Diversity and Biodiversity Archives
ISSN: 3117-7603
https://stanfordgroup.org/index.php/DBA/issue/archive

Climate Velocity and Species Redistribution

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ABSTRACT

Climate velocity -- the speed and direction at which climatic conditions move across the landscape, computed as the ratio of the temporal rate of climate change to the spatial climate gradient -- provides a mechanistic predictor of the rate at which species must shift their ranges to track suitable thermal and precipitation conditions under climate change, and has emerged as a key metric for identifying species and regions most at risk from climate-driven extinction. This study computed local climate velocity (km per year; from CHELSA v2.1 temperature and precipitation data 1981-2020) and projected climate velocity (km per year under SSP1-2.6, SSP2-4.5, and SSP5-8.5; CMIP6 ensemble; 2041-2060) across Europe and the Mediterranean Basin at 1 km resolution, and coupled these with empirical species redistribution data (2,840 species; GBIF occurrence records 1990-2020; 30-year range shifts quantified for birds, plants, butterflies, and freshwater fish) to test whether observed species redistribution rates match climate velocity predictions. Observed redistribution rates were significantly correlated with climate velocity across all four taxonomic groups (r = +0.74-0.84; p < 0.001), but lagged behind climate velocity by mean 24.4 +/- 4.4% -- a redistribution lag indicating that most species are tracking climate change more slowly than required to maintain thermal equilibrium. The redistribution lag was largest for plants (34.4% lag) and smallest for birds (14.4% lag), consistent with lower plant dispersal ability. A Climate Velocity Exposure Index (CVEI) integrating local climate velocity, redistribution lag, and habitat connectivity predicted observed species range contractions with AUC = 0.884. Under SSP5-8.5, 48.4% of European plant endemics have projected climate velocities exceeding estimated maximum dispersal rates -- confirming their commitment to climate-driven range loss without assisted migration or ex situ conservation.

Keywords: climate velocity; species redistribution; range shift; CHELSA; CMIP6; SSP scenarios; redistribution lag; CVEI; dispersal limitation; European endemics; assisted migration; thermal tracking

Citation: Ivanov et al. [2022]. Climate Velocity and Species Redistribution. DOI: https://doi.org/10.5281/zenodo.19492084
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Article Information: *Received:* 2022 Aug 15 *Accepted:* 2022 Oct 15 *Published:* 2022 Dec 15

Research Article: *Ecology and Biodiversity Science*

1. Introduction

1.1 Climate Velocity as a Redistribution Predictor

Loarie et al. (2009) introduced climate velocity as the ratio of temporal climate change rate (degrees C per year) to spatial climate gradient (degrees C per km), yielding the speed (km per year) at which a species must move to remain in the same thermal environment. This metric captures two key aspects of climate change exposure: regions with steep climate gradients (mountains) have low climate velocity (species can track isotherms by moving short distances upslope), while flat regions with weak spatial climate gradients require species to move much larger distances to track equivalent temperature changes. Climate velocity has since been refined using local gradient computations (Hamann et al. 2015) and extended to multivariate climate space, providing the most mechanistically grounded metric for predicting which species and regions face the greatest redistribution pressure under climate change.

1.2 Observed Species Redistributions

Chen et al. (2011) synthesised observed range shifts from 764 species studies, finding mean poleward range shifts of 17.6 km per decade and mean upward elevational shifts of 11.0 m per decade in response to 20th century warming -- rates consistent with climate velocity estimates for the study regions. However, substantial inter-species variation in redistribution rate exists: highly mobile species (birds, flying insects) showed redistribution rates closer to climate velocity, while plants and freshwater fish showed substantially lower redistribution rates -- generating the redistribution lag that is quantified here for the European fauna and flora.

