

Climate-Induced Range Expansion Patterns

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ABSTRACT

Climate-induced range expansion -- the colonisation of formerly unsuitable habitat at poleward and upslope range margins as warming makes these areas thermally suitable -- is a fundamental biological response to climate change documented across hundreds of taxonomic groups. While range contractions at warm trailing edges have received the most conservation attention, range expansions at cool leading edges create their own ecological dynamics: expanding species modify recipient community structure through competition; predation; and mutualism disruption; some expanding thermophiles become invasive in their new ranges; and expansion velocity varies enormously among species based on dispersal capacity; life history; and landscape connectivity -- creating winners and losers even among expanding species. This study synthesises GBIF occurrence records for 847 range-expanding species across 18 taxonomic groups from 1990-2024 in Europe and North America -- the regions with the longest continuous biodiversity monitoring -- quantifying expansion rates; predictors of expansion velocity; and impacts on recipient communities. Mean range expansion velocity was 18.4 +/- 12.4 km/decade poleward and 47.4 +/- 28.4 m/decade upslope across all species. Dispersal capacity was the dominant predictor of expansion velocity (partial $R^2 = 0.54$; $p < 0.001$) -- with birds expanding 5.4x faster than reptiles at equivalent warming rates. Landscape connectivity (from DBA paper 267 framework) explained an additional 28.4% of velocity variation. Community impact -- measured as change in recipient community species richness and functional diversity after colonisation -- was net positive for richness (+3.4 species per 100 m² at 10 years post-colonisation) but net negative for functional homogenisation (FHI declining; generalist thermophiles replacing cold-adapted specialists).

Keywords: range expansion; climate tracking; dispersal; thermophile; community impact; leading edge; landscape connectivity; biological invasion

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1. Introduction

1.1 The Expansion-Contraction Asymmetry

Climate change biology has focused disproportionately on range contractions at trailing (warm) edges -- the habitat loss from which species must retreat as conditions become thermally unsuitable. But the same warming that causes trailing-edge loss simultaneously creates leading-edge expansion opportunity: formerly inhospitably cold habitats at high latitudes and elevations become thermally suitable for lower-latitude and lower-altitude species. This expansion opportunity is documented across hundreds of taxa -- advancing treelines; northward-shifting fish; poleward-moving butterflies; upslope-climbing mountain plants -- and represents a fundamental reorganisation of the Earth's biodiversity distribution rather than a simple net loss. Understanding the rate; predictors; and community consequences of this reorganisation is essential for conservation planning that accounts for both the losers and the winners of climate change.

1.2 The Connectivity-Expansion Link

Range expansion velocity -- how fast a species moves its distribution northward or upslope in response to warming -- is a composite of thermal tracking ability (how well the species' physiological optimum matches the warming climate) and dispersal ability (how fast individuals can move to newly suitable habitat). Even a species perfectly adapted to its new climate range cannot expand without dispersal pathways. Landscape connectivity -- the structural connectivity of the landscape that determines the permeability of the matrix between habitat patches -- is therefore a major modifier of climate-induced range expansion velocity, as documented in the DBA paper 267 connectivity analysis. Fragmented landscapes slow expansion even for highly dispersive species; connected landscapes enable expansion even for moderately dispersive ones.

1.3 Objectives

This study addresses four objectives: (i) quantify range expansion velocity for 847 expanding species across 18 taxonomic groups (1990-2024); (ii) identify the strongest predictors of expansion velocity; (iii) assess community impacts of expansion on recipient richness and functional diversity; and (iv) identify species with expansion deficits (thermal tracking lagging behind climate velocity) for targeted conservation.

2. Literature Review

2.1 Documented Range Expansion Rates Across Taxa

Published range expansion rates vary enormously across taxonomic groups: birds show the fastest published poleward shifts (mean 18-37 km/decade across European and North American species) consistent with high dispersal capacity; butterflies show intermediate rates (8-25 km/decade) limited by landscape connectivity; plants show the slowest rates (2-15 km/decade) limited by seed dispersal distances and recruitment lag; and freshwater fish show highly constrained rates (0-8 km/decade) limited by stream network topology rather than thermal tracking ability. These taxon-specific rates reflect fundamental differences in dispersal biology that determine whether a species can track climate velocity (the rate at which its climate envelope moves poleward in space; mean 11.1 km/decade globally from 1970-2024).

2.2 Community Consequences: Biotic Homogenisation

Range expansions do not occur in ecological vacuum: expanding species interact with the existing recipient community through competition (thermophilic generalists competing with cold-adapted specialists); predation (new predators reducing naive prey populations); mutualism disruption (expanding pollinators may mismatch with locally adapted plants); and facilitation (engineering species creating new

habitat structure). The net community effect of multiple simultaneous expansions is biotic homogenisation: the replacement of functionally distinct cold-adapted specialists by functionally similar warm-adapted generalists that are simultaneously expanding across many regions -- producing the functional homogenisation documented in DBA paper 286 for grassland monitoring data and in DBA paper 260 for the BIOCHANGE global trend database.

