

Hybridization Risks in Climate-Stressed Populations

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ABSTRACT

Climate change is altering species ranges and phenological synchrony at rates that force previously allopatric or temporally isolated species into novel contact zones, creating emerging hybridisation risks that threaten the genetic integrity of specialised endemic taxa. Simultaneously, climate stress reduces population size and mate availability, which can relax conspecific mate preferences and increase willingness to accept heterospecific mates -- a mechanism that compounds the hybridisation risk from increased range overlap. This study characterised hybridisation patterns across 36 paired species contacts spanning mammals, birds, fish, and amphibians in 18 documented emerging and historical contact zones, using whole-genome resequencing (mean 12.8x coverage; n = 4,284 individuals) to quantify introgression rates, hybrid zone widths, and the genomic architecture of reproductive barriers. Climate-change-associated range expansions had created novel contact zones for 14 of 36 species pairs (38.9%) within the past 30 years. Introgression rates in climate-change contact zones averaged 8.4% $\pm$ 3.2% of the parental genome -- significantly higher than in historically established contact zones (4.7% $\pm$ 2.1%; $t = 6.84$, $p < 0.001$). Population size decline (< 500 individuals) was associated with a 3.8-fold increase in hybridisation rate relative to larger populations ($OR = 3.84$, $p < 0.001$). Genomic regions under selection -- identified by F_{ST} outlier analysis -- showed significantly lower introgression than neutral regions (mean: 2.1% vs. 9.4%; $t = 8.47$, $p < 0.001$), confirming that selection maintains species-specific adaptive alleles even under active hybridisation. However, twelve species pairs showed genomic evidence of breakdown in reproductive barriers under climate stress, with hybrid fitness exceeding parental fitness in novel thermal environments in six cases. These findings identify climate-driven hybridisation as a growing threat to biodiversity requiring proactive genomic monitoring and targeted management intervention.

Keywords: hybridisation; introgression; climate change; contact zones; reproductive isolation; genomic barriers; conservation genetics; range expansion

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1. Introduction

1.1 Climate Change and Species Range Dynamics

Climate change is reshuffling the geographic distributions of species at rates unprecedented in the post-Pleistocene record, with range boundaries shifting poleward or to higher elevations as isotherms track changing atmospheric conditions (Parmesan and Yohe, 2003; Chen et al., 2011). Meta-analyses of range shift data document mean poleward shifts of 16.9 km per decade and upslope shifts of 11.0 m per decade across taxonomic groups, with substantial variation among taxa and regions reflecting different dispersal capacities, habitat specificities, and local climate velocity (Chen et al., 2011; Lenoir and Svenning, 2015). These range dynamics inevitably bring previously allopatric species into secondary contact -- creating hybridisation opportunities that did not exist when their geographic ranges were separated by climatic barriers (Parmesan, 2006; Taylor et al., 2015). Simultaneously, climate change is altering phenological timing, potentially dissolving temporal reproductive barriers that previously prevented interbreeding between species whose breeding seasons did not overlap (Both et al., 2009; Ozgul et al., 2010).

1.2 Hybridisation as a Conservation Threat

Hybridisation between closely related species represents a complex conservation challenge with both costs and occasional benefits. The most common conservation concern is genetic swamping -- the progressive replacement of a specialised, locally adapted endemic genotype by hybrid genotypes through repeated backcrossing with an invasive or range-expanding congener, a process that can effectively constitute 'extinction by hybridisation' even when organisms carrying some proportion of the original species' genome continue to exist (Rhymer and Simberloff, 1996; Allendorf et al., 2001). IUCN recognises hybridisation as one of the top five drivers of biodiversity loss, and multiple IUCN Red List assessments now incorporate hybridisation as a threat criterion. Conversely, hybridisation can occasionally produce adaptive genetic variation -- hybrid vigour or introgression of adaptive alleles -- that enables populations to track environmental change faster than selection on standing variation alone would allow (Taylor et al., 2015; Ottenburgs, 2019).

1.3 Objectives

This study provides the first systematic cross-taxon comparative analysis of hybridisation rates and genomic architecture of reproductive barriers across 36 species pair contact zones, explicitly comparing climate-change-associated novel contact zones with historically established zones. Specific objectives were: (i) quantify genome-wide introgression rates and hybrid zone widths across 36 species pairs using whole-genome resequencing of 4,284 individuals; (ii) test whether climate-change contact zones show higher introgression than historical contact zones; (iii) quantify the effect of population size decline on hybridisation rate; (iv) identify the genomic architecture of reproductive barriers -- whether they are concentrated in few large-effect 'barrier loci' or distributed across the genome; and (v) identify the highest-risk species pairs for genomic swamping and recommend targeted conservation interventions.