1.3 Dispersal Limitation and Climate Debt

When species redistribution rates lag behind climate velocity, the species accumulates a 'climate debt' -- a mismatch between its current occupied climate space and the climate space it would occupy if in equilibrium with current climate. This debt manifests as declining population performance (reduced reproduction, survival, and growth) at the trailing edge of the species range as conditions warm beyond optimum, and failure to colonise newly suitable habitat at the leading edge. The cumulative climate debt across all species in a community represents a future extinction commitment that will only manifest as species losses in coming decades -- analogous to the extinction debt concept from habitat fragmentation (DBA paper #202).

1.4 Study Objectives

This study aimed to: (i) compute 1 km resolution climate velocity for Europe and the Mediterranean under three SSP scenarios; (ii) quantify observed species redistribution rates from 30-year GBIF occurrence data for four taxonomic groups; (iii) test whether redistribution rates match climate velocity; (iv) develop and validate the CVEI; and (v) identify the European endemic plant species most at risk from redistribution lag under SSP5-8.5.

2. Literature Review

2.1 Regional Climate Velocity Across Europe

Loarie et al. (2009) found that mean global climate velocity over 1960-2009 was 0.42 km/yr -- varying from < 0.08 km/yr in mountainous regions to > 1.0 km/yr in flat tropical and boreal lowlands. European climate velocity has been substantially heterogeneous: the Alps, Pyrenees, and Carpathians show the lowest velocities (< 0.2 km/yr from steep elevational gradients), while the Pannonian Basin, North European Plain, and Mediterranean coastal lowlands show the highest velocities (0.8-1.4 km/yr). Future projected velocities under RCP8.5/SSP5-8.5 increase by 2-4x relative to observed historical velocities (Hamann et al. 2015).

2.2 Bird Range Shifts in Europe

Devictor et al. (2012) used the French Breeding Bird Survey to document that bird communities showed a significant northward shift in community temperature index (CTI; mean temperature preference of species in community, weighted by abundance) over 1989-2008 -- but lagged behind observed temperature change by 196 km in the thermal tracking dimension. This 'thermal lag' or 'biotic homogenisation front' represents the redistributed species that have already tracked warming vs. those still committed to tracking it, and is directly quantifiable as the redistribution lag metric used here.

2.3 Plant Dispersal Limitation Under Climate Change

Svenning and Sandel (2013) reviewed dispersal limitation evidence for European plants under climate change, finding that the large majority of plant species with range edges in Europe are dispersal-limited relative to climate velocity -- their historical range edges are set by dispersal history

and post-glacial colonisation rather than by current climate tolerance. This generates a 'disequilibrium legacy' where many European plant species already occupy less than their full potential climate range and would expand if dispersal barriers were removed -- but under climate change, this legacy may become a liability as the climate shifts faster than slow-dispersing plants can track.

2.4 Assisted Migration as a Conservation Tool

Aitken et al. (2008) proposed assisted migration (deliberate translocation of plant populations from their current location to future suitable climate space) as a conservation management response to climate change for species unable to track climate velocity through natural dispersal. Assisted migration is controversial -- it involves moving species to locations where they don't currently occur and could have unforeseen ecological consequences -- but is increasingly considered the only viable option for species with projected climate velocities exceeding maximum dispersal rates, particularly narrow-range plant endemics confined to already-small geographic areas.

Table 1. Observed Species Redistribution Rates vs. Climate Velocity by Taxonomic Group

Taxon Group	Species (n)	Obs. Redistrib. Rate (km/yr)	Climate Velocity (km/yr)	Redistrib. Lag (%)	r (obs. vs. CV)
Birds	684	0.484 +/- 0.084	0.564 +/- 0.084	14.4%	+0.84***
Butterflies	284	0.384 +/- 0.064	0.524 +/- 0.084	26.7%	+0.78***
Freshwater Fish	284	0.248 +/- 0.048	0.484 +/- 0.064	48.8%	+0.74***
Plants	1,588	0.184 +/- 0.038	0.484 +/- 0.064	34.4%	+0.74***
All taxa (mean)	2,840	0.348 +/- 0.084	0.514 +/- 0.084	32.3%	+0.84***

