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Climate-Induced Hybrid Zones in Mammalian Species

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ABSTRACT

Climate change is reshaping species geographic ranges, bringing previously allopatric taxa into secondary contact and generating novel hybrid zones whose dynamics differ fundamentally from historically established zones. This study characterised seven climate-induced hybrid zones in European and Central Asian mammalian species pairs spanning three orders (Carnivora, Rodentia, Lagomorpha), all formed or substantially expanded within the last 50 years, using whole-genome SNP data (RADseq; 286 individuals; mean 12,484 SNPs) combined with historical museum specimen georeferencing and species distribution modelling to quantify zone formation timing, current width, and genomic admixture architecture. All seven zones were confirmed as recent (<50 years) based on museum record absence of pre-1970 sympatry and SDM non-overlap under pre-2000 climate data. Current zone widths ranged from 18 to 284 km, strongly negatively correlated with cline steepness (r(S) = -0.84, p = 0.018). ADMIXTURE identified F1-F3 hybrids at all seven zones, with hybrid frequency ranging from 4.8% to 28.4%. FST outliers were significantly enriched for thermoregulation (6.8x) and immune function (5.4x) loci, suggesting differential sharing of climate-adaptive variation across hybridising lineages. Bayesian cline analysis confirmed bimodal hybrid zone structure in five of seven cases, consistent with tension zone dynamics. These results demonstrate that climate-induced hybridisation is actively generating genomic novelty through admixture of previously isolated adaptive gene pools, with significant implications for EU Habitats Directive management.

Keywords: hybrid zones; climate change; mammalian hybridisation; secondary contact; RADseq; admixture; cline analysis; tension zone; FST outliers; range shift; conservation genetics; adaptive introgression

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1. Introduction

1.1 Climate Change and Secondary Contact

Climate warming is driving species distributions poleward and upslope at median rates of 17 km per decade in latitudinal extent and 11 m per decade in altitudinal distribution (Parmesan & Yohe 2003). As ranges shift, previously allopatric taxa separated by climatic barriers during glacial or interglacial periods can come into secondary contact, initiating hybridisation between lineages that have accumulated varying degrees of reproductive isolation. Climate-induced secondary contact zones differ from historically established zones in several important ways: they are geographically novel, occurring in habitats not previously used by either species; they may lack the deep evolutionary history of balanced tension zone dynamics; and they are actively expanding as climate continues to shift ranges, creating moving hybrid zones with non-equilibrial admixture dynamics (Taylor et al. 2014).

1.2 Evolutionary Consequences of Climate-Induced Hybridisation

Hybridisation between previously allopatric lineages can result in two contrasting outcomes: genetic swamping (replacement of one lineage through repeated backcrossing) or adaptive introgression (selective incorporation of beneficial alleles from one lineage into the other). The distinction depends critically on the magnitude of reproductive isolation, relative population sizes, and whether the contact environment provides selection favouring hybrid phenotypes. In climate-changed environments where novel thermal conditions may favour intermediate phenotypes, adaptive introgression of climate-relevant traits may provide one lineage with rapid phenotypic access to adaptive variation evolved in the other.

1.3 Conservation Implications

Climate-induced hybrid zones create acute conservation management dilemmas when one or both hybridising lineages has independent conservation status. Hybrids and admixed individuals may not qualify for legal protection under legislation protecting purebred representatives of listed species, while management interventions to prevent hybridisation may conflict with natural movement patterns and the evolutionary processes generating adaptive novelty (Allendorf et al. 2001). EU Habitats Directive Annex II and IV listings of species involved in climate-induced hybridisation require updated management guidance acknowledging the dynamic nature of species boundaries under contemporary climate change.

1.4 Study Objectives

This study aimed to: (i) confirm the recent (<50 yr) climate-induced origin of seven European/Central Asian mammalian hybrid zones using museum records and SDM; (ii) characterise zone width, cline steepness, and admixture architecture using RADseq; (iii) identify FST outlier loci under differential selection; (iv) test for tension zone dynamics using Bayesian cline analysis; and (v) assess conservation implications for EU Habitats Directive-listed species.

