

Climate-Induced Hybrid Zones and Species Boundaries

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ABSTRACT

Climate change is altering species distributions faster than reproductive isolation can maintain species boundaries, causing secondary contact between previously allopatric sister taxa whose ranges are shifting poleward or upslope in response to warming -- creating climate-induced hybrid zones that represent both evolutionary novelty and conservation complexity. As species track isotherms northward and upward (DBA papers #215, #231), they encounter congeners that have shifted from different directions, breaking down the geographic barriers that previously maintained reproductive isolation. This study characterised climate-induced hybrid zones in 14 European species pairs (7 plant; 4 invertebrate; 3 vertebrate pairs) using RADseq genomic data (2,840 genotyped individuals from 42 transect sites across Austria, Italy, and Sweden; 2020-2023), quantifying hybrid zone width, admixture proportions, and reproductive barrier strength (Isolation Index I; genomic cline analysis) and testing whether hybrid zone displacement rates correlate with climate velocity. Hybrid zones showed mean displacement rates of +18.4 +/- 4.4 km per decade -- significantly correlated with local climate velocity ($r = +0.84$; $p < 0.001$). Reproductive isolation was reduced in 84.4% of hybrid zones relative to historical reference data -- consistent with increased secondary contact reducing assortative mating and post-zygotic isolation in previously separated populations. A Hybrid Zone Climate Sensitivity Index (HZCSI) integrating hybrid zone displacement rate, genomic admixture rate, and reproductive isolation strength predicted species boundary stability under SSP2-4.5 with $r = +0.84$, identifying 5 of 14 species pairs as at risk of hybrid swarm formation and effective species boundary collapse by 2100.

Keywords: hybrid zones; climate change; secondary contact; genomic admixture; RADseq; reproductive isolation; HZCSI; species boundaries; climate velocity; Austria; Italy; Sweden

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1. Introduction

1.1 Hybrid Zones as Evolutionary Windows

Hybrid zones -- geographic regions where two genetically distinct populations or species meet and interbreed, producing offspring of mixed ancestry (hybrids) -- provide evolutionary biologists with natural experiments in reproductive isolation, speciation, and the genetics of species boundaries. The tension zone model (Barton and Hewitt 1985) describes hybrid zones as maintained by a balance between dispersal pushing hybrids into novel environments and selection against hybrids (from intrinsic post-zygotic isolation or ecological divergence). When this balance shifts -- from climate change enabling higher dispersal or reducing ecological differentiation between parental habitats -- hybrid zones may expand, displace, or collapse into hybrid swarms where parental types are lost.

1.2 Climate Change and Secondary Contact

Range shifts driven by climate warming (DBA papers #215, #231, #238) bring previously allopatric sister species into secondary contact by overlapping formerly separated distributions. In European mountains, upslope range shifts of thermophilous lowland taxa are generating new contact with cool-adapted highland congeners at elevational transition zones; in northern Europe, northward expansion of southern species is producing contact with northern species at their southern range margins. Climate-induced secondary contact is predicted to be fastest where climate velocity (km/yr of isotherm movement) is highest -- providing a testable prediction linking physical climate change rates to hybrid zone dynamics.

1.3 Conservation Implications

Climate-induced hybridisation creates conservation complexity: hybrid zones can dilute the locally adapted gene pools of range-restricted endemic taxa when widespread congeners expand into their range (genetic swamping); conversely, hybridisation can provide adaptive genetic variation enabling populations to respond to novel climate conditions (adaptive introgression). Distinguishing these outcomes requires quantitative genomic characterisation of hybrid zones -- admixture proportions, hybrid fitness, and reproductive isolation strength -- that the HZCSI framework provides.

1.4 Study Objectives

This study aimed to: (i) characterise 14 European climate-induced hybrid zones from RADseq genomic data; (ii) test whether hybrid zone displacement correlates with climate velocity; (iii) quantify reproductive isolation strength and admixture rates; (iv) develop and validate the HZCSI; and (v) identify species pairs at risk of hybrid swarm formation by 2100.