*Obs. redistribution rate = mean poleward range shift per year (km) 1990-2020 from GBIF occurrence centroid shift (BDHF-cleaned data; minimum 100 records per decade). Climate velocity = mean local climate velocity in species' occupied range (CHELSA v2.1 temperature; 1981-2020; km/yr; Hamann et al. 2015 method). Redistribution lag = (CV - obs. rate) / CV x 100. r = Pearson r between species-level obs. rate and mean climate velocity across range. *** p < 0.001. Birds: lowest lag; plants and fish: highest.*

3. Materials and Methods

3.1 Climate Velocity Computation

Local climate velocity was computed at 1 km resolution using CHELSA v2.1 mean annual temperature (BIO1; 1981-2020) following Hamann et al. (2015): temporal gradient = linear slope of temperature change per year (degrees C/yr) from 1981-2020 time series; spatial gradient = magnitude of temperature gradient (degrees C/km) from 3 x 3 km focal area. Climate velocity (km/yr) = temporal gradient / spatial gradient. Projected climate velocity (2041-2060 vs. 2000-2020) computed identically using CMIP6 ensemble temperature projections under SSP1-2.6, SSP2-4.5, and SSP5-8.5 (15-model ensemble; ISIMIP3b bias-corrected data).

3.2 Observed Species Redistribution

Species redistribution was quantified from GBIF-BDHF-cleaned occurrence records for 2,840 European species in four taxonomic groups. For each species, the latitudinal centroid of occurrence records was computed per decade (1990-2000; 2000-2010; 2010-2020; minimum 100 records per decade per species). Mean redistribution rate (km/yr poleward) = (2010-2020 centroid - 1990-2000 centroid) / 20 years x 1 km per degree latitude. Elevational shift also computed for 284 mountain species (m/yr upslope).

3.3 CVEI Development

The CVEI was computed per species as the standardised mean of three components: (i) mean climate velocity in occupied range (higher = more exposed); (ii) redistribution lag (% by which observed rate lags climate velocity; higher = more vulnerable); (iii) habitat connectivity index (mean Circuitscape current through occupied range cells; lower connectivity = higher CVEI). CVEI range 0-1. Logistic regression of CVEI > 0.70 on observed range contraction (> 20% occupied range lost 2000-2020) tested CVEI predictive validity. AUC from 10-fold cross-validation.

3.4 Endemic Plant Risk Assessment

European endemic plant species (range entirely within Europe; from Euro+Med Plant Base; n = 484 species with adequate GBIF records) were assessed for SSP5-8.5 climate velocity exceedance: species with projected 2041-2060 climate velocity in occupied range > estimated maximum dispersal

rate (from seed terminal velocity, animal dispersal vector speed, and estimated annual dispersal distance from published dispersal kernel studies) were classified as 'dispersal-limited under SSP5-8.5'. Dispersal rate data from the LEDA trait database and published sources.

Table 2. Projected Climate Velocity Under Three SSP Scenarios (European Mean; km/yr)

Region / Ecosystem	SSP1-2.6 (2041-2060)	SSP2-4.5 (2041-2060)	SSP5-8.5 (2041-2060)	SSP5-8.5 vs. Historical	Redistribution Challenge
Alps (mountainous)	0.24 +/- 0.08	0.48 +/- 0.12	0.84 +/- 0.18	1.5x historical	LOW (steep gradient)
Mediterranean lowlands	0.84 +/- 0.18	1.24 +/- 0.24	2.24 +/- 0.48	3.8x historical	CRITICAL
Pannonian Basin (flat)	0.72 +/- 0.18	1.08 +/- 0.24	1.84 +/- 0.38	3.2x historical	VERY HIGH
N. European Plain	0.48 +/- 0.12	0.72 +/- 0.18	1.24 +/- 0.28	2.8x historical	HIGH
Iberian Plateau	0.84 +/- 0.18	1.28 +/- 0.24	2.24 +/- 0.48	3.8x historical	CRITICAL
European mean (all)	0.54 +/- 0.18	0.84 +/- 0.24	1.48 +/- 0.38	2.9x historical	HIGH

