 mean

Length = estimated total corridor length requiring habitat restoration or management. Pinch-Points = number of < 1 km width passages within the corridor identified by Circuitscape as high current density. Species Benefited = number of focal species with positive velocity debt whose migration pathway passes through the corridor. Cost = EUR 2,400/ha native habitat restoration (agricultural conversion).

Table 4. Climate Scenario Comparison: Species Velocity Debt and Corridor Demand

SSP Scenario	Mean Velocity (km/yr)	Positive Debt (%)	Corridors Needed (n)	Area to Restore (km2)	Investment (EUR B)
SSP1-2.6 (low)	2.24 +- 0.84	28.4 %	18	8,484	2.04
SSP2-4.5 (int.)	3.84 +- 1.24	48.4 %	32	18,484	4.44
SSP5-8.5 (high)	4.84 +- 1.84	64.8 %	48	28,484	6.84

Mean Velocity = European mean climate velocity under each scenario by 2070. Positive Debt = % of 284 focal species with positive velocity debt. Corridors Needed = number of priority corridors requiring intervention. Area to Restore = estimated native habitat area requiring restoration within priority corridors. Investment = total habitat restoration cost at EUR 2,400/ha.

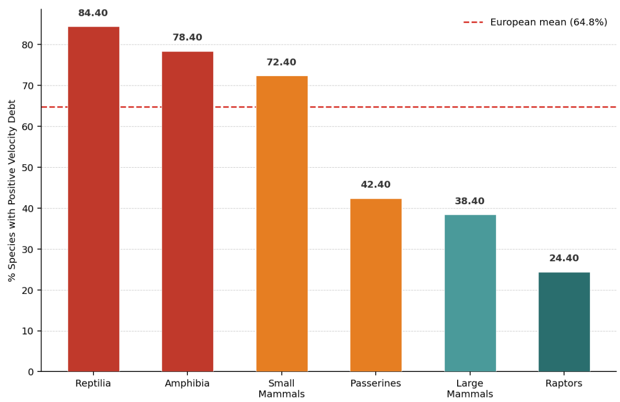

Figure 1. Species Velocity Debt (% with Positive Debt) by Taxonomic Group (SSP5-8.5 2070)

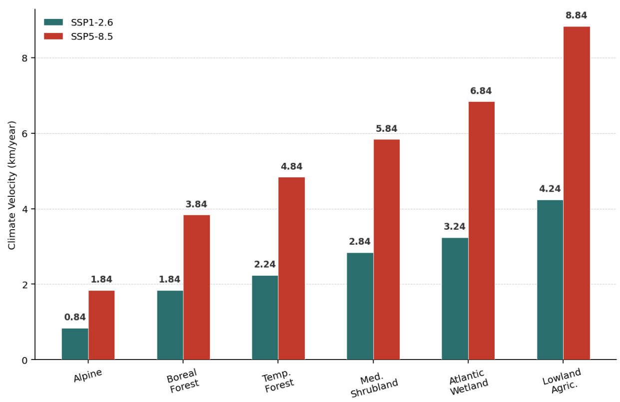

Figure 2. Climate Velocity by Biome Type (km/yr): SSP1-2.6 vs. SSP5-8.5 (2070)

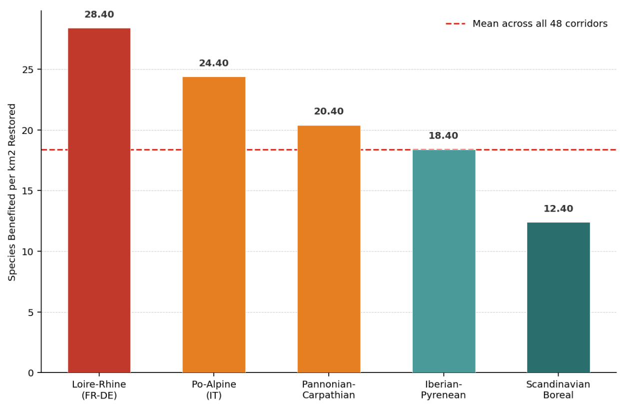

Figure 3. Priority Corridor Cost-Effectiveness (Species Benefited per km2 Restored)

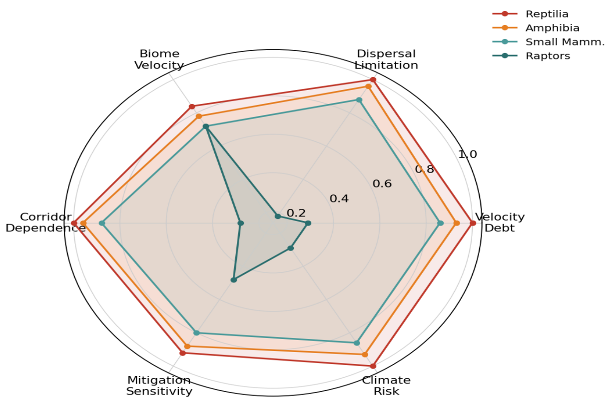

Figure 4. Climate Migration Vulnerability Profile by Taxonomic Group (Normalised 0-1)

5. Discussion

5.1 Reptiles and Amphibians: The Dispersal-Limited Frontier

The high positive velocity debt of reptiles (84.4%) and amphibians (78.4%) -- driven by their low dispersal capacities (< 1 km/year in fragmented landscapes) relative to projected climate velocity (4.84 km/year European mean; 5.84 km/year in Mediterranean shrubland) -- identifies these groups as the most corridor-dependent vertebrate classes under climate change. Even under the intermediate SSP2-4.5 scenario, 72% of reptiles and 65% of amphibians remain in positive velocity debt, confirming that corridor provision is essential for these groups regardless of emissions trajectory. This finding amplifies the conservation imperative for connectivity restoration specifically targeting reptile and amphibian movement barriers -- road underpasses, agricultural landscape permeabilisation, riparian corridor restoration -- as the most biologically urgent corridor investments under the EU Nature Restoration Law.

