

Selection through soft and incomplete sweeps underlies postglacial ecotype differentiation in an Arctic wide-ranging ungulate

Xavier Dallaire

`xavier.dallaire.2@ulaval.ca`

Université Laval <https://orcid.org/0000-0003-2375-561X>

Glenn Yannic

Université Savoie Mont Blanc <https://orcid.org/0000-0002-6477-2312>

Joëlle Taillon

Ministère de l'Environnement, de la Lutte Contre les Changements Climatiques, de la Faune et des Parcs

Martin-Hugues St-Laurent

Université du Québec à Rimouski

Claude Robert

Université Laval

Steeve Côté

Université Laval <https://orcid.org/0000-0002-4875-1917>

Aaron Shafer

Trent University <https://orcid.org/0000-0001-7652-225X>

Article

Keywords:

Posted Date: October 28th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11319271/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: There is no duality of interest

1 Selection through soft and incomplete sweeps 2 underlies postglacial ecotype differentiation in an 3 Arctic wide-ranging ungulate

4 Abstract

5 Ecotypes offer a window into the earliest stages of adaptive divergence, before
6 reproductive isolation is complete. In eastern Canada, migratory and boreal caribou
7 (*Rangifer tarandus caribou*) represent a striking example of recent ecological
8 divergence, differing primarily in movement strategy despite ongoing gene flow. We
9 used low- and high-coverage whole-genome sequencing from migratory and boreal
10 populations in Quebec and Labrador to characterize the timing, demographic history,
11 and genomic signatures of this divergence. Demographic modeling supported a
12 secondary contact scenario, with an estimated divergence time roughly 7,000–
13 11,700 years ago, coinciding with the last deglaciation period. Despite weak overall
14 population structure (genome-wide $F_{ST} = 0.02$) and evidence of continued gene flow,
15 we identified distinct genomic peaks of differentiation, nearly half of which coincided
16 with divergent haplotype length (XP-nSL), a pattern consistent with recent,
17 incomplete soft selective sweeps rather than classic hard sweeps. Combining
18 differentiation-, diversity-, and haplotype-based statistics proved essential for

detecting this subtle selection signature. Candidate genes under selection point to a polygenic architecture spanning bone and connective tissue development (including antler-related pathways), mitochondrial energy metabolism, and other traits plausibly linked to the ecological differences between ecotypes. Together, our results suggest that caribou ecotypes are not fixed evolutionary endpoints but a dichotomy that can re-emerge from standing genetic variation as opportunity arises.

Introduction

Ecotype is a widely used term in ecology to describe group-specific phenotypic variation that may be linked to morphology, physiology, or behaviour. While ecotypes can occupy a wide space along the ecological speciation spectrum (Nosil, 2012), their adaptive divergence is maintained by partial barriers to gene flow. This contrasts with the classic threshold for defining species that involves irreversible reproductive isolation such as hybrid unviability or sterility (Lowry, 2012). Partial and reversible barriers to gene flow can involve differences in phenology or habitat use during the mating season, reduced fitness in hybrids, or strong selection against individuals dispersing outside their native habitat (Johannesson et al., 2026). As these barriers can have both spatial and temporal dimensions, ecotype pairs can be maintained in either allopatry (e.g., guppies *Poecilia reticulata* in high- and low predation environments, Torres-Dowdall et al., 2012), parapatry (e.g., forest and prairie deer mice *Peromyscus maniculatus*, Hager et al., 2022), or sympatry (e.g., full- and new-moon midge *Clunio marinus*, Fuhrmann et al., 2023).

There is an ongoing debate as to whether ecotypes and even species can routinely emerge without an initial period of geographical isolation (Jiggins, 2006; Bolnick & Fitzpatrick, 2007; Foote, 2018). Theory predicts that selection can overcome gene flow if it is strong enough (Endler, 1977; Lenormand, 2002). However, demographic modeling of ecotype divergence rarely supports continuous gene flow following a population split (e.g. Rougemont et al., 2017, but see Butlin et al., 2014 in *Littorina saxatilis*), and secondary contact following isolation in distinct glacial refugia has been associated with many cases of ecotypic divergence (e.g. Rougeux et al., 2019; Backenstose et al., 2024). By contrast, during the earliest stages of sympatric or parapatric divergence, phenotypic plasticity might allow the colonization of a novel habitat, promoting survival and establishment before positive selection can favor alleles that lead to heritable local adaptation, even though there is little empirical evidence to support this hypothesis (Levis & Pfennig, 2016; Levis et al., 2018; Castillo et al., 2024; Coates et al., 2025).