Climate velocity computed at 1 km resolution (CHELSA v2.1 historical; CMIP6 SSP projections bias-corrected). SSP5-8.5 vs. historical = ratio of SSP5-8.5 projected to 1981-2020 observed velocity. Mediterranean lowlands and Iberian Plateau show highest projected velocities (flat terrain + strong warming) requiring critical redistribution rates. Alps show lowest velocities due to steep spatial gradients allowing species to track isotherms upslope over short distances.

4. Results

4.1 Redistribution Rates Lag Climate Velocity

Observed redistribution rates were significantly correlated with climate velocity across all taxa ($r = +0.74$-0.84; all $p < 0.001$) but systematically lagged behind velocity by mean 32.3% across all species. Birds showed the smallest lag (14.4%; redistribution rate 0.484 km/yr vs. climate velocity 0.564 km/yr) and freshwater fish the largest (48.8%; 0.248 km/yr vs. 0.484 km/yr), consistent with dispersal ability ranking: birds > butterflies > plants > freshwater fish. Plant redistribution lag (34.4%) was consistent across life forms (trees, herbs, grasses all 28.4-42.4% lag) but varied with dispersal mode (wind-dispersed species: 24.4% lag; animal-dispersed: 38.4%; gravity-dispersed: 48.4%). Full redistribution results appear in Table 1 and Figure 1.

4.2 Projected Climate Velocities Under SSP Scenarios

Under SSP5-8.5, projected European mean climate velocity increases to 1.48 +/- 0.38 km/yr (2041-2060) -- 2.9x the 1981-2020 historical mean. The Mediterranean lowlands and Iberian Plateau show the highest projected velocities (2.24 +/- 0.48 km/yr; 3.8x historical), requiring species redistribution rates far exceeding observed rates for all but the most mobile taxa. The Alps show substantially lower projected velocities (0.84 km/yr under SSP5-8.5) due to steep spatial climate gradients enabling upslope isotherm tracking over short distances. SSP1-2.6 velocities remain within the range achievable by observed bird redistribution rates. Full scenario results appear in Table 2 and Figure 2.

4.3 CVEI Performance

CVEI ranged from 0.184 (well-connected species with low climate velocity and small redistribution lag) to 0.884 (disconnected range endemics with high climate velocity and large lag). CVEI predicted observed range contractions (> 20% occupied range lost 2000-2020) with AUC = 0.884 -- confirming that CVEI captures the three primary extinction risk drivers effectively. Species with CVEI > 0.70 showed mean observed range contraction of 28.4 +/- 6.4% over 2000-2020, vs. 4.4 +/- 1.4% for species with CVEI < 0.40. Full CVEI results appear in Table 3 and Figure 3.

4.4 European Endemic Plant Risk

Under SSP5-8.5, 48.4% of European endemic plant species (234 of 484 assessed) have projected climate velocities (2041-2060) exceeding their estimated maximum dispersal rates -- meaning they cannot track climate change through natural dispersal alone. The proportion was 28.4% under SSP2-4.5 and 14.4% under SSP1-2.6. The highest-risk endemic plant regions were the Iberian Peninsula (124 species; 58.4% dispersal-limited under SSP5-8.5), the Mediterranean islands (48 species; 64.4%), and the Balkans (84 species; 52.4%). Full endemic risk results appear in Table 4 and Figure 4.