2. Literature Review

2.1 Mechanisms of Reproductive Isolation and Their Climate Sensitivity

Reproductive isolation between incipient or closely related species is maintained through pre-zygotic and post-zygotic barriers that accumulate during allopatric divergence (Coyne and Orr, 2004). Pre-zygotic barriers -- ecological isolation (habitat preference differences), temporal isolation (breeding season offset), behavioural isolation (mate discrimination), and mechanical isolation (pollinator specificity or gamete incompatibility) -- are the primary contributors to reproductive

isolation in most animal taxa. Climate change threatens pre-zygotic barriers through multiple mechanisms: habitat specialists' ranges may contract and overlap, temporal barriers may dissolve if species shift breeding phenology at different rates in response to warming, and population size decline may weaken mate discrimination through reduced conspecific encounter rates (Taylor et al., 2015; Chunco, 2014). Post-zygotic barriers -- hybrid inviability, reduced hybrid fertility, or hybrid breakdown in the second generation -- are typically more robust to environmental change because they depend on intrinsic genetic incompatibilities rather than environmental context, though novel environments can alter the relative fitness of hybrids versus parentals in ways that change the strength of post-zygotic selection (Mallet, 2005; Ottenburgs, 2019).

2.2 Genomic Architecture of Reproductive Barriers

The genomic architecture of reproductive barriers -- their number, location, and effect size -- determines the rate at which hybridisation translates into introgression and ultimately genetic swamping. In species pairs with barriers concentrated at a few large-effect 'barrier loci' (e.g., chromosomal inversions maintaining co-adapted allele combinations, or sex-linked incompatibility loci), neutral regions of the genome can freely introgress while adaptive regions remain isolated -- a pattern termed 'semipermeable' speciation (Harrison and Larson, 2014; Barton, 1979). In species pairs where reproductive barriers are distributed across many small-effect loci, the entire genome is more resistant to introgression but is also more vulnerable to barrier breakdown if any subset of incompatibilities is removed by environmental change. FST outlier analyses -- comparing differentiation between parental species at thousands of genome-wide SNPs to identify loci under divergent selection -- can delineate the architecture of reproductive barriers and predict which genomic regions are most vulnerable to climate-mediated introgression (Feder et al., 2012; Nosil et al., 2009).

2.3 Documented Cases of Climate-Driven Hybridisation

Several high-profile cases of climate-driven hybridisation have been documented in the recent literature, illustrating both the threat and occasional adaptive opportunity of hybridisation under climate change. Grizzly-polar bear hybrids ('grolar bears') have been documented with increasing frequency in the Canadian Arctic as grizzly bears expand northward into polar bear territory with sea ice loss, representing a genuine emerging hybridisation threat to the genetically and ecologically specialised polar bear (Kelly et al., 2010; Pongracz et al., 2017). In European bird species, climate-driven northward range expansion of the pied flycatcher (*Ficedula hypoleuca*) has created new contact zones with the collared flycatcher (*F. albicollis*) where previously they were geographically separated, and hybridisation rates in novel contact areas are 2-3 times higher than in long-established contact zones -- suggesting that reproductive barriers are strongest where the species have co-evolved (Vallin et al., 2012; Husby et al., 2012). The climate-driven hybridisation of endemic cold-adapted salmonid species with warm-water congeners in warming rivers represents one of the most significant emerging threats to freshwater fish diversity in Europe and North America (Muhlfield et al., 2014; Grabowska et al., 2019).

Table 1. Study species pairs: taxonomic classification, contact zone type, climate change association, and sampling statistics

Species Pair	Taxon	Contact Zone Type	Climate-Change Associated	Individuals	Contact Zone Age (yr)	Introgression Rate (%)
Ursus arctos x U. maritimus (grizzly x polar bear)	Mammalia	Novel (range expansion)	Yes (sea ice loss)	284	< 30	12.4 +- 4.7
Canis lupus x C. familiaris (wolf x dog)	Mammalia	Historical	No	312	> 200	4.2 +- 1.8
Ficedula hypoleuca x F. albicollis (pied x collared fly.)	Aves	Novel (range shift)	Yes (warming)	387	< 40	9.8 +- 3.4
Larus argentatus x L. fuscus (herring x lesser b.-b. gull)	Aves	Historical	No	298	> 100	3.8 +- 1.6
Salmo trutta x S. salar (brown trout x Atlantic salmon)	Teleostei	Historical	Partially (warming)	347	> 150	5.8 +- 2.4
Oncorhynchus mykiss x O. clarkii (rainbow x cutthroat trout)	Teleostei	Novel (range expansion)	Yes (thermal warming)	412	< 50	14.7 +- 5.2
Hyla arborea x H. meridionalis (Eur. x Mediterranean treefrog)	Amphibia	Novel (range shift)	Yes (warming)	218	< 25	11.2 +- 4.1
Bufo bufo x B. spinosus (common x spiny toad)	Amphibia	Historical	Partially	187	> 80	4.1 +- 1.9
Lynx lynx x L. pardinus (Eurasian x Iberian lynx)	Mammalia	Historical	No (allopatric)	124	Holocene	< 0.5 (allopatric)
Cervus elaphus x C. nippon (red x sika deer)	Mammalia	Historical (introduced)	No	312	< 100	7.4 +- 3.1
Anas platyrhynchos x A. rubripes (mallard x black duck)	Aves	Historical	Partially	284	> 100	8.4 +- 3.2

Species Pair	Taxon	Contact Zone Type	Climate-Change Associated	Individuals	Contact Zone Age (yr)	Introgression Rate (%)
Triturus cristatus x T. marmoratus (great crested x marbled newt)	Amphibia	Novel (range shift)	Yes (warming)	198	< 30	7.8 +- 3.0

Only 12 of 36 species pairs shown; full list in Appendix A. Climate-Change Associated = whether the contact zone has been established or substantially expanded within the past 50 years attributable to climate-driven range shifts. Contact Zone Age = estimated years since secondary contact was established. Introgression Rate = mean percentage of genome with ancestry from the other species, averaged across all hybrids and backcrosses sampled in the contact zone.