The genomic basis of ecotypic divergence has been identified in many systems (reviewed in Johannesson et al., 2026). Examples include the repeated implication of specific genes in marine and freshwater three-spined sticklebacks (*Gasterosteus aculeatus*, Kingman et al., 2021) and the role of chromosomal inversions in ecotypes of *Littorina saxatilis* (Koch et al., 2022; Castillo et al., 2024). Such findings have largely emerged from comparisons of genomic variation between ecotypes, with genome-wide scans of genetic differentiation providing a common approach for identifying candidate regions underlying ecological divergence (Hoban et al., 2016).

However, interpreting these patterns of differentiation as signatures of selection requires caution. Metrics such as F_{ST} can conflate reduced diversity with reduced gene flow, since it is inflated in low-recombination or low-diversity regions regardless of selection (Cruickshank & Hahn, 2014) and can be driven by demography alone (Excoffier et al., 2009). Genome-wide scans are nonetheless powerful to detect the signature of hard selective sweeps, where positive selection on a *de novo* mutation creates a dominant haplotype and decreases genetic variation in proximity (Maynard Smith & Haigh, 1974). Alternatively, soft selective sweeps create more subtle genomic signatures, since selection acts on multiple pre-existing haplotypes simultaneously. Soft sweeps might be more common in practice (Messer & Petrov, 2013; Schrider & Kern, 2017) but can be harder to detect, especially if they are incomplete. Haplotype-based metrics have shown increased power compared to F_{ST} scans to detect soft and incomplete selective sweeps and are not dependent on recombination rates (Ferrer-Admetlla et al., 2014; Szpiech et al., 2021).

Caribou and reindeer (both *Rangifer tarandus*) have a circumpolar range where ecotypes represent ecologically differentiated populations that vary in habitat use, movement behaviour, and life-history strategies (COSEWIC, 2011). Eastern Canada is inhabited by the woodland caribou (*R. tarandus caribou*) subspecies, which comprises populations of the migratory, boreal and mountain ecotypes. Mitochondrial and microsatellite data indicate that caribou in Quebec and Labrador derive predominantly from a lineage that persisted through the Last Glacial Maximum in an eastern North American refugium prior to their northward expansion (Bergerud

84 et al., 2008; Yannic et al., 2014), with negligible introgression from the Beringian
85 lineage from which it diverged approximately 70,000 years ago (Taylor et al., 2021;
86 Hold et al., 2024). In Quebec, the migratory and boreal ecotypes provide a striking
87 example of ecological divergence and differ mainly in their amplitude of movement.
88 Migratory caribou form large herds that travel hundreds to thousands of km in yearly
89 migrations from calving grounds in the tundra, where they aggregate to reduce
90 predation risk and access seasonal food sources (Bergerud et al., 2008), to taiga
91 wintering areas that allow for lichen foraging (Sharma et al., 2009). In contrast,
92 individuals from boreal populations move over much shorter distances, travel in
93 smaller, less cohesive groups, show weaker directionality, and space out to calve
94 (COSEWIC, 2011). Partial reproductive isolation between ecotypes appears to be
95 maintained through spatio-temporal separation, as overlap in habitats generally
96 occurs after the end of the mating season (Boulet et al., 2007), although some GPS-
97 tracked caribou have been observed to change migratory behaviour across their
98 lifetime (MELCCFP, unpublished data). Similar migratory-sedentary dichotomies
99 recur around the globe at the tundra-boreal transition, but emerging genomic work is
100 revealing that this differentiation is shallow and polygenic, with independent origins
101 rather than through a shared genetic basis (Cavedon et al., 2022; Pokharel et al.,
102 2023; Delgado et al., 2026). Identifying the genomic basis of these divergent
103 ecological strategies can help elucidate how natural selection shapes genetic
104 variation in recent ecotype differentiation, particularly when divergence is
105 maintained despite gene flow.

Previous studies on *R. tarandus* of the North American lineage have examined peaks of differentiation between the boreal and migratory ecotype using high-coverage sequencing on limited sample sizes (Prunier et al., 2022; Delgado et al., 2026) and demographic inference based on one-dimensional site-frequency spectra (SFS; Dedato et al., 2022). In this study, we leverage low and high coverage whole genomes from migratory and boreal populations in Quebec and Labrador to gather additional insight on the recent divergence of ecotypes and their subsequent gene flow and adaptation. Specifically, we first compared two-population demographic models to estimate the divergence time of ecotypes and migration rates while considering both continuous and discontinuous gene flow. We then compared F_{ST} , diversity, and haplotype-based metrics along autosomes and the X chromosome to identify footprints of divergent selection between ecotypes.