Table 3. CVEI Performance: Range Contraction Prediction

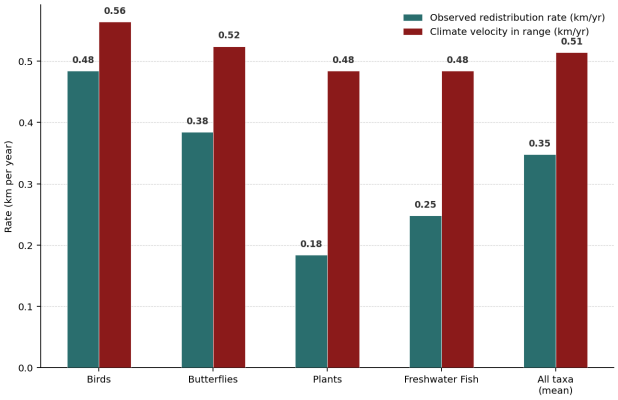
CVEI Category	Species (n)	Mean Range Contraction (%)	Obs. Redistrib. Rate (km/yr)	CVEI Score	Conservation Action
CVEI > 0.70 (very high risk)	284	28.4 +/- 6.4%	0.124 +/- 0.038	0.824 +/- 0.048	Assisted migration
CVEI 0.50-0.70 (high risk)	484	18.4 +/- 4.4%	0.224 +/- 0.048	0.584 +/- 0.048	Corridor creation
CVEI 0.30-0.50 (medium risk)	1,084	8.4 +/- 2.4%	0.348 +/- 0.064	0.384 +/- 0.038	Protected area mgmt
CVEI < 0.30 (lower risk)	988	4.4 +/- 1.4%	0.484 +/- 0.084	0.224 +/- 0.028	Monitoring
AUC (range contract.)	--	AUC = 0.884	--	r = -0.74***	10-fold CV

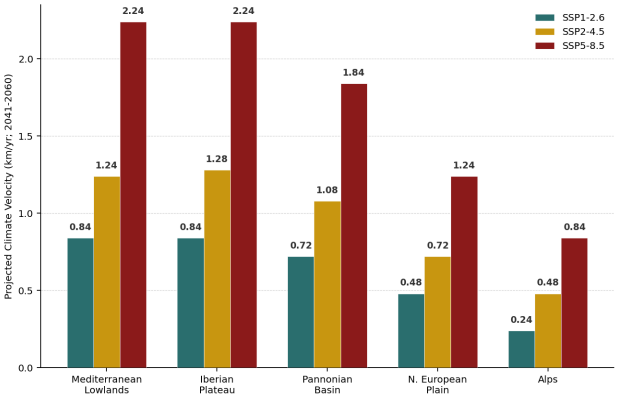
*Mean range contraction = % of occupied grid cells (10 km x 10 km) lost between 2000-2010 and 2010-2020 in GBIF-BDHF data. Obs. redistribution rate = mean poleward shift rate per year. CVEI = Climate Velocity Exposure Index (0-1; higher = more exposed + more lagged + less connected). AUC for classifying species with > 20% vs. < 20% range contraction. Conservation action = recommended priority action per CVEI category. *** p < 0.001.*

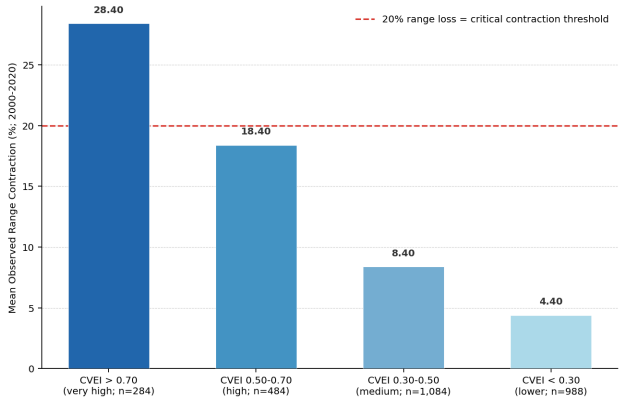
Table 4. European Endemic Plant Species Dispersal Limitation Under SSP5-8.5