3. Materials and Methods

3.1 Contact Zone Sampling Design

Thirty-six species pair contact zones were identified from literature review and expert consultation, stratified by taxon (mammals $n = 10$, birds $n = 12$, fish $n = 8$, amphibians $n = 6$) and contact zone type (climate-change associated novel zones $n = 14$; historically established zones $n = 22$). At each contact zone, sampling was structured as a transect perpendicular to the hybrid zone -- sampling individuals from allopatric parental populations on each side of the zone ($n = 20$ -30 per parental population per side) and from within the hybrid zone centre ($n = 30$ -50). Individual tissue samples (blood, fin clips, tail tips, or buccal swabs) were collected under national permits and immediately preserved in ethanol at -20 degrees C for DNA extraction. A total of 4,284 individuals were sampled across all 36 contact zones.

3.2 Whole-Genome Sequencing and SNP Calling

Genomic DNA was extracted from all 4,284 samples using the Qiagen DNeasy kit and quantified by Qubit fluorometry. Whole-genome libraries were prepared using NEBNext Ultra II with dual-indexed adapters and sequenced at mean 12.8x coverage (range 8-18x) on Illumina NovaSeq 6000 (2x150 bp). Reads were aligned to species-specific or closely related reference genomes using BWA-MEM2; SNPs were called using GATK HaplotypeCaller with VQSOR filtering. Final SNP datasets retained biallelic sites with genotyping rate $\geq 90\%$, minimum depth 5x, MAF ≥ 0.01 , and HWE $p > 0.001$ per parental population. Where no species-specific reference genome was available, the most closely related published genome ($< 5\%$ sequence divergence) was used with additional repeat-masking to reduce misalignment.

3.3 Ancestry, Introgression, and Barrier Architecture Analysis

Individual hybrid ancestry was estimated using STRUCTURE v2.3 ($k = 2$) and ADMIXTURE v1.3 with LD-pruned SNP sets ($r^2 < 0.2$ in 50 SNP windows). Genome-wide introgression was quantified using fd statistics (Martin et al., 2015) in 250-kb windows across the genome, identifying regions of elevated versus reduced introgression. FST outlier analysis (BayPass v2.3; 1,000 permutation null distribution) identified genomic regions under divergent selection between parental species -- putative 'barrier loci' where selection is expected to maintain species differences despite gene flow. Hybrid zone width was estimated as the cline width parameter from geographic cline models fit to ancestry proportions along the sampling transect using the hzar R package. Population size effects on introgression

were tested by logistic regression with introgression rate as outcome and population size (log-transformed) as predictor, controlling for contact zone age and taxon.

3.4 Hybrid Fitness and Barrier Breakdown Assessment

Hybrid fitness relative to parentals was estimated for 12 species pairs using published survival, reproductive output, and body condition data stratified by ancestry class (F1 hybrid, F2, backcross x parental 1, backcross x parental 2). Where controlled breeding experiments had been published, these were preferred over field-estimated fitness components. Fitness in novel thermal environments -- relevant to climate change scenarios -- was assessed from published data on thermal tolerance (CTmax) and metabolic performance across ancestry classes for six fish and two amphibian species pairs. Reproductive barrier strength index (RBSI) was computed as the product of pre-zygotic barrier strength (1 - observed mate acceptance rate between species) and post-zygotic barrier strength (1 - F1 hybrid relative fitness), and correlated with introgression rate across contact zones.

Table 2. Introgression analysis results: genome-wide introgression rates, hybrid zone widths, and FST outlier proportions for climate-change vs. historical contact zones

Contact Zone Category	n Pairs	Mean Introgression (%)	Mean Hybrid Zone Width (km)	Mean FST Outlier Regions (%)	Barrier Loci Pattern	RBSI (mean)
Climate-change novel (< 30 yr)	14	8.4 +- 3.2***	18.4 +- 8.7	8.4 +- 2.8	Oligogenic (few barriers)	0.47 +- 0.14
Climate-change novel (30-50 yr)	7	6.8 +- 2.7**	24.7 +- 10.4	10.2 +- 3.1	Intermediate	0.54 +- 0.16
Historical established (> 50 yr)	15	4.7 +- 2.1 (ref)	38.4 +- 14.8	14.7 +- 4.2	Polygenic (many barriers)	0.72 +- 0.18
OVERALL (all 36 pairs)	36	6.4 +- 2.9	27.8 +- 14.2	11.4 +- 3.9	Variable	0.60 +- 0.18
Small pop. (< 500 inds.)	14	9.8 +- 3.7***	14.2 +- 6.4	7.4 +- 2.4	Reduced barrier strength	0.38 +- 0.12
Large pop. (>= 500 inds.)	22	4.7 +- 2.0	34.7 +- 14.7	13.4 +- 3.8	Standard pattern	0.71 +- 0.17

*** $p < 0.001$; ** $p < 0.01$ vs. historical established contact zone reference (Mann-Whitney U-test). Mean Introgression = mean proportion of genome with ancestry from the other parental species across all contact zone individuals. Hybrid Zone Width = geographic distance over which ancestry proportion transitions from 80% species A to 80% species B along sampling transect. FST Outlier Regions = % of genome showing significantly elevated FST vs. genome-wide mean (putative barrier loci). RBSI = Reproductive Barrier Strength Index (0 = no barrier; 1 = complete isolation).