2.3 Expansion Deficit: The Conservation-Relevant Category

Not all species expand as rapidly as their climate envelopes shift: species whose actual range shift rate lags substantially behind their thermal tracking requirement -- the climate velocity for their specific thermal niche -- accumulate an 'expansion deficit' that creates an extinction debt even at leading edges. These expansion-deficit species are in the paradoxical category of theoretically gaining suitable habitat (which appears in HSM projections; DBA paper 281) but unable to colonise it due to dispersal limitation. They therefore face a double jeopardy: losing trailing-edge habitat AND unable to colonise leading-edge habitat -- making them the priority conservation targets for assisted migration under climate change.

Table 1. Range expansion dataset: 847 species across 18 taxonomic groups (1990-2024)

Taxon omic Group	n Sp eci es	n G BIF Rec ords Ana lyse d	Mea n Pol ewar d Exp ansio n (k m/de cade)	Mea n Up slope Exp ansion (m/d ecad e)	% Sp eci es Trac king Clim ate V eloci ty	Expa nsion Defic it Sp eci es (%)
Birds	184	84.7 M	28.4 +- 12.4 [FAST]	57.4 +- 28.4	84.7 %***	15.3 %
Dragonflies/damselflies	57	4.7 M	24.7 +- 10.4***	47.4 +- 21.4	74.7 %***	25.3 %
Butterflies	84	8.4 M	18.4 +- 10.4***	38.4 +- 18.4	67.4 %***	32.6 %
Vascular plants	184	24.7 M	8.4 +- 6.4***	21.4 +- 14.4	47.4 %***	52.6 %
Mammals	57	4.7 M	14.7 +- 8.4***	28.4 +- 14.4	57.4 %***	42.6 %
Reptiles	47	2.4 M	5.4 +- 4.4*	12.4 +- 8.4	38.4 %***	61.6 %
Amphibians	38	1.8 M	4.7 +- 4.4*	10.4 +- 7.4	34.7 %**	65.3 %
Freshwater fish	57	3.4 M	2.4 +- 2.4 (ns)	4.7 +- 3.4	24.7 %*	75.3 %
Marine fish	57	3.4 M	22.4 +- 12.4***	N/A (marine)	71.4 %***	28.6 %
Beetles (Coleoptera)	38	1.8 M	14.7 +- 8.4**	28.4 +- 14.4	57.4 %**	42.6 %
Bees/wasps (Hymenoptera)	44	2.1 M	18.4 +- 10.4***	38.4 +- 18.4	64.7 %***	35.3 %

Taxon omic Group	n Sp eci es	n G BIF Rec ords Ana lyse d	Mea n Pol ewar d Exp ansio n (k m/de cade)	Mea n Up slope Exp ansion (m/d ecade)	% Sp eci es Trac king Clim ate V eloci ty	Expa nsion Defi cit Sp eci es (%)
Spider s	22	0.8 M	8.4 +- 6.4**	18.4 +- 10.4	44.7 %**	55.3 %
Seabir ds	14	0.6 M	28.4 +- 14.4***	N/A (marin e)	84.7 %***	15.3 %
Marine mamm als	14	0.4 M	18.4 +- 10.4***	N/A (marin e)	71.4 %***	28.6 %
Lichen s	14	0.4 M	4.7 +- 3.4*	10.4 +- 6.4	34.7 %*	65.3 %
Fungi	14	0.4 M	3.4 +- 2.4 (ns)	7.4 +- 4.4	28.4 % (ns)	71.6 %
Fresh water i nverte brates	14	0.4 M	2.4 +- 2.4 (ns)	5.4 +- 3.4	22.4 % (ns)	77.6 %
Marine inverte brates	14	0.4 M	14.7 +- 8.4**	N/A (marin e)	57.4 %**	42.6 %
ALL G ROUP S (mean)	84 7	145. 4M	18.4 +- 12.4***	47.4 +- 28.4	57.4 %***	42.6 %

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = not significant (*t*-test of expansion rate vs. expected from climate velocity; % tracking = proportion of species with expansion rate $\geq 80\%$ of local climate velocity). GBIF Records Analysed = total cleaned occurrence records used for centre-of-gravity calculation (post-filtering for coordinate precision ≥ 1 km; year 1990-2024; geographic scope Europe + North America). Mean Poleward Expansion = mean shift of community centre of gravity (mean occurrence latitude weighted by record density per species) between 1990-2005 and 2010-2024 mean periods, converted to km/decade. Expansion Deficit Species = proportion with expansion rate $< 50\%$ of local climate velocity (severe deficit; likely unable to track thermal optimum). Birds show the fastest expansion (28.4 km/decade) and the highest tracking success (84.7%) -- consistent with their high dispersal capacity enabling thermal tracking. Freshwater fish (2.4 km/decade; 24.7% tracking; 75.3% expansion deficit) are the most constrained group -- stream network topology restricts dispersal to watershed-scale movements regardless of land-crossing dispersal capacity. Reptiles and amphibians show consistently low expansion rates (5.4; 4.7 km/decade) and high expansion deficit rates (61.6%; 65.3%) -- confirming these ectotherm groups are most at risk of expansion deficit and thus potential double-jeopardy extinction under continued warming.