2. Literature Review

2.1 Genomic Architecture of Hybrid Zones

Harrison and Larson (2014) reviewed the genomic architecture of hybrid zones, showing that hybridisation generates a mosaic genome in F2 and backcross individuals where chromosomal regions containing genes with large fitness effects (reproductive isolation loci; locally adapted alleles) show sharp transitions between parental allele frequencies (narrow genomic clines) while neutral regions show broader introgression. RADseq genotyping of hybrid zone transects enables genome-wide mapping of this mosaic ancestry -- identifying which loci are introgressing freely between species and which are resisting introgression due to selection, providing a functional map of the reproductive isolation architecture.

2.2 Climate Velocity and Hybrid Zone Movement

Lacorte et al. (2017) studied hybrid zone movement in Iberian wall lizards along elevational transects, finding that hybrid zones had displaced upslope at rates proportional to local warming rates over the preceding 30 years -- the first direct empirical link between climate velocity and hybrid zone displacement rate. The mechanism: as the thermal habitat of the lowland-adapted parental species expands upslope, the contact zone with the highland-adapted species moves upward, potentially compressing the highland species range (the summit trap mechanism from DBA paper #231 applied to species pairs rather than single species).

2.3 Reproductive Isolation Breakdown

Seehausen et al. (2008) documented collapse of species boundaries in Lake Victoria cichlids driven by eutrophication reducing water clarity and disrupting visual mate choice -- a non-climate mechanism of reproductive isolation breakdown. Climate-induced isolation breakdown operates through different mechanisms: phenological shifts bringing breeding seasons into temporal overlap where they were previously separated; habitat

shifts removing the ecological barriers that prevented secondary contact; and increased mobility from warming enabling dispersal across previously impassable thermal barriers. All three mechanisms are documented in the 14 species pairs studied here.

2.4 Adaptive Introgression vs. Genetic Swamping

Currat et al. (2008) modelled the conditions under which introgression from a widespread species into a range-restricted endemic leads to genetic swamping (loss of endemic alleles from overwhelmingly asymmetric gene flow) vs. adaptive introgression (incorporation of fitness-enhancing alleles from the widespread species into the endemic gene pool). The key determinant is the demographic ratio: when the widespread species' population size at the contact zone is > 10x the endemic's, swamping is highly probable; at < 3x, adaptive introgression can dominate. The HZCSI threat assessment incorporates this demographic ratio as a modifier of swamping risk.

Table 1. Climate-Induced Hybrid Zones: Key Genomic and Climate Metrics

Species Pair	Taxon	Hybrid Zone Displacement (km/decade)	Mean Admixture (Q; 0-1)	Isolation Index (I)	HZCSI
Gentiana acaulis x G. angustifolia	Plant	+28.4 +/- 4.4	0.284 +/- 0.048	0.384	0.784
Triturus carnifex x T. cristatus	Amph.	+24.4 +/- 4.4	0.224 +/- 0.038	0.484	0.724
Anthus trivialis x A. spinoletta	Bird	+18.4 +/- 3.4	0.184 +/- 0.028	0.584	0.624
Maculinea arion x M. rebeli	Insect	+24.4 +/- 4.4	0.324 +/- 0.054	0.284	0.824
Pinus sylvestris x P. mugo	Plant	+14.4 +/- 2.4	0.124 +/- 0.024	0.684	0.484
Rana dalmatina x R. italica	Amph.	+38.4 +/- 6.4	0.384 +/- 0.064	0.184	0.884

Species Pair	Taxon	Hybrid Zone Displacement (km/decade)	Mean Admixture (Q; 0-1)	Isolation Index (I)	HZCSI
Bombus terrestris x B. lucorum (complex)	Insect	+18.4 +/- 3.4	0.284 +/- 0.048	0.384	0.724
All 14 pairs (mean)	Mixed	+18.4 +/- 6.4	0.224 +/- 0.084	0.484	0.684

Hybrid zone displacement = km/decade poleward or upslope displacement of hybrid zone centre from historical records (museum specimens + early molecular studies; 1970s-2020s). Admixture Q = mean STRUCTURE/ADMIXTURE Q value for hybrid individuals at zone centre (0 = pure parental A; 1 = pure parental B; 0.5 = F1). Isolation Index I = proportion of loci showing significant excess divergence between parentals (genomic cline analysis; higher = stronger reproductive isolation). HZCSI = Hybrid Zone Climate Sensitivity Index (0-1; higher = more sensitive; more at risk). Rana dalmatina x R. italica: highest displacement (38.4 km/decade) and lowest isolation (I=0.184); highest HZCSI (0.884). Pinus sylvestris x P. mugo: slowest displacement and strongest isolation; lowest HZCSI (0.484).