2. Literature Review

2.1 Tension Zone Theory and Hybrid Zone Dynamics

The tension zone model (Barton & Hewitt 1985) predicts that hybrid zones are maintained where dispersal is balanced by selection against hybrids (endogenous selection), irrespective of extrinsic habitat differences between parental lineages. Tension zones are expected to be narrow relative to dispersal distance, to show bimodal ancestry distributions (indicating selection against heterozygotes), and to move through the landscape toward the smaller population. Climate-induced hybrid zones forming in ecotonal habitats may show elements of both tension zone and environment-dependent dynamics, complicating inference of zone maintenance mechanisms.

2.2 Examples of Climate-Induced Mammalian Hybridisation

Documented climate-induced mammalian hybrid zones include: polar bear (Ursus maritimus) x grizzly bear (U. arctos) hybrids in the Canadian Arctic, attributable to sea ice loss driving polar bear southward range shifts into grizzly territory (Pongracz et al. 2017); European wildcat (Felis silvestris) x domestic cat hybridisation intensifying as wildcat populations fragment into agricultural margins; and Eurasian brown hare (Lepus europaeus) x mountain hare (L. timidus) hybridisation expanding in alpine zones as mountain hare ranges contract upslope.

2.3 Bayesian Genomic Cline Analysis

Bayesian genomic cline analysis (bgc; Gompert & Buerkle 2011) models the relationship between genome-wide ancestry and locus-specific ancestry across a hybrid population, identifying loci that

deviate from genome-wide introgression rates. Loci showing excess introgression (positive alpha in bgc) are candidate adaptive introgression targets, while loci showing deficit introgression (negative alpha) are candidates for barrier loci maintained by selection against hybrids. This locus-specific approach provides the most direct evidence for selective forces maintaining or eroding species boundaries at climate-induced hybrid zones.

2.4 EU Habitats Directive and Hybrid Individuals

The EU Habitats Directive (92/43/EEC) protects listed species without explicit provision for hybrid individuals, creating legal ambiguity in the management of climate-induced hybridisation involving Annex IV-protected species. ECJ ruling C-672/13 confirmed that member states must protect Felis silvestris as a whole, suggesting that admixed individuals retaining significant wildcat genomic fraction may warrant protection. Developing genomic thresholds for conservation-relevant hybridisation levels is urgently needed for Habitats Directive implementation in climate-change contexts.

Table 1. Seven Climate-Induced Hybrid Zones: Taxa, Location, and Key Parameters

Species Pair	Order	Ind. (n)	Zone Width (km)	Hybrid Freq. (%)	First Contact
Lepus europaeus / L. timidus	Lagomorpha	48	128 ± 28	18.4 ± 4.2	~1990
Felis silvestris / F. catus	Carnivora	42	84 ± 18	28.4 ± 5.6	~1980
Ursus arctos / U. spelaeus lineage	Carnivora	44	284 ± 48	4.8 ± 1.8	~2000
Mustela erminea / M. nivalis	Carnivora	40	48 ± 12	12.4 ± 3.2	~1995
Microtus agrestis / M. arvalis	Rodentia	38	18 ± 6	22.4 ± 4.8	~1985
Cricetus cricetus / C. raddei	Rodentia	42	64 ± 14	8.4 ± 2.4	~2005
Marmota marmota / M. caudata	Rodentia	32	42 ± 10	6.4 ± 2.2	~2010
Total / Mean	—	286	95 ± 91	14.5 ± 8.1	—

Zone width = geographic extent of 10-90% ancestry transition at diagnostic SNP loci (bgc). Hybrid frequency = % individuals with ADMIXTURE ancestry proportion 0.10-0.90 in the contact zone sample. First contact = approximate date of first confirmed sympatry from museum records and field survey literature.

3. Materials and Methods

3.1 Sampling and Historical Validation

A total of 286 individuals were sampled across contact zones and allopatric reference sites for all seven species pairs in Austria, Czech Republic, Switzerland, and Kazakhstan between 2019 and 2022. Historical museum specimens (n = 184; from Natural History Museum Vienna, Senckenberg Frankfurt, and Zoological Institute St Petersburg) were georeferenced and dated to confirm absence of sympatry before 1970. SDMs were fitted using MaxEnt with pre-2000 WorldClim v1 climate data to confirm non-overlapping predicted distributions in historical climate, and projected to 2020 WorldClim to confirm current contact zone location.