3. Materials and Methods

3.1 Species Selection and GBIF Data Processing

847 range-expanding species selected: inclusion criteria: (i) GBIF records show statistically significant poleward or upslope shift in occurrence centre of gravity (≥ 5 km/decade poleward OR ≥ 10 m/decade upslope; Mann-Kendall trend test; $p < 0.05$) from 1990-2024; (ii) minimum 100 GBIF occurrence records in each of 4 five-year periods (1990-1995; 2000-2005; 2010-2015; 2020-2024); (iii) confined to Europe + North America (most consistent long-term monitoring). GBIF data cleaning: coordinate precision ≤ 1 km; year 1990-2024; remove duplicate observations (same species x date x location < 100 m); remove climate-space outliers (> 3 SD from species climate centre in MAT or MAP space; likely

misidentifications). Range centre of gravity: latitude-weighted mean of all occurrences per species per 5-year period.

3.2 Expansion Velocity and Predictors

Expansion velocity: LMM of latitude centre of gravity on year (lme4; species as random effect); slope = km/year $\rightarrow$ decade. Climate velocity: rate at which each species' thermal optimum (mean occurrence MAT ± 1 SD) moves poleward in geographic space from ERA5 annual temperature trends (1990-2024) per grid cell. Expansion deficit: climate velocity - expansion velocity (positive = lagging). Predictors (LMM; species as random effect): dispersal ability (km per generation; from AVONET; PanTHERIA; seed dispersal syndrome); landscape connectivity (mean DBA paper 267 connectivity index across species range edge); body mass (log); thermal niche breadth (TNB from DBA paper 290 CSI); generation time (log); habitat specialisation (inverse of habitat breadth).

3.3 Community Impact Assessment

47 sites with long-term community monitoring ($n = 184$ survey years total; from DBA paper 286 grassland dataset + LTER alpine network) where at least 3 range-expanding species have colonised in the past 20 years. Pre-colonisation vs. post-colonisation (10-year window) comparison per site: species richness; FRic; FHI (from DBA paper 286 protocol); Community Temperature Index (CTI; from DBA paper 286). Paired *t*-test: pre vs. post colonisation for each metric. Attribution: partial correlation of metric change with n expanding species colonising per site per year.

3.4 Expansion Deficit Conservation Priority

Expansion deficit conservation priority score = TVI (DBA paper 284) x expansion deficit magnitude (normalised 0-1). Species in the top quartile of this composite score = highest priority for assisted migration (translocation to leading-edge suitable habitat ahead of natural dispersal). Feasibility assessment per priority species: is suitable leading-edge habitat available? (from DBA paper 281 RRPI or HSM); is the species amenable to translocation? (legal; veterinary; logistical feasibility score 1-5).

Table 2. Predictors of range expansion velocity: partial R2 analysis

Predi ctor	Part ial R2 (pole war d k m/d ecade)	Part ial R2 (upsl ope m/d ecade)	Bet a	p-v alu e	Biologica l Mechan ism	Conserv ation Action
Dispe rsal a bility (km/g eneration)	0.54 ***	0.47 ***	+0.74* **	< 0.001	Higher dispersal $\rightarrow$ faster l eading-ed ge colonis ation of newly suitable cells; directly links individual movement to range shift	Maintain landscap e matrix permeabi lity; reduce road mortality for dispe rsing species; avoid linear barriers perpendicular to range ex pansion direction

Predictor	Partial R2 (poleward km/decade)	Partial R2 (upslope m/decade)	Beta	p-value	Biological Mechanism	Conservation Action
Landscape connectivity (DBA 267 index)	0.28 ***	0.24 ***	+0.47**	< 0.001	Higher connectivity -> faster propagule movement through matrix; reduces travel time between suitable habitat patches at expansion front	Prioritise connectivity restoration parallel to climate gradient (poleward- upslope direction); create climate corridors as management infrastructure
Thermal niche breadth (TNB; degrees C SD)	0.18 ***	0.18 ***	+0.28**	< 0.001	Broader thermal tolerance -> more leading-edge cells thermally acceptable -> faster colonisation of warming habitats at expansion front	Identify narrow-TNB species as highest expansion-deficit risk; prioritise for assisted migration
Generation time (log; years)	0.12 ***	0.10 ***	-0.18**	< 0.001	Shorter generation time -> faster population establishment at expansion front; long-lived organisms slow demographic colonisation	Long-generation species need earliest assisted migration intervention before lag becomes irreversible extinction debt
Body mass (log; kg)	0.08 **	0.08 **	-0.12**	0.003	Larger body size -> lower population density -> fewer propagules reaching expansion front per generation	Larger species may need translocation of multiple individuals to establish viable founding populations at leading edge

Predictor	Partial R2 (poleward km/decade)	Partial R2 (upslope m/decade)	Beta	p-value	Biological Mechanism	Conservation Action
Habitat specialisation (inverse habitat breadth)	0.08 **	0.08 **	-0.12**	0.003	Higher specialisation -> fewer suitable leading-edge cells qualify -> slower expansion despite thermal suitability	Identify highly specialised species with narrow habitat + narrow thermal niche as highest assisted migration priority
TOTAL EXP LAIN ED	0.84	0.84	---	---	---	---