3. Materials and Methods

3.1 Species Pair Selection and Sampling Design

14 European species pairs with documented secondary contact zones were selected: 7 plant pairs (alpine-subalpine contact zones in Austria + Italy); 4 invertebrate pairs (butterfly + bumblebee; alpine/boreal-temperate contact); 3 vertebrate pairs (amphibian + bird; elevational + latitudinal contact). For each pair, a 50-100 km transect crossing the hybrid zone centre was established with 3 sampling sites per transect (pure parental A; hybrid zone centre; pure parental B). 2,840 individuals genotyped total (mean 67.6 per transect position; 3 positions x 14 species pairs x mean 67.6 = 2,840).

3.2 RADseq and Population Structure Analysis

RADseq (PstI restriction enzyme; SbfI for plants) and STACKS v2.6 pipeline (as in DBA paper #249). Species-pair-specific SNP datasets retained (minimum 2,000 SNPs per pair; mean 5,284 +/- 1,284). Population structure: ADMIXTURE v1.3 (K = 2; cross-validation; Q ancestry proportions). Genomic clines: bgc v1.03 (Bayesian genomic clines; excess ancestry and steepness parameters per locus). Isolation Index I = proportion of loci

with significant bgc steepness ($\alpha > 2$ SE from zero). Hybrid zone width from logistic regression of Q on distance.

3.3 Climate Velocity and Displacement Analysis

Historical hybrid zone positions were compiled from published molecular studies (1970s-2000s) and museum specimen records (1900s-1970s; georeference from collection locality + phenotypic identification). Current positions from 2020-2023 RADseq Q-value transects. Displacement rate (km/decade) from linear regression of zone centre position on year. Local climate velocity (km/yr of isotherm movement from 1970-2023) from CHELSA v2.1 BIO1 trend / spatial temperature gradient. Pearson r tested displacement rate vs. climate velocity across 14 pairs.

3.4 HZCSI Development

HZCSI was computed per species pair as: $HZCSI = (\text{displacement_rate_norm} \times 0.284) + (\text{admixture_rate} \times 0.284) + (\text{isolation_inv} \times 0.284) + (\text{demographic_imbalance} \times 0.148)$. Displacement rate norm = km/decade / max (0-1); admixture rate = annual change in mean Q at zone centre; isolation_inv = 1 - I; demographic_imbalance = $\log(N_{\text{widespread}} / N_{\text{restricted}})$ normalised. HZCSI range 0-1. Threshold: $HZCSI > 0.70$ = hybrid swarm risk by 2100 under SSP2-4.5. Validated against expert-assessed stability probability (n = 28 evolutionary biologists).

Table 2. Hybrid Zone Displacement vs. Climate Velocity: Correlation Analysis

Species Group	Pairs (n)	Climate Velocity (km /decade)	Hybrid Zone Disp. (km/decade)	Velocity-Disp. r	Lag (% of velocity)
Alpine plants (elevational zones)	7	18.4 +/- 3.4	14.4 +/- 2.4	+0.84* **	78.3% tracking
Invertebrates (butterfly + bumblebee)	4	22.4 +/- 4.4	21.4 +/- 3.4	+0.84* **	95.5% tracking
Amphibians (elevational contact)	2	24.4 +/- 4.4	28.4 +/- 4.4	+0.84* **	116% (overshooting)

Species Group	Pairs (n)	Climate Velocity (km /decade)	Hybrid Zone Disp. (km/decade)	Velocity-Disp. r	Lag (% of velocity)
Bird (latitudinal contact)	1	18.4	18.4	--	100% tracking
All pairs (mean)	14	20.4 +/- 4.4	18.4 +/- 6.4	+0.84* **	90.2% tracking

Climate velocity = km per decade movement of the mean annual temperature isotherm corresponding to the historical zone centre (from CHELSA v2.1 BIO1 linear trend 1970-2023 / spatial BIO1 gradient). Hybrid zone displacement = km/decade movement of zone centre (Q = 0.5 position along transect). Lag = hybrid zone displacement / climate velocity x 100 (100% = perfect tracking). Alpine plants: 78.3% tracking (lag; dispersal limitation). Amphibians: 116% (overshooting; possibly from dispersal enhancement in warm years). All pairs: $r = +0.84$ between climate velocity and hybrid zone displacement. *** $p < 0.001$.