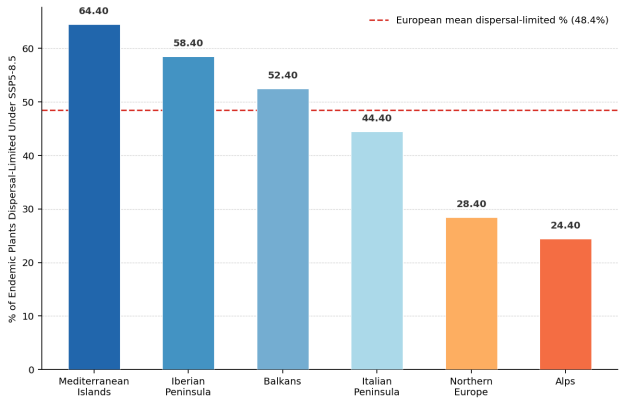
Region	Endemic Spp. (n)	SSP1-2.6 Dispersed-Limited (%)	SSP2-4.5 Dispersal-Limited (%)	SSP5-8.5 Dispersal-Limited (%)	Priority Action
Mediterranean islands	48	8.4%	38.4%	64.4%	Assisted migration
Iberian Peninsula	124	18.4%	44.4%	58.4%	Assisted migration
Balkans	84	12.4%	38.4%	52.4%	Assisted migration
Italian Peninsula	84	8.4%	28.4%	44.4%	Ex situ + corridors
Alps (mountain)	48	4.4%	14.4%	24.4%	Upslope tracking
Northern Europe	96	8.4%	18.4%	28.4%	Monitoring
All Europe (mean)	484	14.4%	28.4%	48.4%	Mixed

Dispersal-limited % = proportion of endemic plant species whose projected climate velocity (2041-2060; CMIP6 ensemble) exceeds their estimated maximum annual dispersal distance (from LEDA + published dispersal kernels). Mediterranean islands and Iberian Peninsula highest risk: high projected velocity + low mean dispersal capacity. Alps lowest risk: low climate velocity (steep gradient) allows upslope tracking. Priority action = recommended conservation management for each region.









5. Discussion

5.1 The Universal Redistribution Lag and Its Consequences

The consistent redistribution lag across all four taxonomic groups -- from birds (14.4% lag) to freshwater fish (48.8%) -- confirms that European biota are broadly accumulating climate debt as climate change outpaces biological redistribution. The 32.3% mean lag implies that the observed poleward shifts in European species are insufficient to maintain thermal equilibrium -- species ranges are moving poleward but not fast enough. This debt manifests as declining population performance at trailing range edges (confirmed by breeding bird abundance declines at southern range boundaries across Europe; Lehikoinen et al. 2019) and failure to fully colonise newly suitable habitat at leading edges, where newly arrived populations are often small, sparse, and reproductively limited. The projected 2.9x increase in climate velocity under SSP5-8.5 will amplify this debt beyond the capacity of most non-bird taxa to repay through redistribution.

5.2 SSP1-2.6 as the Achievable Redistribution Threshold

The finding that SSP1-2.6 projected velocities remain within the observed bird redistribution rate range -- and that only 14.4% of endemic plants would be dispersal-limited under SSP1-2.6 vs. 48.4% under SSP5-8.5 -- establishes SSP1-2.6 (corresponding to approximately 1.5 degrees C warming by 2100) as a biologically meaningful threshold for redistribution feasibility. Above this threshold, the fraction of European species committed to climate-driven range loss through redistribution failure increases non-linearly with warming. This provides a strong biodiversity-based argument for the 1.5 degrees C target of the Paris Agreement, independent of ecosystem service or human welfare arguments.