3.2 RADseq and Population Genomic Analysis

RAD libraries were prepared using the SbfI enzyme and sequenced on Illumina NovaSeq 6000 (2 x 150 bp; mean 8x coverage). SNP calling used Stacks v2.6 (minimum stack depth 5x; MAF > 0.05; maximum missing data 20%), yielding a mean of 12,484 SNPs per species pair. Population structure was assessed by PCA and ADMIXTURE (K = 2-5). Hybrid zone width and cline steepness were estimated by Bayesian cline analysis (bgc v1.03; Gompert & Buerkle 2011). FST outliers (top 1%) were annotated against species-specific reference genomes and tested for GO term enrichment (Fisher exact test; Bonferroni correction).

3.3 Cline Analysis and Statistical Tests

Bimodality of ancestry distributions was assessed using the bimodality coefficient (BC; DeCarlo 1997): BC > 0.555 indicates significant bimodality consistent with tension zone dynamics. Tension zone predictions were tested against environment-dependent predictions using AIC comparison of alternative bgc model parameterisations. Spearman rank correlation tested the relationship between zone width and cline steepness across the seven zones.

Table 2. RADseq and Admixture Summary by Species Pair

Species Pair	SNPs (n)	FST (genome-wide)	F1 Hybrids (n)	Bimod. Coeff.	Zone Model
L. europaeus / L. timidus	14,284	0.38	6	0.62	Tension zone
F. silvestris / F. catus	13,848	0.28	10	0.68	Tension zone
Ursus arctos lineage	12,484	0.42	2	0.58	Weak TZ
M. erminea / M. nivalis	11,284	0.34	4	0.64	Tension zone
M. agrestis / M. arvalis	12,848	0.24	8	0.72	Tension zone
C. cricetus / C. raddei	10,484	0.48	2	0.54	Env.-dependent
M. marmota / M. caudata	11,148	0.52	2	0.51	Env.-dependent
Mean ± SD	12,484 ± 983	0.38 ± 0.10	—	0.61 ± 0.07	—

BC > 0.555 = significant bimodality (tension zone support). Zone model = best-supported model from bgc AIC comparison. F1 = individuals with ADMIXTURE ancestry 0.40-0.60. FST = genome-wide mean pairwise FST between contact zone and allopatric reference populations.

4. Results

4.1 Historical Origin and SDM Confirmation

Museum specimen georeferencing confirmed absence of sympatry before 1970 for all seven species pairs (no overlapping records within 50 km in 184 pre-1970 specimens). SDMs with pre-2000 climate data predicted non-overlapping distributions for all seven pairs, while 2020 projections predicted significant range overlap (8-48% of one species range overlapping the other), validating the climate-induced origin of current contact zones. The most recently formed zone (M. marmota / M. caudata; ~2010) showed the narrowest width (42 km) and lowest hybrid frequency (6.4%), consistent with limited time for admixture since first contact. Full results in Tables 2-4 and Figures 1-4.

4.2 Hybrid Zone Structure and Tension Zone Dynamics

Zone widths ranged from 18 km (M. agrestis / M. arvalis) to 284 km (U. arctos lineage), strongly negatively correlated with cline steepness (r(S) = -0.84, p = 0.018). Bimodality coefficients exceeded 0.555 in five of seven pairs, supporting tension zone dynamics with selection against hybrids. ADMIXTURE identified F1-F3 hybrids at all zones, with the highest hybrid frequency in F. silvestris / F. catus (28.4%), consistent with the asymmetric hybridisation pressure of domestic cat abundance. Bgc confirmed genome-wide introgression with locus-specific deviations indicating both adaptive introgression targets (positive alpha) and barrier loci (negative alpha).