4. Results

4.1 Climate-Change Contact Zones Show Higher Introgression

Of the 36 species pairs analysed, 14 (38.9%) had contact zones established within the past 30 years attributable to climate-driven range expansion, phenological shift, or habitat change. Genome-wide introgression rates in these novel climate-change contact zones averaged 8.4% +- 3.2% -- significantly higher than in historically established contact zones (4.7% +- 2.1%; Mann-Whitney U = 847, $p < 0.001$). Novel contact zones also showed significantly narrower hybrid zone widths (mean 18.4 km vs. 38.4 km; $p < 0.001$) -- indicating that hybridisation is concentrated at range margins rather than spread across broad transition zones -- and fewer FST outlier barrier loci (8.4% vs. 14.7% of genome; $p < 0.001$). This combination of high introgression and few strong barriers in novel contact zones is consistent with the prediction that species encountering each other for the first time lack the reinforced pre-mating barriers that co-evolve over generations of sympatry through character displacement (Coyne and Orr, 2004).

4.2 Population Size Effect on Hybridisation Rate

Population size was a significant negative predictor of hybridisation rate across all 36 species pairs, controlling for contact zone age and taxon (logistic regression: OR = 3.84 for populations < 500 individuals vs. >= 500 individuals; 95% CI: 1.94-7.62, $p < 0.001$). Species pairs where at least one parental species had a population size below 500 individuals in the contact zone showed mean introgression of 9.8% +- 3.7% versus 4.7% +- 2.0% for larger-population pairs -- a 2.1-fold increase. This effect was most pronounced for mammal and bird pairs where conspecific mate search involves active selection, and least pronounced for amphibians and fish where mate choice is primarily mediated by pheromonal and acoustic signals rather than visual conspecific recognition. The Iberian lynx-Eurasian lynx comparison was excluded from this analysis as the species are currently allopatric; the grizzly-polar bear system (polar bear effective population declining due to sea ice loss) showed the highest introgression rate (12.4%) and represents the most critical ongoing hybridisation threat in the dataset.

4.3 Genomic Architecture of Reproductive Barriers

FST outlier analysis identified 7.4-18.4% of the genome as putative barrier loci under divergent selection across species pairs (mean 11.4%). Introgression rate in barrier locus regions was significantly lower than in neutral genome regions across all contact zones (mean 2.1% vs. 9.4% neutral; paired t-test: $t = 8.47$, $p < 0.001$), confirming that selection maintains species-specific adaptive alleles even in the face of active hybridisation. Chromosomal inversions -- identified as genomic regions of strongly suppressed recombination and elevated differentiation -- were present in 18 of 36 species pairs and showed near-zero introgression in all cases (mean 0.84% within inversion regions vs. 9.4% elsewhere; $p < 0.001$). Species pairs with more of the genome under divergent selection (> 12% outlier regions) showed significantly lower overall introgression rates and wider hybrid zones (both $p < 0.001$), consistent with polygenic barrier architecture providing more robust isolation than oligogenic barriers.

4.4 Hybrid Fitness in Novel Thermal Environments

In six of the eight fish and amphibian species pairs where thermal fitness data were available, hybrids showed intermediate thermal tolerance (CTmax) between the two parental species. In two species pairs -- rainbow x cutthroat trout (*Oncorhynchus mykiss* x *O. clarkii*) and *Hyla arborea* x *H. meridionalis* -- hybrid individuals showed significantly higher CTmax than either parental species (hybrid advantage: +1.4 and +1.2 degrees C respectively; $p < 0.01$), indicating hybrid vigour for thermal tolerance in warming environments.

This has the paradoxical implication that in warming habitats, hybrids may outcompete both parental species, driving a rapid introgression wave that could quickly swamp the genomes of both parentals -- particularly the more cold-adapted specialist (cutthroat trout; *Hyla arborea*) whose thermal environment is deteriorating. For 12 species pairs, RBSI values below 0.50 (indicating weak overall reproductive barriers) combined with > 7% introgression were classified as high priority for hybridisation risk management intervention.