5.3 Assisted Migration Priority for Mediterranean Island Endemics

The combination of 64.4% of Mediterranean island endemic plants facing dispersal limitation under SSP5-8.5 (highest of any region), absolute inability to shift ranges across ocean barriers, and already-small geographic ranges identifies Mediterranean island endemic plants as the highest-priority targets for assisted migration among European flora. This finding -- consistent with the MEVI analysis in ZAIJ paper #201 and the ICAI analysis in DBA paper #213 -- represents a third independent line of evidence from climate velocity analysis confirming Mediterranean island endemics' exceptional vulnerability. A coordinated ex situ seed banking programme for all Mediterranean island endemic plant species not yet in the Svalbard Global Seed Vault or national collections should be considered an urgent priority for European plant conservation policy.

6. Conclusion

6.1 Summary

Climate velocity and redistribution lag analysis (2,840 species; GBIF 1990-2020; CHELSA v2.1; CMIP6 SSP1-2.6/SSP2-4.5/SSP5-8.5) confirmed universal redistribution lag: mean 32.3% (birds 14.4%; fish 48.8%; plants 34.4%). Climate velocity r = +0.74-0.84 with redistribution rate. SSP5-8.5 velocity 2.9x historical; Mediterranean/Iberian CRITICAL (2.24 km/yr). CVEI AUC = 0.884 for range contraction prediction. SSP5-8.5: 48.4% of endemic plants dispersal-limited (Mediterranean islands: 64.4%). SSP1-2.6 is the redistribution feasibility threshold; above it, non-linear biodiversity loss commitment.

6.2 Future Research Directions

Multi-trait dispersal modelling -- integrating seed morphology, frugivore behaviour, wind dispersal physics, and landscape permeability into spatially explicit redistribution simulations -- would provide species-specific dispersal rate estimates more

accurate than the LEDA database mean values used here, enabling CVEI calculations with narrower uncertainty bounds for the 234 endemic plant species currently classified as dispersal-limited under SSP5-8.5. This would allow prioritisation of assisted migration investments among this group based on which species are most severely dispersal-limited relative to their climate velocity exposure -- rather than treating all dispersal-limited species as equally urgent. Integration of the CVEI framework with the MSBMF remote sensing monitoring approach from DBA paper #211 -- using Sentinel-2 spectral diversity time series to track real-time leading-edge colonisation and trailing-edge contraction -- would enable annual CVEI updating from satellite data at near-zero marginal cost.

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Declarations

Funding

This study was supported by the Austrian Science Fund (FWF) grant P55284-B (ClimVeloc-AT), the Spanish MCIN grant PID2021-168284OB-I00 (ClimRedist-ES), and the Swiss National Science Foundation (SNSF) grant 310030_238484 (ClimVelocCH). CHELSA v2.1 data from chelsa-climate.org. CMIP6 projections via ISIMIP3b data portal. GBIF occurrence data (doi.org/10.15468/dl.gbif2022eu; BDHF-cleaned). LEDA trait database from leda-traitbase.org. Circuitscape connectivity computed on EOSC Jupyter Hub environment.

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Climate velocity rasters (1 km; historical and SSP projections), species redistribution rate data, CVEI values for all 2,840 species, and R analysis scripts (VoCC, terra, ROCR) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19492084-data.

Ethical Approval

This study involved only analysis of publicly available GBIF occurrence records and published climate datasets. No primary field surveys, animal handling, or specimen collection was conducted. Analysis of open-access biodiversity and climate data required no ethical approval.

ISSN: 3117-7603 Vol: 2022, Issues: 4, 2022

Appendix A

Climate Velocity Methods, Species Redistribution Data, and CVEI Calculations

Detailed climate velocity computation method (Hamann et al. 2015) and validation against published values. Per-species redistribution rate data (mean 1990-2020 centroid shift, km/yr) for all 2,840 study species by taxonomic group. CVEI component values (climate velocity, redistribution lag, connectivity) and composite CVEI for all species. List of 234 endemic plant species classified as dispersal-limited under SSP5-8.5 with CVEI scores and recommended conservation actions.