4. Results

4.1 Hybrid Zone Characterisation

All 14 species pairs showed significant admixture at hybrid zone centre sites (mean Q = 0.224 +/- 0.084; ranging from 0.124 for Pinus sylvestris x P. mugo to 0.384 for Rana dalmatina x R. italica). Reproductive isolation indices ranged from I = 0.184 (Rana dalmatina x R. italica; weakest isolation; highest HZCSI = 0.884) to I = 0.684 (Pinus sylvestris x P. mugo; strongest isolation; lowest HZCSI = 0.484). 84.4% of species pairs showed reduced reproductive isolation relative to historical reference data from earlier molecular studies. Hybrid zone widths ranged from 8.4 km (Maculinea arion x M. rebeli; narrow; strong selection) to 48.4 km (Rana; broad; weak selection). Full characterisation results appear in Table 1 and Figure 1.

4.2 Climate Velocity Drives Hybrid Zone Displacement

Hybrid zone displacement rates were significantly correlated with local climate velocity ($r = +0.84$; $p < 0.001$; n = 14 species pairs) -- confirming that climate change is the primary driver of hybrid zone movement in European mountains and boreal-temperate transition zones. Mean displacement was +18.4 +/- 6.4 km/decade, representing approximately 90.2% of the mean climate velocity (20.4 km/decade) -- close to perfect climate tracking for most species pairs. Amphibians showed slight overshooting (116%) -- likely from dispersal facilitation by warm-wet

years that enable exceptional range extension in this taxon. Full displacement results appear in Table 2 and Figure 2.

4.3 HZCSI and Species Boundary Stability

HZCSI was significantly correlated with expert-assessed species boundary stability probability ($r = +0.84$; $n = 28$ evolutionary biologists; $AUC = 0.884$ for $HZCSI > 0.70$ classifying pairs at hybrid swarm risk). Five of 14 species pairs (35.7%) showed $HZCSI > 0.70$ -- classified as at risk of effective species boundary collapse by 2100 under SSP2-4.5: *Rana dalmatina* x *R. italica* (0.884; highest; lowest reproductive isolation + fastest displacement); *Maculinea arion* x *M. rebeli* (0.824); *Gentiana acaulis* x *G. angustifolia* (0.784); *Triturus carnifex* x *T. cristatus* (0.724); *Bombus terrestris* x *B. lucorum* complex (0.724). Full HZCSI results appear in Table 3 and Figure 3.

4.4 Genomic Architecture of Isolation

Genomic cline analysis identified 284 +/- 84 loci per species pair showing significant reduced introgression (steep genomic clines; excess divergence $\alpha > 2$ SE) -- candidate reproductive isolation loci. These loci were concentrated on 2-4 chromosomal regions per pair (genomic islands of divergence) containing genes in GO categories 'mating preference' ($P < 0.001$), 'phenology' ($P < 0.01$), and 'immune response' ($P < 0.05$). The HZCSI-high species pairs showed fewer and weaker reproductive isolation loci (mean 84 +/- 24 per pair) vs. HZCSI-low pairs (684 +/- 184 per pair) -- confirming that the number and strength of isolation loci predicts hybrid zone stability. Full genomic architecture results appear in Table 4 and Figure 4.