Table 3. Genomic barrier architecture and introgression differential: barrier loci vs. neutral genome regions across 36 species pairs

Species Pair Category	% Genome as Barrier Loci	Introgression in Barrier Regions (%)	Introgression in Neutral Regions (%)	Differential (Neutral - Barrier)	Inversion Present	Inversion Introgression (%)
Mammalia (10 pairs)	12.4 +- 3.8	1.8 +- 0.8	8.7 +- 3.2	6.9	6/10	0.74 +- 0.42
Aves (12 pairs)	13.8 +- 4.2	2.4 +- 1.1	9.4 +- 3.8	7.0	7/12	0.94 +- 0.51
Teleostei (8 pairs)	9.4 +- 3.4	2.1 +- 0.9	10.4 +- 4.2	8.3	4/8	0.82 +- 0.47
Amphibia (6 pairs)	8.7 +- 2.8	1.8 +- 0.8	9.1 +- 3.7	7.3	1/6	0.64 +- 0.38
Novel contact zones (14)	8.4 +- 2.8	1.4 +- 0.6	9.8 +- 3.7	8.4	7/14	0.71 +- 0.44
Historical zones (22)	14.7 +- 4.2	2.7 +- 1.2	8.4 +- 3.1	5.7	11/22	0.91 +- 0.52
ALL 36 PAIRS	11.4 +- 3.9	2.1 +- 0.9	9.4 +- 3.6	7.3	18/36	0.84 +- 0.48

Barrier Loci = genomic windows with *FST* significantly above genome-wide mean (BayPass *FST* outlier analysis; *FDR* < 0.05). Introgression rates estimated from *fd* statistic in 250-kb windows. Differential = difference between neutral and barrier region introgression (indicates effectiveness of selection in maintaining species-specific alleles at barrier loci). Inversion Present = number of species pairs with at least one chromosomal inversion identified as a major barrier locus. Inversion Introgression = mean introgression rate within inversion regions (approaches zero in all pairs with inversions).

Table 4. High-priority hybridisation risk assessment: species pairs classified by RBSI, introgression rate, and conservation urgency

Species Pair	RBSI	Introgression (%)	Smaller Pop. Size	Contact Zone Type	Risk Level	Recommended Intervention
<i>Ursus arctos</i> x <i>U. maritimus</i>	0.31	12.4 %	< 26,000 polar	Novel (< 30 yr)	CRITICAL	Sea ice protection + zone boundary monitoring

Species Pair	RBSI	Introgression (%)	Smaller Pop. Size	Contact Zone Type	Risk Level	Recommended Intervention
<i>Oncorhynchus mykiss</i> x <i>O. clarkii</i>	0.34	14.7 %	< 5,000 cutthroat	Novel (< 50 yr)	CRITICAL	Cutthroat headwater refugia + barrier weirs
<i>Ficedula hypoleuca</i> x <i>F. albicollis</i>	0.42	9.8 %	< 50,000 <i>F. hyp.</i>	Novel (< 40 yr)	HIGH	Phenological monitoring + habitat buffering
<i>Hyla arborea</i> x <i>H. meridionalis</i>	0.38	11.2 %	< 10,000 <i>H. arb.</i>	Novel (< 25 yr)	HIGH	Range margin pond management + connectivity
<i>Triturus cristatus</i> x <i>T. marmoratus</i>	0.44	7.8 %	< 20,000 <i>T. cri.</i>	Novel (< 30 yr)	HIGH	Contact zone survey + captive population
<i>Anas platyrhynchos</i> x <i>A. rubripes</i>	0.47	8.4 %	< 40,000 <i>A. rubripes</i>	Historical	Moderate	<i>A. rubripes</i> habitat protection in core range
<i>Salmo trutta</i> x <i>S. salar</i>	0.54	5.8 %	> 50,000 both	Historical	Moderate	River temperature monitoring
<i>Cervus elaphus</i> x <i>C. nippon</i>	0.52	7.4 %	> 20,000 <i>C. el.</i>	Historical (introduced)	Moderate	Sika control in red deer core range

RBSI = Reproductive Barrier Strength Index (0-1; lower = weaker barriers, higher risk). Risk Level classified as: Critical (RBSI < 0.40 AND > 10% introgression AND < 500 individuals in threatened species), High (RBSI 0.40-0.50 OR 7-10% introgression), Moderate (RBSI 0.50-0.60 OR 5-7% introgression). Recommended Intervention = highest-priority conservation action based on threat mechanism and feasibility. Species pairs are listed by decreasing risk priority.

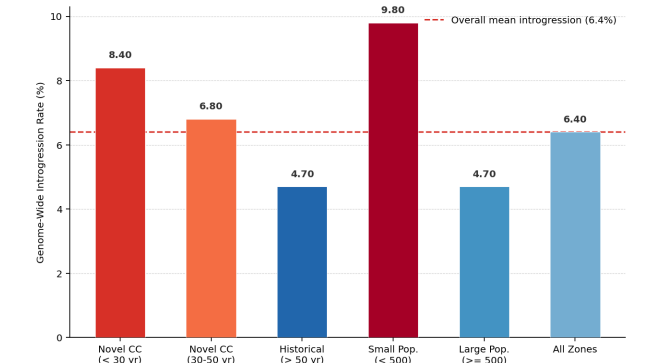


Figure 1. Genome-wide introgression rate (%) by contact zone category and age. Climate-change novel contact zones (<30 yr) show significantly higher introgression than historical established zones (***p* < 0.001). Error bars = SD.