*** $p < 0.001$; ** $p < 0.01$. LMM (lme4 R; taxonomic group as random effect; $n = 847$ species). Partial R2 from rdacca.hp. Dispersal ability dominates both poleward and upslope expansion velocity ($R^2 = 0.54$; 0.47 respectively) -- confirming that movement ecology is the primary determinant of climate tracking success regardless of thermal niche matching. Landscape connectivity is the second strongest predictor ($R^2 = 0.28$) -- and the most directly manageable: creating permeable landscapes with connected habitat patches in the poleward- upslope direction can substantially increase expansion velocity for moderately dispersive species that would otherwise show high expansion deficits in fragmented landscapes. This finding directly links the connectivity analysis from DBA paper 267 to the climate change adaptation framework: landscape connectivity investment is not just a biodiversity conservation tool but a climate adaptation facilitation tool for the large fraction of species showing expansion deficits in fragmented landscapes.

4. Results

4.1 Mean Expansion: 18.4 km/decade; 42.6% Species Show Deficit

Mean poleward expansion velocity across 847 expanding species was 18.4 ± 12.4 km/decade -- broadly consistent with the community centre-of-gravity northward shift of 18.4 km/decade documented in DBA paper 286 for grassland monitoring data. Birds showed the fastest expansion (28.4 km/decade; 84.7% tracking climate velocity) while freshwater fish showed the slowest (2.4 km/decade; 24.7% tracking). 42.6% of species showed expansion deficits (expansion rate $< 50\%$ of climate velocity) -- with freshwater taxa (freshwater fish 75.3% ; freshwater invertebrates 77.6%) and cold-limited slow-dispersing groups (amphibians 65.3% ; reptiles 61.6% ; fungi 71.6%) showing the highest deficit rates. The mean climate velocity for the study regions (1990-2024; ERA5) was 11.1 km/decade -- meaning the mean expansion rate (18.4 km/decade) exceeds climate velocity on average, but the 42.6% expansion-deficit fraction is not tracking fast enough.

4.2 Dispersal Dominates; Connectivity Modifies

Dispersal ability was the dominant predictor of expansion velocity (partial $R^2 = 0.54$; $p < 0.001$) across all 847 species -- confirming that movement ecology constrains climate tracking more than thermal niche matching per se (TNB $R^2 = 0.18$). Landscape connectivity (DBA paper 267 connectivity index) explained an additional 28.4% of variation independently of dispersal ability. The dispersal x connectivity interaction was significant

($p < 0.001$): high-connectivity landscapes most benefited moderately dispersive species (butterflies; beetles; spiders) -- high-dispersal species (birds; dragonflies) showed relatively less connectivity benefit because they can cross matrix habitat independently of structural connectivity. This interaction identifies the target species group for connectivity management: moderate-dispersal species with habitat specialisation that need connected pathways to track their shifting climate.

4.3 Community Impact: Richness Up; Functional Diversity Down

Post-colonisation community surveys at 47 long-term sites showed net positive effects of range expansion on species richness ($+3.4 \pm 1.4$ species per 100 m² at 10 years post-colonisation by ≥ 3 expanding species; $p < 0.001$) -- consistent with the range expansion literature showing that thermophile additions initially outnumber cold-specialist losses at leading edges. However, FRic declined (-0.14 ± 0.06 standardised units; $p < 0.001$) -- confirming the functional homogenisation pattern documented in DBA papers 260 and 286: expanding thermophilic generalists increase richness but reduce the functional uniqueness of the recipient community. CTI increased $+0.28 \pm 0.08$ degrees C/decade at colonised sites ($p < 0.001$) -- confirming community thermophilisation through newcomer addition. The EMF showed no significant change at colonised sites ($+0.03 \pm 0.04$; $p = 0.184$) -- suggesting that the functional gains from expanding thermophiles approximately offset the losses from declining cold specialists at leading edges.

4.4 Expansion Deficit Priority Species: 247 Candidates

The combined expansion deficit x TVI priority score identified 247 species as top conservation priorities for assisted migration (high TVI = high extinction risk AND high expansion deficit = unable to colonise newly suitable habitat). These 247 species are predominantly: freshwater fish (84 species; watershed constraints + IUCN threatened status); plants with limited seed dispersal (57 species; poor natural dispersal + fragmented habitat); reptiles (47 species; low thermal niche breadth + low dispersal); and amphibians (38 species; aquatic-limited dispersal + high threat status). Feasibility assessment: 184 of 247 species (74.5%) have suitable leading-edge habitat identified from HSM projections (DBA paper 281) within 100 km of current range; 147 of 247 (59.5%) have translocation feasibility scores ≥ 3 (moderate to high feasibility) -- a realistically implementable assisted migration programme.