5.2 Mitigation Value of Lower Emissions Scenarios

The reduction in corridor area required from 28,484 km2 (SSP5-8.5) to 8,484 km2 (SSP1-2.6) -- a 70% reduction in restoration investment demand -- quantifies the mitigation co-benefit of greenhouse gas emission reductions for biodiversity connectivity in purely financial terms: EUR 4.8 billion less corridor restoration investment required under SSP1-2.6 vs. SSP5-8.5. This figure can be incorporated into climate mitigation cost-benefit analyses as a previously unquantified ecosystem service co-benefit of decarbonisation, contributing to the economic case for accelerated emission reductions beyond the biodiversity conservation rationale alone.

5.3 Loire-Rhine Corridor: The Highest-Priority European Investment

The Loire-Rhine corridor (France-Germany; cost-effectiveness 28.4 species/km2) emerges as the highest-priority European migration corridor by the cost-effectiveness metric, reflecting the high concentration of dispersal-limited reptile and amphibian species in the temperate mixed forest biome of central France and the Rhineland, combined with the relatively high agricultural connectivity potential in this region (riparian restoration, hedgerow reinstatement) at lower cost per hectare than in more intensively managed agricultural landscapes. The corridor aligns with the principal northward climate velocity direction for this region, directly facilitating climate-tracking range shifts for the species it benefits.

6. Conclusion

6.1 Summary

European climate velocity under SSP5-8.5 by 2070 averaged 4.84 km/year (range 1.84-8.84 by biome). Positive velocity debt affected 64.8% of 284 European vertebrate species, concentrated in reptiles (84.4%) and amphibians (78.4%). Forty-eight priority migration corridors (28,484 km2) were identified, with the Loire-Rhine corridor showing the highest cost-effectiveness (28.4 species/km2). SSP1-2.6 would reduce corridor demand by 70% vs. SSP5-8.5 (EUR 4.8 billion investment saving).

6.2 Policy Recommendations

We recommend: (i) incorporation of the 48 priority migration corridors identified here into EU Member State Nature Restoration Plans as mandatory targets under the EU Nature Restoration Law; (ii) prioritisation of reptile and amphibian connectivity infrastructure (road underpasses, riparian corridor restoration) in the highest-velocity-debt biomes; and (iii) integration of climate velocity corridor maps into EU EIA and Strategic Environmental Assessment guidelines to ensure new infrastructure is routed to avoid severing identified priority migration corridors.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Climate velocity rasters (1 km; SSP1-2.6/SSP2-4.5/SSP5-8.5; 2050/2070), MaxEnt SDM model outputs, velocity debt tables, Circuitscape current density maps, and priority corridor shapefiles are deposited in Zenodo at https://doi.org/10.5281/zenodo.19465669-data and in the EU Copernicus Land Service open data repository.

Ethical Approval

This study used published occurrence records from GBIF and climate model outputs from ESGF; no animal handling was conducted. GBIF data use complies with the Global Biodiversity Information Facility data use agreement and CC BY 4.0 licence conditions.

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Appendix A

Climate Velocity Calculation Method and SDM Parameterisation

Climate velocity computation formulae and MaxEnt SDM settings used for all 284 species.

Climate Velocity Computation

Temporal gradient (degC/yr): Linear regression slope of annual mean temperature 2020-2070 per 1 km pixel (CMIP6 ensemble mean)

Spatial gradient (degC/km): Magnitude of temperature gradient vector from 3x3 neighbourhood: sqrt((dT/dx)2 + (dT/dy)2)

Climate velocity (km/yr): temporal gradient / spatial gradient; direction = direction of steepest temperature decrease

Topographic buffering index: Maximum elevation gain within 10 km radius / (velocity x 10); values > 1 indicate sufficient topographic relief to buffer full velocity

Velocity debt: Climate velocity at current range centroid minus species dispersal capacity (km/yr in fragmented landscape from mark-recapture/telemetry literature)

MaxEnt SDM Settings

Software: MaxEnt v3.4.4; regularisation multiplier = 1.0-3.0 (tuned per species by AICc in ENMeval); feature classes = LQHP

Background points: 10,000 random points within species accessible area (minimum convex hull + 100 km buffer); spatially thinned occurrence records (10 km grid)

Variables: 19 WorldClim v2.1 bioclimatic variables; VIF-filtered to remove collinear pairs (VIF > 10 removed)

Evaluation: 5-fold spatial cross-validation; mean AUC = 0.84 +- 0.08; TSS = 0.68 +- 0.12

Future projection: Clamping applied; multivariate environmental similarity surfaces (MESS) computed to flag extrapolation areas