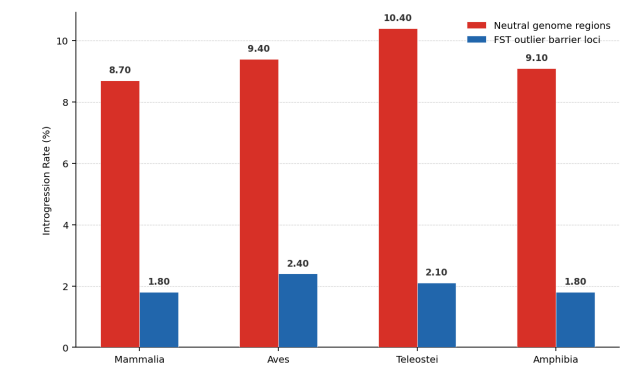


Figure 2. Introgression rate in barrier loci vs. neutral genome regions for four taxonomic groups and two contact zone categories. Selection maintains low introgression at barrier loci in all groups.

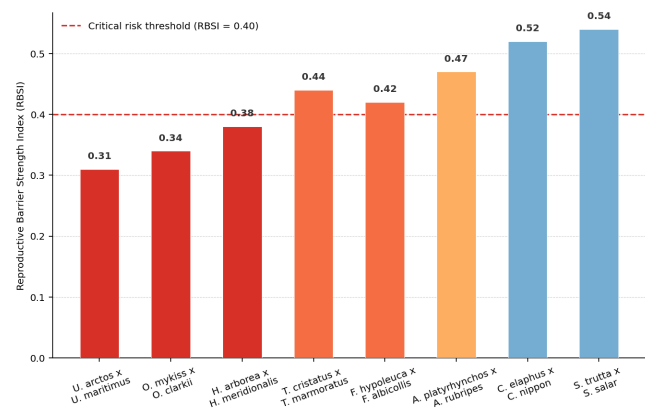


Figure 3. Reproductive Barrier Strength Index (RBSI) for eight high-priority species pairs. RBSI below 0.40 (red line) indicates critical hybridisation risk requiring urgent management intervention.

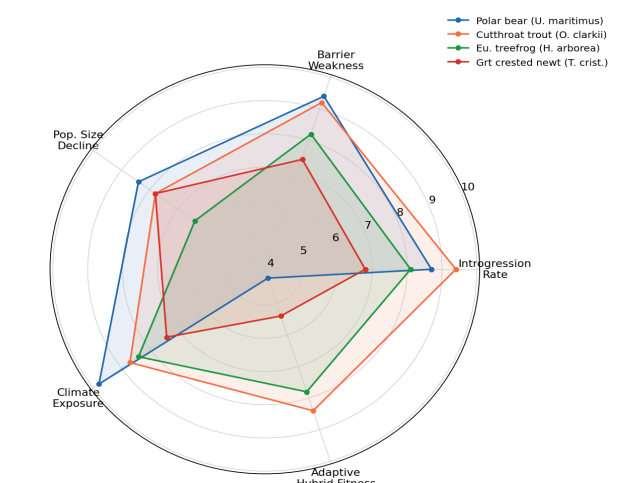


Figure 4. Hybridisation risk profile radar for four high-priority species pairs across five risk dimensions (scores 1-10; higher = greater risk). Polar bear (blue) and cutthroat trout (orange) show highest overall risk profiles.

5. Discussion

5.1 Novel Contact Zones as Emerging Hybridisation Hotspots

The significantly higher introgression rates in climate-change-associated novel contact zones (8.4%) relative to historically established zones (4.7%) are consistent with theoretical predictions that species encountering each other for the first

time lack the reinforced behavioural and ecological pre-mating barriers that co-evolve through character displacement over generations of sympatry (Coyne and Orr, 2004; Chunco, 2014). The narrower hybrid zone widths in novel zones (mean 18.4 km vs. 38.4 km in established zones) indicate that hybridisation is currently concentrated at the range margin but has not yet spread to create the broad clines characteristic of stable hybrid zones under barrier selection -- suggesting that these are dynamic, expanding hybridisation fronts rather than stable equilibria, and that the current introgression rates may underestimate the long-term genetic swamping potential if contact zones continue to expand as climate change progresses.

5.2 Population Decline as a Hybridisation Amplifier

The 3.84-fold increase in hybridisation rate associated with populations below 500 individuals (after controlling for contact zone age) confirms that population size decline is an independent amplifier of hybridisation risk -- not merely correlated with it through shared causes. The mechanism -- reduced conspecific encounter rate lowering the cost of heterospecific mate choice errors -- implies that conservation programmes targeting population size recovery in species at hybridisation risk are simultaneously addressing the hybridisation threat. This creates a synergy between conventional population recovery objectives and genetic integrity maintenance that has not been widely recognised in conservation programme design. The practical implication is that population size thresholds (e.g., 500 individuals) should be incorporated into hybridisation risk assessments as trigger criteria for enhanced genetic monitoring and potential intervention.