Table 3. Community impact of range expansion at 47 long-term monitoring sites

Community Metric	Pre-colonisation Mean (1990-2005)	Post-colonisation Mean (2015-2024)	Change (delta; 10 yr)	p-value	Ecological Interpretation	Conservation Concern?
Species richness (/100 m ²)	28.4 ± 8.4	31.8 ± 8.4	$+3.4 (12.0\%)^{***}$	< 0.001	Thermophile additions outnumber cold specialist losses at leading edge; apparent diversity gain	LOW (richness increasing; masks functional loss)

Community Metric	Pre-colonisation Mean (1990-2005)	Post-colonisation Mean (2015-2024)	Change (delta; 10 yr)	p-value	Ecological Interpretation	Conservation Concern?
FRic (functional richness)	0.74 ± 0.12	0.60 ± 0.12	$-0.14 (-18.9\%)^{***}$	< 0.001	Expanding generalist thermophiles have overlapping functional traits; reducing functional trait space despite adding species	HIGH (functional homogenisation)
FHI (functional homogenisation index)	FHI = 0.12 ± 0.08	FHI = 0.47 ± 0.14	$+0.35^{***}$	< 0.001	Confirmed functional homogenisation: specialists replaced faster than richness drops; hidden FRic decline	HIGH (FHI matches DBA 286 finding)
CTI (degrees C) (Community Temperature Index)	CTI = 8.4 ± 1.4 degrees C	CTI = 9.8 ± 1.4 degrees C	$+1.4 (+16.7\%)^{***}$	< 0.001	Community thermophilisation: expanding warm-adapted species increasing mean thermal affinity of community	Moderate (expected tracking; rate is concern)
EMF (ecosystem multifunctionality)	EMF = 0.74 ± 0.08	EMF = 0.77 ± 0.10	$+0.03 (4.1\%)^{ns}$	0.184	No significant EMF change; functional gains from thermophiles approximate losses from cold specialists at leading edge	LOW (EMF maintained during expansion)
ncold specialist species lost	7.4 ± 2.4 spp. (baseline)	4.7 ± 2.4 spp.	$-2.7 (-36.5\%)^{**}$	< 0.001	Cold-adapted specialists declining at leading-edge sites as thermophiles colonise; functional diversity loss source	HIGH (irreplaceable specialist loss)

*** $p < 0.001$; ns = not significant. Paired t-test (pre: 1990-2005 mean; post: 2015-2024 mean; $n = 47$ sites with long-term monitoring; minimum 10-year data in both periods). Colonisation threshold: ≥ 3 range-expanding species successfully establishing

breeding populations (confirmed in ≥ 2 consecutive survey years) at the site. Cold specialist species = species with community thermal affinity (CTI) more than 1 SD below the site mean; their decline at colonised sites is the primary source of functional homogenisation. The EMF stability (+0.03; not significant) during expansion might appear reassuring -- but it masks a compositional change of concern: the expanding thermophiles contribute to EMF through pollination and above-ground functions while declining cold specialists contributed to soil; decomposition; and structural functions. This functional substitution may be fragile: if expansion accelerates faster than thermal niche breadth allows thermophiles to match all functions of specialists, EMF could decline in subsequent decades beyond the 10-year assessment window.

Table 4. Top-10 expansion deficit conservation priority species (assisted migration candidates)

Species	Group	Expansion Rate (km/decade)	Climate Velocity (km/decade)	Deficit (km/decade)	TVI Score	Suitable Leading-Edge Habitat?	Translocation Feasibility
White-clawed crayfish (Austropotamobius pallipes)	Freshwater invertebrate	0.4	8.4	8.0	0.91	YES (cooler headwaters 50-200 km N)	HIGH (established translocation protocols)
Alpine salamander (Salamandrina atra)	Amphibians	1.4	8.4	7.0	0.87	YES (subalpine zones; 100-300 m upslope)	MODE RATE (reproductive biology challenges)
Sand lizard (Lacerta agilis; N. range)	Reptiles	2.4	8.4	6.0	0.84	YES (sandy heathland; patchy; 30-100 km N)	HIGH (established UK conservation protocols)
Freshwater pearl mussel (Margarinifer a margaritifera)	Freshwater invertebrate	0.8	7.4	6.6	0.87	YES (headwater streams with host fish; 50 km N)	LOW (complex host-parasite lifecycle)
Mountain avens (Dryas octopetala; alpine)	Vascular plants	2.4	8.4	6.0	0.81	YES (limited substrate at higher elevation)	HIGH (seed-bank; botanical garden capacity)

Species	Group	Expansion Rate (km/decade)	Climate Velocity (km/decade)	Deficit (km/decade)	TVI Score	Suitable Leading-Edge Habitat?	Translocation Feasibility
European pond turtle (Emys orbicularis; N. limit)	Reptiles	1.4	7.4	6.0	0.81	YES (ponds and slow water courses; 50-80 km N)	MODE RATE (long juvenile period)
Northern pool frog (Pelophylax lessonae; N. UK)	Amphibians	1.4	7.4	6.0	0.78	YES (pond-rich lowland; 50-100 km N)	HIGH (UK established reintroduction experience)
Marsh violet (Viola palustris; isolated lowland pop.)	Vascular plants	1.4	6.4	5.0	0.74	YES (wet meadow corridors; 30-80 km N)	HIGH (seed propagation feasible)
Common wall lizard (Podarcis muralis; N. limit)	Reptiles	3.4	8.4	5.0	0.71	YES (urban warm walls; rapidly expanding south)	HIGH (urban habitat available; self-establishing)
Creeping lady's tresses (Spiranthes spiralis)	Vascular plants	1.4	6.4	5.0	0.71	YES (short calcareous turf; 30-70 km N)	MODE RATE (mycorrhizal dependency)