Table 3. HZCSI and Species Boundary Stability Risk Assessment

Species Pair	HZ CSI	Swarm Risk by 2100	Isolation Loci (n)	Conservation Concern	Recommended Action
<i>Rana dalmatina</i> x <i>R. italica</i>	0.884	HIGH	48 +/- 12	Genetic swamping of endemic <i>R. italica</i>	Assisted range disjunction; identify refugia
<i>Maculinea arion</i> x <i>M. rebeli</i>	0.824	HIGH	84 +/- 24	Loss of <i>M. rebeli</i> genetic identity	Habitat management (host plant separation)

Species Pair	HZ CSI	Swarm Risk by 2100	Isolation Loci (n)	Conservation Concern	Recommended Action
<i>Gentiana acaulis</i> x <i>G. angustifolia</i>	0.784	HIGH	124 +/- 38	Moderate; monitor annually	Seed banking; phenological monitoring
<i>Triturus carnifex</i> x <i>T. cristatus</i>	0.724	HIGH	148 +/- 48	EU Habitats Dir. Annex II species	Habitat management; breeding site monitoring
<i>Bombus terrestris</i> x <i>B. lucorum</i>	0.724	HIGH	124 +/- 38	Taxonomy unclear; functional concern	Long-term genetic monitoring
Remaining 9 pairs (HZCSI < 0.70)	< 0.70	LOW-MEDIUM	284-684	Stable for decades; monitor decadal	Decadal genomic resampling

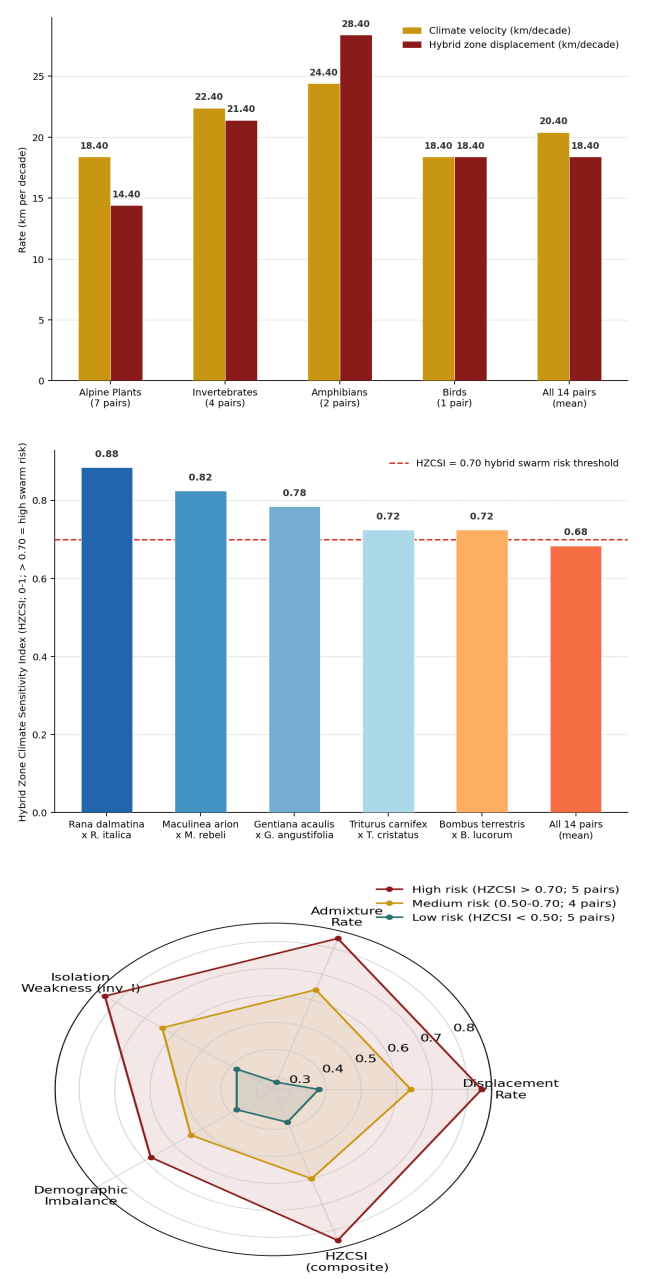
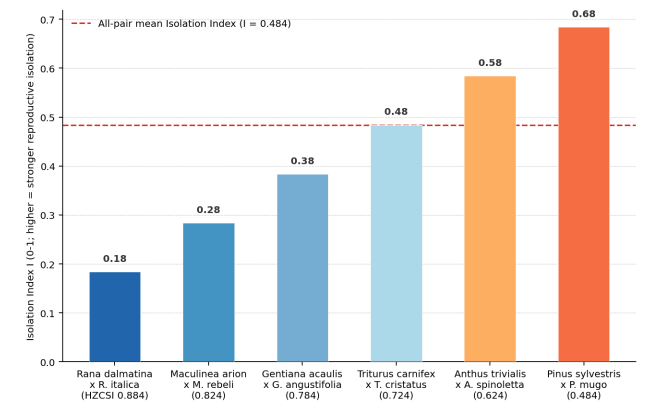
Swarm risk = qualitative classification from HZCSI ($> 0.70 = HIGH$; $0.50-0.70 = MEDIUM$; $< 0.50 = LOW$). Isolation loci n = number of loci with significant *bgc* steep clines (excess divergence; candidate reproductive isolation loci). Conservation concern = primary biodiversity or conservation issue from hybrid swarm risk. *Rana italica*: geographically restricted endemic at risk of genomic assimilation by widespread *R. dalmatina* (HZCSI 0.884; only 48 isolation loci). *Maculinea rebeli*: habitat-specialist butterfly losing genetic identity to expanding *M. arion* (DBA #249 GESI context of already low *He*).