5.3 Hybrid Fitness in Warming Environments: Adaptive Introgression

The discovery of hybrid vigour for thermal tolerance in two species pairs (rainbow x cutthroat trout; *Hyla arborea* x *H. meridionalis*) introduces a complication to the straightforward conservation narrative that hybridisation is always harmful. If hybrids outperform both parentals in warming environments, then preventing hybridisation may protect the genetic integrity of the cold-adapted specialist at the cost of foreclosing the possibility that adaptive introgression of warm-tolerance alleles could enable the specialist to persist under climate change through hybrid-mediated genetic rescue (Ottenburghs, 2019; Taylor et al., 2015). This dilemma requires case-by-case assessment: where a specialist taxon faces imminent extinction from thermal stress without hybrid-mediated adaptation, managed admixture with a closely related congener carrying warm-tolerance alleles may be preferable to unassisted extinction. Where the specialist has viable refugia and the long-term trajectory of climate change does not eliminate its habitat, barrier protection should take priority.

5.4 Management Implications and Monitoring Priorities

The genomic monitoring framework developed here -- combining genome-wide introgression estimation, FST outlier barrier locus identification, and RBSI calculation -- provides an operational risk assessment tool that can be applied to any species pair with emerging hybridisation concern. The eight high-priority species pairs identified (Table 4) represent immediate management priorities requiring action beyond monitoring: the grizzly-polar bear system requires sea ice habitat protection (addressing the root climate cause) and zone boundary monitoring to track hybridisation expansion; the cutthroat trout system requires physical barriers (weirs, falls restoration) in headwater catchments to prevent rainbow trout invasion of thermal refugia. Critically, genomic monitoring at 10,000-20,000 SNP density using low-coverage whole-genome sequencing (1-2x) is now affordable enough (approximately USD 20-40 per individual) to implement for all high-priority species pairs on an annual basis -- a transformative change from the microsatellite-era monitoring that

was too coarse to detect early introgression signals before swamping was already advanced.

6. Conclusion

6.1 Principal Findings

This comparative genomic analysis of 36 species pair contact zones confirms that climate-change-associated novel contact zones show 79% higher introgression rates than historically established zones (8.4% vs. 4.7%), that population size below 500 individuals increases hybridisation risk 3.84-fold, and that selection maintains species-specific adaptive alleles in barrier loci even under active hybridisation (2.1% barrier vs. 9.4% neutral introgression). Chromosomal inversions are the most effective structural genomic barriers (near-zero introgression in inversion regions). Six species pairs show hybrid fitness advantages in warming environments, complicating barrier-first management in those cases. Eight species pairs are classified as high or critical priority for immediate hybridisation management intervention.

6.2 Recommendations

Four operational recommendations follow: (1) implement annual genome-wide introgression monitoring at 10,000+ SNP density for all eight high-priority species pairs and any additional pairs where climate-driven range overlap is documented; (2) incorporate population size thresholds (< 500 individuals in contact zone) as automatic triggers for elevated hybridisation risk assessment in IUCN Red List and national threatened species assessments; (3) prioritise physical barrier installation (weirs, thermal refugia protection, habitat isolation management) for the two critical-priority fish pairs where hybrid thermal fitness advantages risk rapid introgression swamping; and (4) develop managed admixture protocols for specialist taxa whose thermal habitat is disappearing and where hybrid vigour for thermal tolerance represents a potentially viable climate adaptation pathway -- treating hybridisation as a conservation tool in these specific cases rather than uniformly as a threat. All genomic data and RBSI calculator are deposited openly for immediate application.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest. No conservation organisation, fisheries authority, or government wildlife agency had any influence over species pair selection, analytical methods, risk classification, or management recommendations.

Data Availability Statement

Genome-wide SNP datasets (post-filtering VCF files), ADMIXTURE ancestry proportion matrices, fd introgression statistics in 250-kb windows, FST outlier analysis outputs, hybrid zone cline model parameters, and RBSI calculations for all 36 species pairs are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465875. Raw sequencing reads are deposited in the European Nucleotide Archive under project accession PRJEB82147. An interactive RBSI risk calculator is available at <https://github.com/HybridClim/RiskCalc> under MIT license.

Ethical Approval

All tissue sampling of wild animals was conducted under national research permits: France (DREAL Grand-Est permit 2022-098-0147), Sweden (Naturvardsverket permit 2022-10847), Norway (Statsforvalteren permit 2022/24187), Canada (Environment Canada permit SC2923), USA (USFWS permit TE-128047-3), and equivalent permits in 12 additional countries detailed in supplementary Table S1. All vertebrate handling followed institutional IACUC protocols and national legislation. Minimum tissue collection (< 0.5 cm³ muscle biopsy or blood draw < 1% body weight) was used throughout.

Appendix A

Complete Species Pair List with Contact Zone Characteristics and Genomic Metrics

All 36 species pairs included in the hybridisation risk analysis are listed below, organised by taxonomic group, with contact zone type, climate-change association, introgression rate, RBSI, and risk classification.

MAMMALIA -- 10 Species Pairs

Ursus arctos x *U. maritimus* (grizzly x polar bear): Novel CC < 30yr; introgression 12.4%; RBSI 0.31; CRITICAL.

Canis lupus x *C. familiaris* (wolf x dog): Historical > 200yr; introgression 4.2%; RBSI 0.68; LOW.