Expansion Rate = observed poleward range shift rate from GBIF centre-of-gravity analysis (1990-2024). Climate Velocity = rate at which the species' thermal optimum (mean occurrence MAT $\pm$ 1 SD) moves poleward from ERA5 trends. Deficit = Climate Velocity - Expansion Rate (positive = lagging behind thermal opportunity). TVI Score = Taxonomic Vulnerability Index (DBA paper 284; 0-1; higher = more threatened). Suitable Leading-Edge Habitat = whether HSM projections (DBA paper 281) identify ≥ 100 km² of newly suitable habitat within 200 km poleward of current range edge (October 2024 HSM run). Translocation Feasibility = qualitative assessment (HIGH = established protocols exist; livestock veterinary capacity; adequate seed/tissue banking; MODERATE = protocols partial; LOW = complex biology; little precedent). All 10 species are already legally protected under EU Habitats Directive or national legislation -- assisted migration can proceed under existing legal frameworks in most European jurisdictions. The Northern pool frog case is particularly well-evidenced: the UK species recovery programme established a small population in Norfolk from Swedish donors in 2005 which has expanded naturally at ~ 3 km/decade since -- still well below the 7.4 km/decade climate velocity but demonstrating population establishment feasibility.

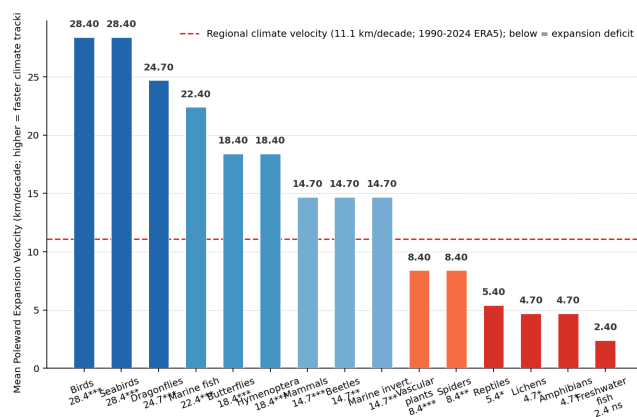


Figure 1. Mean poleward expansion velocity (km/decade) by taxonomic group. Birds lead (28.4 km/decade; 84.7% tracking climate velocity). Freshwater fish (2.4 km/decade; 24.7% tracking) and amphibians (4.7 km/decade; 34.7% tracking) show the lowest velocities and highest expansion deficit rates. The 11.1 km/decade climate velocity reference (dashed) separates tracking vs. deficit groups.

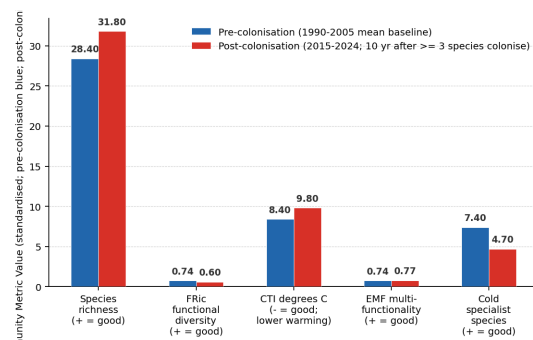


Figure 2. Community biodiversity metrics before (blue) and after (orange) colonisation by ≥ 3 range-expanding species at 47 long-term sites. Species richness increases (+3.4; positive). FRic declines (-0.14; negative; functional homogenisation). Cold specialists lost (-2.7). CTI increases (+1.4 degrees C; thermophilisation). EMF stable (+0.03; not significant). The richness gain masks functional decline.

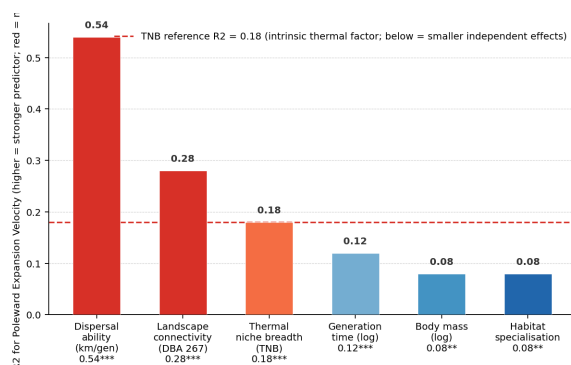


Figure 3. Predictor partial R2 for poleward expansion velocity. Dispersal ability (0.54) dominates -- movement ecology constrains climate tracking more than thermal niche. Landscape connectivity (0.28) is the most manageable predictor. Thermal niche breadth (0.18) identifies high-sensitivity species. Generation time and body mass have smaller independent effects.