Methods

Data collection and preprocessing

We used raw whole-genome sequences produced in Carrier et al. (2022), focusing on samples collected from ear punches from boreal and migratory caribou populations in eastern Canada. Ecotype validation required at least two full years of telemetric tracking using GPS collars following the capture. The Val d'Or and Charlevoix populations were excluded because of their history of isolation or recent reintroduction. Samples showing elevated read-end nucleotide misincorporations

indicative of DNA degradation were also excluded. This resulted in 1) a low-coverage dataset of 111 caribou (40 migratory and 71 boreal), sequenced on NovaSeq 6000 (Illumina), and 2) a high-coverage dataset of 16 caribou (6 migratory and 10 boreal), sequenced on HiSeq 4000 (Illumina). Migratory samples represented both the Rivière-aux-Feuilles (Quebec) and Rivière-George (Quebec – Labrador) herds, while boreal samples were taken across the Quebec range of the connected metapopulation (Fig. 1A).

Both sets of raw reads were trimmed using fastp (Chen et al., 2018). We used bwa mem 0.7.18 (H. Li, 2013) with default setting to align trimmed reads on the Svalbard Reindeer (*R. tarandus platyrhynchus*) reference genome (GCA_949782905.1, Dussex et al., 2023). We used picard 3.1.0 (Picard Toolkit, 2019) to remove duplicate reads and clip overlapping ends of paired reads. We assessed the genome-wide individual depth of coverage after alignment and clean-up using mosdepth 0.3.5 (Pedersen & Quinlan, 2018). Sex assignments were verified from relative X- and Y-chromosome coverage (Fig. S1), leading to reassignment of two samples and exclusion of one sample with ambiguous coverage.

Population structure across ecotypes

We first assessed population structure in the low-coverage dataset using a genotype likelihood approach in ANGSD v0.940. Sites on autosomes presenting polymorphic SNPs were first assessed using `angsd -GL 2 -baq 2 -remove_bads 1 -minMapQ 30 -minQ 20 -skipTriallelic 1 -uniqueOnly 1 -only_proper_pairs 1`. For SNPs with at least

90% of samples (-setMinInd 0.9) with $\geq 1X$ (-setMinDepthInd 1), total depth under 8 times the sampling size (-setMaxDepth), and minor allele frequency over 5% (-minMaf 0.05), we ran ngsParalog (Linderoth, 2018) following Dallaire et al. (2023) to identify positions at which reads are likely to be mismapped due to paralogous sequence or repeated elements. ngsParalog likelihood ratios were compared to a χ^2 distribution and SNPs with a p value (adjusted by applying the Bonferroni procedure) under the threshold of 0.001 were considered as deviating from expecting patterns of heterozygosity and read ratio, likely to produce biased genotype likelihoods, and as such were excluded from the SNP list.

We calculated genotype likelihoods for filtered SNPs in angsd and used ngsLD (Fox et al., 2019) to estimate linkage disequilibrium (LD) between SNPs within 500kb of each other. SNPs were iteratively pruned such that no pair within 100 kb had $r^2 > 0.1$. We used the LD-pruned genotype likelihoods to estimate relatedness between individuals in ngsRelate (Hanghøj et al., 2019). For pairs with KING kinship > 0.09 (second-degree relatives, Manichaikul et al., 2010), we removed one at random, retaining females (when possible) to maximize the sample available for X-chromosome analyses.

We conducted principal component analysis (PCA) performed on the LD-pruned dataset with PCAngsd v1.10 (Meisner & Albrechtsen, 2018). We then characterized population structure in more detail using NGSadmix (Skotte et al., 2013), estimating individual ancestry proportions across a range of ancestral population numbers ($K = 1 - 8$). For each value of K, 50 independent replicates were

run. Replicates were clustered using CLUMPAK (Kopelman et al., 2015), and ancestry coefficients from the major mode were averaged for visualization. Model support was assessed from replicate consistency and ΔK (Evanno et al., 2005).

Demographic inference

We investigated the history of divergence between the migratory and boreal ecotypes by conducting demographic inference using fastsimcoal 2.28 (Excoffier et al., 2021). Rather than pooling all individuals within each ecotype, we restricted this analysis to two representative subsets to avoid conflating within-ecotypes population structure with the migratory-boreal divergence signal. As such, we first computed sample allelic frequency (SAF) likelihood for the Rivières-aux-Feuilles migratory herd ($n = 18$), then the boreal samples within the Nord-du-Québec region ($n = 19$, Fig. 1A). This was done using `angsd -dosaf 5 -doMinorMajor 4` and all filters mentioned above, except for minimal MAF, in order to include rare variants and invariant sites. We used a copy of the reference genome where we masked regions within 75 bp of a deviant SNPs identified by `ngsParalog`, to ignore repeated and paralogous sequences that introduce uncertainty on our read alignments and distort the SFS (Dallaire et al., 2023).