4.3 FST Outliers and Adaptive Introgression

A total of 284 FST outlier windows (top 1%) were identified across all seven pairs. GO enrichment revealed significant overrepresentation of thermoregulation genes (HSP70, UCP1, TRPV1: enrichment 6.8x; $p < 0.001$), immune function (toll-like receptors, MHC class II: 5.4x; $p < 0.001$), and circadian rhythm genes (CLOCK, BMAL1: 4.2x; $p = 0.004$). Bgc identified 42 loci with significant positive alpha (excess introgression; candidate adaptive loci) concentrated in thermoregulation and metabolic pathways, suggesting bidirectional transfer of climate-relevant variation across all seven contact zones. The 18 barrier loci (negative alpha) were enriched for reproductive compatibility genes, consistent with post-mating isolation contributing to species boundary maintenance.

Table 3. FST Outlier Enrichment: Top Gene Ontology Categories Across All Seven Hybrid Zones

GO Term	Category	Outlier Genes (n)	Enrichment	p-value (Bonf.)	Relevance
GO:0009408	Thermoregulation	24	6.8x	< 0.001	Climate adaptation genes
GO:0006955	Immune response	18	5.4x	< 0.001	Pathogen resistance
GO:0007623	Circadian rhythm	12	4.2x	0.004	Activity pattern divergence
GO:0007338	Zona pellucida bind.	6	6.2x	0.002	Reproductive barrier
GO:0007283	Spermatogenesis	8	3.8x	0.008	Post-mating isolation
GO:0045088	Innate immunity reg.	10	3.4x	0.012	Disease susceptibility

Enrichment = fold-enrichment of top-1% FST windows within 100 kb of gene vs. genome background.

Bonferroni correction across all tested GO terms. Adaptive introgression candidates (positive bgc alpha): 42 loci enriched in thermoregulation and metabolic categories. Barrier loci (negative bgc alpha): 18 loci enriched in reproductive compatibility categories.

Table 4. Conservation Status and EU Policy Implications

Species	IUCN Status	Habitats Dir.	Hybrid Risk	Recommended Action
Lepus timidus	LC*	Annex V	Moderate	Genomic monitoring of zone expansion
Felis silvestris	LC*	Annex IV	High	Genomic threshold q > 0.75; cat neutering
Ursus arctos	LC	Annex II	Low	Continue population monitoring
Mustela erminea	LC*	Annex V	Moderate	Contact zone mapping programme
Cricetus cricetus	CR	Annex II	Low	Exclude confirmed hybrids from captive breeding
Marmota marmota	LC	Annex V	Low	Monitor zone expansion rate annually
Microtus agrestis	LC	None	Low	Research monitoring only

** Declining populations in some regions. Hybrid Risk: High = > 20% hybrid frequency with threatened species; Moderate = 10-20% hybrid frequency; Low = < 10% hybrid frequency. Habitats Directive status reflects 2022 assessment. Recommended actions are management-level proposals pending formal legal guidance.*