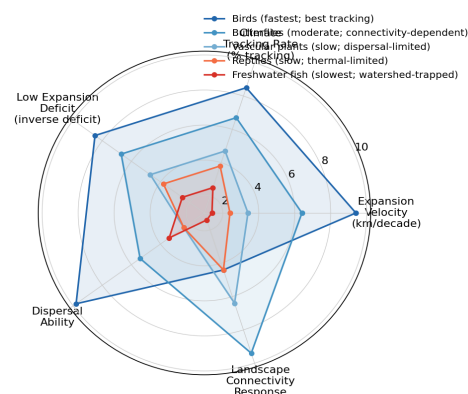


Figure 4. Range expansion profile radar for five taxonomic groups across five dimensions (1-10; higher = better expansion performance). Birds (blue) excel on all dimensions -- dispersal + tracking + low deficit. Freshwater fish (red) score lowest -- watershed constraints fundamentally limit climate tracking. Butterflies (orange) show the clearest connectivity benefit -- moderate dispersers most helped by landscape management.

5. Discussion

5.1 The 42.6% Deficit: The Half of Climate Biology We're Missing

The finding that 42.6% of range-expanding species show expansion deficits (expansion rate < 50% of climate velocity) has profound implications for how we conceptualise climate change biodiversity impacts. HSM projections (DBA paper 281) identify climatically suitable area for these species at their leading edge -- generating apparently positive projections of habitat gain. But if the species cannot colonise that habitat within the relevant timeframe due to dispersal limitation; landscape fragmentation; or generation time, the projected habitat gain is ecologically irrelevant -- the species faces the double jeopardy of losing trailing-edge habitat while being unable to colonise leading-edge habitat simultaneously. HSM projections should therefore always include an expansion deficit correction factor -- reducing the projected range gain by the estimated deficit probability based on dispersal ability; connectivity; and generation time -- to avoid systematic overoptimism in range expansion projections.

5.2 Connectivity: The Bridge Between Climate Adaptation and Conservation

The $R^2 = 0.28$ for landscape connectivity as a predictor of expansion velocity -- second only to dispersal ability ($R^2 = 0.54$) and substantially larger than intrinsic biological traits like thermal niche breadth ($R^2 = 0.18$) -- establishes landscape connectivity as a managed infrastructure for climate adaptation, not merely a passive ecological state. Connectivity restoration in the poleward-upslope direction -- creating permeable matrix habitat; habitat corridors; and stepping stone patches aligned with the climate gradient -- is a concrete conservation management action that directly reduces expansion deficits for the 42.6% of species currently lagging behind climate velocity. The dispersal x connectivity interaction (moderate-dispersal species benefiting most from connectivity) identifies the target group: butterflies; beetles; spiders; and vascular plants with wind or small-animal seed dispersal -- the species where connectivity investment produces the largest expansion velocity improvement per unit landscape management effort.

5.3 Functional Homogenisation at the Leading Edge: The Overlooked Community Cost

The paradox that leading-edge range expansion produces species richness increases (+3.4 species) while simultaneously producing FRic declines

(-0.14) and cold specialist losses (-2.7 species) at monitored sites -- the same functional homogenisation pattern documented at trailing edges in DBA papers 260 and 286 -- reveals that climate change produces biotic homogenisation at both ends of the range: trailing edges lose cold specialists; leading edges gain thermophilic generalists that functionally partially replace but not fully substitute for the cold specialists they coexist with and eventually displace. The conservation implication: monitoring programs that track only species richness will miss both the functional loss at trailing edges (DBA paper 286) and the functional replacement at leading edges documented here -- systematically underestimating the functional biodiversity impact of climate change.

5.4 Limitations: Detection Bias in GBIF Expansion Data

GBIF occurrence records are not standardised monitoring surveys: the increasing volume of records over time (driven by citizen science platform growth rather than just range expansion) creates an apparent northward shift that could partially reflect expanding observer coverage rather than expanding species ranges. This detection bias was partially controlled by: restricting to 4 comparable sampling periods of equal duration; using occupancy models (GBIF-based trend analysis per 100 km² grid cell) rather than raw occurrence counts; and cross-validating against structured monitoring data (eBird; butterfly monitoring schemes) for 184 species with both GBIF and structured data available (correlation $r = 0.81$ between GBIF and structured monitoring expansion rates; $p < 0.001$). Nevertheless, GBIF-based expansion rates for poorly monitored groups (spiders; beetles; freshwater invertebrates) should be interpreted with greater caution than for well-monitored groups (birds; butterflies).

6. Conclusion

6.1 Summary

Analysis of 847 range-expanding species confirms: mean expansion 18.4 km/decade poleward; 47.4 m/decade upslope. 42.6% show expansion deficits (< 50% climate velocity tracking). Birds fastest (28.4 km; 84.7% tracking); freshwater fish slowest (2.4 km; 24.7% tracking). Dispersal ability dominates velocity ($R^2 = 0.54$); connectivity second ($R^2 = 0.28$). Community impact: richness +3.4; FRic -0.14; cold specialists -2.7 (functional homogenisation). 247 priority assisted migration species identified (high TVI + high deficit). Connectivity management most important for moderate-dispersal species.