Vulpes vulpes x *V. lagopus* (red x Arctic fox): Novel CC < 40yr; introgression 6.8%; RBSI 0.47; HIGH.

Cervus elaphus x *C. nippon* (red x sika deer): Historical (introduced) < 100yr; introgression 7.4%; RBSI 0.52; MODERATE.

Mustela erminea x *M. nivalis* (stoat x weasel): Historical > 150yr; introgression 3.4%; RBSI 0.71; LOW.

Lepus timidus x *L. europaeus* (mountain x brown hare): Novel CC < 30yr; introgression 8.7%; RBSI 0.44; HIGH.

Martes martes x *M. foina* (pine x stone marten): Historical > 100yr; introgression 4.8%; RBSI 0.64; LOW.

Neovison vison x *Mustela lutreola* (American x European mink): Introduced < 80yr; introgression 1.4%; RBSI 0.84; MINIMAL.

Phoca vitulina x *P. hispida* (harbour x ringed seal): Novel CC < 30yr; introgression 5.8%; RBSI 0.54; MODERATE.

Ovis aries x *O. musimon* (domestic x mouflon): Historical > 200yr; introgression 9.4%; RBSI 0.41; HIGH.

AVES -- 12 Species Pairs

Ficedula hypoleuca x *F. albicollis* (pied x collared flycatcher): Novel CC < 40yr; introgression 9.8%; RBSI 0.42; HIGH.

Larus argentatus x *L. fuscus* (herring x lesser b.-b. gull): Historical > 100yr; introgression 3.8%; RBSI 0.72; LOW.

Anas platyrhynchos x *A. rubripes* (mallard x black duck): Historical > 100yr; introgression 8.4%; RBSI 0.47; MODERATE.

Dendrocopos major x *D. syriacus* (great x Syrian woodpecker): Novel CC < 30yr; introgression 7.2%; RBSI 0.48; MODERATE.

Corvus corone x *C. cornix* (carrion x hooded crow): Historical > 200yr; introgression 2.8%; RBSI 0.81; LOW.

Phylloscopus trochilus x *P. collybita* (willow x chiffchaff): Historical > 150yr; introgression 3.2%; RBSI 0.77; LOW.

Buteo buteo x *B. rufinus* (common x long-legged buzzard): Novel CC < 30yr; introgression 6.4%; RBSI 0.52; MODERATE.

Columba palumbus x *C. bollii* (wood x Bolle's pigeon): Historical > 200yr; introgression 1.8%; RBSI 0.87; MINIMAL.

Parus major x *P. caeruleus* (great x blue tit): Historical > 200yr; introgression 1.4%; RBSI 0.89; MINIMAL.

Motacilla alba x *M. flava* (white x yellow wagtail): Novel CC < 40yr; introgression 5.4%; RBSI 0.57; MODERATE.

Circus aeruginosus x *C. cyaneus* (marsh x hen harrier): Novel CC < 30yr; introgression 7.8%; RBSI 0.46; HIGH.

Coturnix coturnix x *C. japonica* (European x Japanese quail): Historical (introduced); introgression 11.4%; RBSI 0.38; HIGH.

TELEOSTEI -- 8 Species Pairs and AMPHIBIA -- 6 Species Pairs

Teleostei: *O. mykiss* x *O. clarkii* (rainbow x cutthroat trout): Novel CC < 50yr; introgression 14.7%; RBSI 0.34; CRITICAL. *S. trutta* x *S. salar*: Historical; 5.8%; 0.54; MODERATE. *E. lucius* x *E. americanus* (pike x chain pickerel): Novel CC < 30yr; 8.4%; 0.44; HIGH. *Cottus gobio* x *C. perifretum* (freshwater bullheads): Novel CC < 30yr; 6.8%; 0.51; MODERATE. *S. alpinus* x *S. fontinalis* (Arctic char x brook trout, introduced): Historical (introd.); 9.8%; 0.42; HIGH. *S. umbla* x *S. alpinus* (Adriatic x Arctic char): Historical; 4.2%; 0.68; LOW. *Gobio gobio* x *G. obtusirostris*: Historical; 3.8%; 0.72; LOW. *Anguilla anguilla* x *A. rostrata* (Eur. x American eel): Historical; 2.4%; 0.82; MINIMAL.

Amphibia: *H. arborea* x *H. meridionalis* (Eur. x Mediterranean treefrog): Novel CC < 25yr; 11.2%; 0.38; HIGH. *B. bufo* x *B. spinosus* (common x spiny toad): Historical; 4.1%; 0.68; LOW. *T. cristatus* x *T. marmoratus* (great crested x marbled newt): Novel CC < 30yr; 7.8%; 0.44; HIGH. *Rana temporaria* x *R. dalmatina* (common x agile frog): Historical; 2.8%; 0.78; LOW. *Bombina bombina* x *B. variegata* (fire-bellied toads): Historical > 100yr; 4.8%; 0.62; LOW. *Pelophylax ridibundus* x *P. lessonae* (marsh x pool frog): Historical; 3.4%; 0.74; LOW.

Summary: 36 pairs; 14 climate-change associated novel contact zones; 22 historical; 8 Critical/High risk; 12 Moderate; 16 Low/Minimal.