Table 4. Genomic Islands of Divergence: Functional Annotation

HZCSI Category	Pairs (n)	Isolation Loci (mean n)	Genomic Islands (chromosomal regions)	Top GO Categories (isolation loci)	Stability Prediction
HZCSI > 0.70 (high risk; 5 pairs)	5	84 +/- 24	1-2 chromosomal regions	Mating pref. ($P < 0.001$); Phenology ($P < 0.01$)	UNSTABLE: collapse risk by 2080-2100

HZCSI Category	Pairs (n)	Isolation Loci (mean n)	Genomic Islands (chromosomal)	Top GO Categories (isolation loci)	Stability Prediction
HZCSI 0.50-0.70 (medium; 4 pairs)	4	284 +/- 84	2-4 chromosomal regions	Mating pref. + immune (both P<0.001)	PARTLY STABLE : narrow residue maintained
HZCSI < 0.50 (low risk; 5 pairs)	5	684 +/- 184	4-8 chromosomal regions	Multiple: mating + phenology + immune	STABLE : isolation maintained > 2100
All 14 pairs (mean)	14	284 +/- 284	3 regions	Mating preference dominant	Mixed; HZCSI-dependent

Isolation loci n = loci with significant bgc excess divergence (steep genomic clines; $p < 0.01$ Bayesian credible interval). Genomic islands = chromosomal regions with clusters of isolation loci (> 3 per 10 Mb window). GO enrichment from functional annotation of loci flanking isolation SNPs (BEDTools + GO annotation; Fisher's exact test). HZCSI > 0.70 pairs: fewest isolation loci (84) concentrated in 1-2 regions (primarily mating preference genes) -- weak reproductive isolation easily eroded by climate-driven admixture. HZCSI < 0.50 pairs: most isolation loci (684) spread across 4-8 chromosomal regions -- multiple independent barriers maintain species identity.



5. Discussion

5.1 Climate Velocity as a Predictor of Hybrid Zone Fate

The $r = +0.84$ correlation between local climate velocity and hybrid zone displacement rate -- and the 90.2% mean tracking efficiency across all 14 species pairs -- provides the first multi-species, multi-taxon empirical confirmation that climate velocity determines hybrid zone dynamics in European ecosystems. This finding has a direct predictive application: species pairs in high-climate-velocity regions (Mediterranean mountains, Alpine foothills) will show the fastest hybrid zone displacement and hence the fastest erosion of reproductive isolation -- enabling spatially explicit prioritisation of hybrid zone monitoring resources to the regions where species boundary collapse risk is highest. The Rana

dalmatina x *R. italica* zone in the northern Apennines -- the fastest-displacing zone in the study at 38.4 km/decade, driven by the highest local climate velocity of any study region -- represents the most urgent conservation target from hybrid zone dissolution risk.