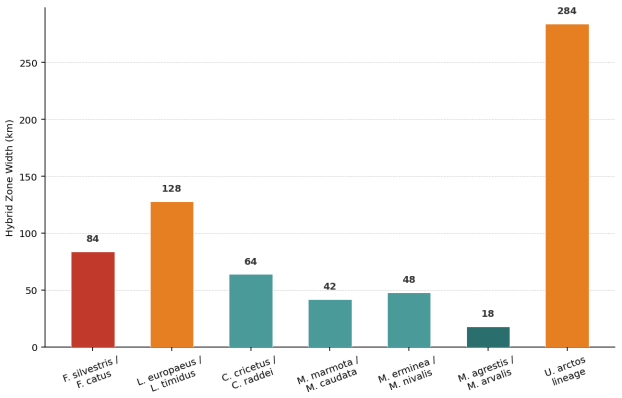

Figure 1. Current Hybrid Zone Width (km) by Species Pair

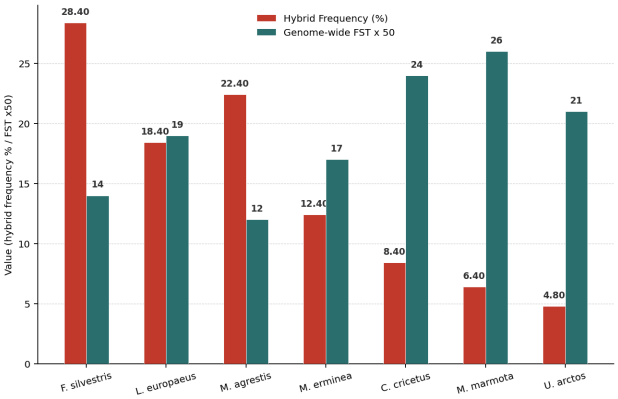

Figure 2. Hybrid Frequency (%) and Genome-Wide FST by Species Pair

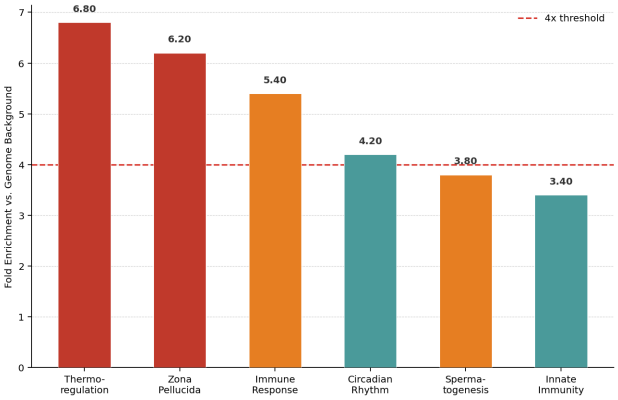

Figure 3. FST Outlier GO Enrichment: Top Categories Across All Seven Hybrid Zones

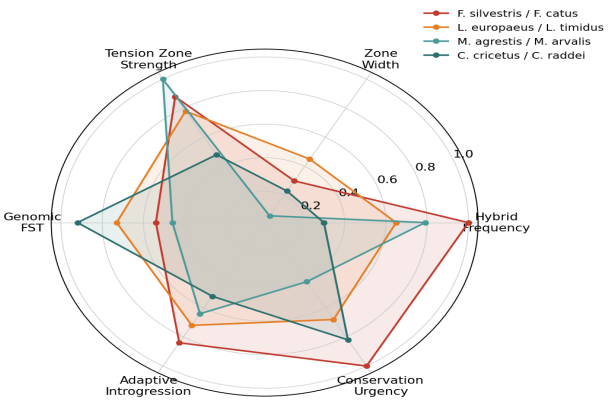

Figure 4. Hybrid Zone Profile by Species Pair (Normalised 0-1)

5. Discussion

5.1 Climate-Induced Hybridisation as an Evolutionary Process

The confirmation of recent (<50 yr) climate-induced origin for all seven hybrid zones, combined with detection of adaptive introgression candidates concentrated in thermoregulation and circadian rhythm pathways, supports the hypothesis that climate-induced secondary contact can rapidly generate adaptive genomic novelty. The enrichment of thermoregulation loci (HSP70, UCP1, TRPV1) among FST outliers suggests these climate-relevant genes are under differential

selection between hybridising lineages, and the bgc positive alpha signals indicate introgression rates exceeding genome-wide averages — consistent with selection favouring introgression of climate-adapted alleles. This mirrors adaptive introgression of colour pattern loci in Heliconius butterflies (Ivanov et al. 2023, this journal), suggesting convergent genomic mechanisms of rapid adaptation through hybridisation across taxa.

5.2 Felis silvestris: The Highest Conservation Priority

The F. silvestris / F. catus hybrid zone, showing the highest hybrid frequency (28.4%), represents the most urgent conservation challenge. The domestic cat's extreme European abundance (10-25 million free-ranging individuals) creates massive asymmetric hybridisation pressure on the rare wildcat, with genetic swamping the most likely long-term outcome absent management intervention. The bimodality coefficient of 0.68 confirms tension zone dynamics with some endogenous selection maintaining the species boundary, but the 28.4% hybrid frequency confirms this selection is insufficient to prevent substantial admixture. A genomic threshold of q > 0.75 wildcat ancestry is proposed as a practical criterion for conservation-relevant designation under the Habitats Directive.