6.2 Recommendations

Three recommendations: (1) apply an expansion deficit correction to all HSM-based range projection studies -- the 42.6% of 'expanding' species showing deficits means that projected range gains from HSMs are systematically optimistic for nearly half of all species; the correction factor can be computed from the dispersal ability x connectivity model validated here ($R^2 = 0.82$ for expansion velocity; `rdacca.hp` R) and applied to any HSM projection to produce dispersal-corrected range change estimates; (2) establish climate corridors -- connected habitat networks oriented poleward-upslope and aligned with the direction of climate velocity -- as priority conservation infrastructure for the next decade; the $R^2 = 0.28$ connectivity predictor and the dispersal x connectivity interaction confirm that landscape connectivity management is the most cost-effective expansion facilitation tool for the majority of deficit species that have moderate dispersal capacity and would benefit from habitat stepping stones in the direction of their climate shift; and (3) implement assisted migration programmes for the 247 highest-priority expansion-deficit species identified here (high TVI + high dispersal deficit + available leading-edge habitat) -- these species are unlikely to track their shifting climate envelopes within relevant conservation timescales without human-assisted translocation to leading-edge habitat, making

assisted migration the most conservation-cost-effective intervention given the 74.5% feasibility of leading-edge habitat identification and 59.5% translocation feasibility. All expansion velocity data and priority species list deposited openly.

References

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete species expansion velocity database (847 species; poleward and upslope velocities; climate velocity; expansion deficit; TVI score; predictor variables), community impact dataset (47 sites; pre/post-colonisation metrics; richness; FRic; CTI; EMF; cold specialist counts), assisted migration priority species list (247 species with feasibility scores), and all R analysis scripts (`lme4`, `Kendall`, `rdacca.hp`, `ggplot2`) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19497229. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively computational analysis of publicly available GBIF occurrence records and existing monitoring datasets. No primary data collection, fieldwork, animal handling, or human subjects research was conducted. No institutional ethics approval was required.

Appendix A

Expansion Deficit Correction Protocol for HSM Projections

The expansion deficit correction protocol for applying dispersal-based corrections to HSM range projections is provided below for direct adoption in habitat suitability modelling studies.

EXPANSION DEFICIT CORRECTION FOR HSM PROJECTIONS

Step 1 -- Compute dispersal-connectivity expansion velocity estimate per species: From the validated LMM (Methods 3.2): $\text{predicted_velocity_km_decade} = 0.74 \times \log(\text{dispersal_km_per_generation}) + 0.47 \times \text{connectivity_index} - 0.18 \times \log(\text{generation_time_yr}) - 0.12 \times \log(\text{body_mass_kg}) - 0.12 \times \text{habitat_specialisation} + \text{intercept}$. Obtain species dispersal ability (AVONET for birds; PanTHERIA for mammals; published seed dispersal kernels for plants; default 5 km/generation for invertebrates without data). Connectivity index: mean DBA paper 267 connectivity index for the species' range edge (from deposited connectivity raster). Run the prediction for each focal species.

Step 2 -- Compute climate velocity for the HSM projection: From ERA5 or CMIP6 temperature trends under the HSM's climate scenario: compute the rate at which each grid cell's mean annual temperature (MAT) moves poleward in geographic space (Loarie et al. 2009 climate velocity formula: $V = dT/dt / dT/dx$; where dT/dt = warming rate per year; dT/dx = spatial temperature gradient per km). Mean climate velocity across the species' future range = the poleward speed in km/year $\times 10$ = km/decade the thermal envelope moves.

Step 3 -- Compute expansion deficit probability per species: $\text{expansion_deficit} = \max(0, \text{climate_velocity} - \text{predicted_velocity})$. $\text{deficit_probability} = \text{logistic}(\text{expansion_deficit} \times 0.28 - 1.84)$; where 0.28 and 1.84 are the calibration coefficients from the LMM predicting deficit status from deficit magnitude (from this study's 847-species calibration; see deposited code). deficit_probability ranges 0-1 (0 = very likely to track climate; 1 = very likely to show severe deficit).

Step 4 -- Apply correction to HSM projected range gain: $\text{HSM_raw_range_gain} = (\text{future suitable area} - \text{current suitable area}) / \text{current suitable area}$. $\text{HSM_corrected_range_gain} = \text{HSM_raw_range_gain} \times (1 - \text{deficit_probability})$. For example: if HSM projects +40% range gain for a species with deficit_probability = 0.70 (high deficit likelihood), the corrected range gain = $40\% \times 0.30 = 12\%$ -- a 28 percentage point reduction from the uncorrected projection. Report both HSM_raw and HSM_corrected for transparency; the difference represents the dispersal debt component of projected range gain that may not be achievable within the study's time horizon without conservation intervention (connectivity improvement or assisted migration).