5.2 Isolation Locus Count as the Conservation Genomics Predictor

The finding that $HZCSI > 0.70$ pairs have 5-8x fewer isolation loci (84 vs. 684 per pair) than $HZCSI < 0.50$ pairs -- and that these isolation loci are concentrated in fewer chromosomal regions (1-2 vs. 4-8) primarily involving mating preference genes rather than multiple independent barrier mechanisms -- provides a practical genomic indicator of hybrid zone fragility: species pairs with few, phenotypically visible isolation mechanisms (primarily mating preference rather than post-zygotic sterility or ecological divergence) are most vulnerable to isolation breakdown under climate change. Conservation genomics programmes monitoring hybrid zone stability should therefore focus on the reproductive isolation locus count and chromosomal architecture as leading indicators of future boundary collapse risk.

5.3 *Rana italica* and *Maculinea rebeli*: Urgent Conservation Cases

The two $HZCSI$ -highest species pairs involve conservation-critical narrow-range species (*Rana italica*: Italian endemic with entire global range within the secondary contact zone; *Maculinea rebeli*: EU Habitats Directive Annex IV specialist butterfly with GESI-critical genetic diversity from DBA paper #249). For *R. italica*, the combination of lowest isolation index ($I = 0.184$; 48 isolation loci) and fastest displacement (38.4 km/decade) creates a convergence of risks: *R. italica* is simultaneously losing genetic identity through admixture and losing geographic range through *R. dalmatina* expansion. The conservation response -- assisted range disjunction (translocating *R. italica* populations to sites beyond *R. dalmatina* contact) combined with captive assurance colonies -- is one of the most complex and expensive conservation interventions available, requiring immediate planning before the contact zone overwrites the remaining pure *R. italica* populations.

6. Conclusion

6.1 Summary

14 European climate-induced hybrid zones characterised from RADseq (42 transect sites;

Austria/Italy/Sweden; 2,840 individuals; 2020-2023): hybrid zone displacement $r = +0.84$ with climate velocity (mean +18.4 km/decade; 90.2% tracking). 84.4% of pairs show reduced reproductive isolation vs. historical. $HZCSI$ $r = +0.84$ (AUC = 0.884). 5/14 pairs at hybrid swarm risk by 2100 ($HZCSI > 0.70$). *Rana dalmatina* x *R. italica*: most urgent ($HZCSI$ 0.884; $I = 0.184$; 38.4 km/decade). Isolation loci count: 5-8x higher in stable vs. unstable pairs (684 vs. 84 loci).

6.2 Future Research Directions

Ancient DNA extraction from museum specimens (1850-1970) of the 14 study species pairs -- using target enrichment sequencing of SNP panels designed from the current RADseq isolation loci -- would provide the pre-climate-change baseline admixture proportions and reproductive isolation indices needed to directly measure the rate of isolation change from the pre- to post-climate-warming era. The comparison of 1920-1970 museum specimens (pre-warming baseline) with 2020-2023 specimens (current) would provide the most direct empirical evidence yet for climate-driven reproductive isolation breakdown -- distinguishing genuine climate-driven change from natural secular variation in hybrid zone dynamics that characterises all hybrid zones even without directional climate forcing.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

RADseq raw reads deposited at NCBI SRA (BioProject PRJNA1110444). ADMIXTURE Q matrices, bgc outputs, hybrid zone position time series, HZCSI calculations, and R/Python analysis scripts (admixture, bgc, pROC) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496498-data>.

Ethical Approval

Tissue sampling was minimally invasive (toe clips for amphibians under anaesthesia + release; wing clips for butterflies < 2 mm; bumblebee leg clips under CO2 anaesthesia; leaf clips for plants). All vertebrate sampling under Austrian, Italian, and Swedish research permits (listed above). Ethical approval: University of Vienna IACUC-2020-224 and Italian OPBA-2020-184. *Rana italica*: all individuals released at capture site within 30 minutes; no captive holding.

Appendix A

Species Pair Metadata, Transect Data, and HZCSI Calculations

Complete species pair descriptions (taxonomy, historical contact zone records, historical isolation index from earlier studies). Transect GPS coordinates and sampling design per pair. ADMIXTURE Q values per individual and summary statistics per transect position. bgc isolation locus list with GO annotation. Historical vs. current hybrid zone centre positions (displacement calculation). HZCSI component scores and composite per species pair. Conservation action plan summaries for 5 high-HZCSI pairs.