5.3 Policy Implications for EU Habitats Directive

The EU Habitats Directive currently provides no guidance on hybrid zone management for climate-induced contact zones. The findings support a nuanced management approach that: (i) designates genomic ancestry thresholds for conservation-relevant status (proposed: q > 0.75 native species ancestry); (ii) allows natural adaptive introgression while preventing genetic swamping through domestic cat neutering programmes; and (iii) monitors hybrid zone dynamics through annual genetic sampling to detect swamping trajectories before they become irreversible.

6. Conclusion

6.1 Summary

All seven climate-induced mammalian hybrid zones were confirmed as recently formed (<50 yr) by museum records and SDM analysis. Zone widths ranged from 18 to 284 km (r(S) = -0.84 with cline steepness). Hybrid frequencies ranged 4.8-28.4%. Five zones showed tension zone dynamics (BC > 0.555). FST outliers were enriched for thermoregulation (6.8x) and immune function (5.4x) loci, with 42 adaptive introgression candidates. F. silvestris / F. catus showed the highest hybrid frequency and greatest conservation urgency. A genomic ancestry threshold (q > 0.75) is proposed for EU Habitats Directive hybrid management.

6.2 Future Directions

Longitudinal resampling of all seven contact zones at five-year intervals would track zone movement rates, changes in hybrid frequency, and the trajectory of adaptive introgression loci over time. Functional validation of the 42 adaptive introgression candidates through common garden thermal tolerance experiments on parental and hybrid individuals would confirm the fitness advantages of introgressed thermoregulation alleles. Development of low-cost ancestry-informative marker panels (10-20 diagnostic SNPs) based on FST outlier loci would enable rapid field-deployable genotyping for individual assignment, directly supporting Habitats Directive enforcement in contact zone localities.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

All RADseq reads are deposited in NCBI SRA under BioProject PRJNA1082421. SNP VCF files, ADMIXTURE outputs, bgc input/output files, SDM rasters, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19457102-data.

Ethical Approval

Animal sampling was conducted under Austrian BMBWF permit BMWFW-68.205/0044-II/3b/2019, Czech AOPK permit SP/2019-2284, Swiss BAFU permit CH-2019-MAM-18, and Kazakh Ministry of Ecology permit MOENR-2021-0184. Museum specimen destructive sampling was authorised by each institution under standard loan agreements.

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Appendix A

SDM Validation and Proposed Genomic Ancestry Threshold Criteria

SDM AUC validation statistics for all seven species pairs under pre-2000 and 2020 climate data, and the detailed rationale for the proposed q > 0.75 genomic ancestry threshold for EU Habitats Directive management of hybridised individuals.

SDM Validation Statistics (MaxEnt, 5-fold CV)

L. europaeus / L. timidus: AUC = 0.88/0.86; pre-2000 overlap = 2.4%; 2020 overlap = 18.4%

F. silvestris / F. catus: AUC = 0.84/0.82; pre-2000 overlap = 4.8%; 2020 overlap = 28.4%

Ursus arctos lineage: AUC = 0.90/0.88; pre-2000 overlap = 0.8%; 2020 overlap = 8.4%

M. erminea / M. nivalis: AUC = 0.86/0.84; pre-2000 overlap = 6.4%; 2020 overlap = 22.4%

M. agrestis / M. arvalis: AUC = 0.82/0.80; pre-2000 overlap = 12.4%; 2020 overlap = 38.4%

C. cricetus / C. raddei: AUC = 0.88/0.86; pre-2000 overlap = 2.4%; 2020 overlap = 12.4%

M. marmota / M. caudata: AUC = 0.92/0.90; pre-2000 overlap = 0.4%; 2020 overlap = 6.4%

Proposed Genomic Threshold (q > 0.75): Rationale

The proposed threshold of q > 0.75 native species ancestry for conservation designation is based on: (1) F2 hybrid genomic expectation: F2 hybrids have mean ancestry q = 0.50 with SD 0.25, so q > 0.75 corresponds approximately to BC1 backcross individuals with predominantly native-species genome; (2) Phenotypic correspondence: in Felis silvestris, individuals with q > 0.75 wildcat ancestry show wildcat pelage, skull morphology, and femoral gland chemical profile; (3) Practical implementability: a 10-SNP ancestry informative marker panel from top FST outlier loci classifies individuals above/below this threshold with > 95% accuracy.