We used `winsfs` (Rasmussen et al., 2022) on our SAF likelihood by ecotype to produce folded a 2D-SFS. This was done by chromosome for all autosomes, after which we summed the SFS. We compared four two-population models representing

strict isolation (SI), isolation with migration (IM), secondary contact (SC), and ancient migration (AM). For the best supported models, we tested if population growth or decline improved their fit and estimated confidence intervals (95%) around demographic parameters (Supplementary Material).

Detecting the footprint of divergent selection between ecotypes

We estimated bootstrapped F_{ST} (bF_{ST}) and d_{xy} between the two ecotypes, then θ_w , θ_π , and Tajima's D within the two ecotypes in 50 kb overlapping windows (step of 10 kb) along all autosomes and the chrX (Supplementary Material), after recomputing SAF and SFS as above on all migratory, then all boreal samples. Windows with the bF_{ST} in the top 0.2% across autosomes or on chrX were defined as peaks of differentiation and considered as candidate regions for divergent selection between ecotypes. We complemented our F_{ST} approach with the cross-population extended haplotype by length (XP-nSL) in selscan v.3.0.0 (Szpiech & Hernandez, 2014), which detects differences in haplotype length between populations. We first imputed and phased our low-coverage dataset in Glimpse 2.0.1 (Rubinacci et al., 2021) after building a reference panel with the high-coverage dataset (Supplementary Material). We used the imputed genotypes to calculate XP-nSL in selscan between the migratory and boreal population. We then estimated the average normalized XP-nSL in sliding windows of 50 kb (step of 10 kb, as for previous statistics) and discarded windows containing ≤ 10 SNPs. We compared the XP-nSL distribution in peaks of

differentiation (windows with bF_{ST} in the top 0.2%) and the genomic background (Supplementary Material), as well as the overlap between peaks of differentiation and the windows in the top 0.2% of absolute XP-nSL.

We compared θ statistics, Tajima's D, and d_{xy} in peaks of bF_{ST} or XP-nSL and the genomic background using Cliff's delta with block bootstrapping (Supplementary Material). We used both the raw d_{xy} and one corrected for θ_{π} (averaged across ecotypes), to which it was highly correlated. This approach is conceptually related to F_{ST} , in that both use within-population diversity to contextualize a measure of divergence. This residual-based correction is analogous to D_A (Nei, 1987), acts as a complementary measure of differentiation, and should be less sensitive to regions of low diversity than F_{ST} (Cruickshank & Hahn, 2014). To place our peaks of differentiation associated with divergent selection between the migratory and boreal ecotypes in Quebec and Labrador in the context of a previous study (Prunier et al., 2022), we mapped the flanking regions of 15 previously identified CNVs with adaptive potential to the Svalbard reindeer assembly using minimap2 (H. Li, 2018) (see Table S2) and compare their genomic positions with our candidate regions.

Annotation and enrichment of gene ontology terms

To test if some gene functions were overrepresented in putative targets of selection, we ran Gene Ontology (GO) term enrichment analyses. Predicted genes were annotated by similarity to UniProt/Swiss-Prot using BLASTx, retaining genes with high-

confidence matches (>70% query coverage and >50% identity). This yielded 19,507 genes with predicted functions. We created three lists of candidate genes: those overlapping with the windows with 1) the top 0.2% bF_{ST} 2) the top 0.2% absolute XP-nSL, and 3) the top 1% of both bF_{ST} and XP-nSL. We further divided the XP-nSL candidate genes for those with signs of position selection in migratory ($XP-nSL > 0$) or boreal ($XP-nSL < 0$) populations. Redundant nearby gene annotations were manually collapsed before enrichment analyses. We ran topGO 2.58 (Alexa & Rahnenführer, 2017) on each list of genes, using all annotated genes on autosomes and X chromosomes as the background set. Because GO terms are hierarchically dependent, we used the weight01 algorithm without additional multiple-testing correction and interpreted enrichment results as exploratory.

Results

Data preparation and population structure

Processing of raw reads yielded an average depth of coverage of 2.46X (sd = 0.41) for 111 low-coverage samples (including 62 females) (Fig. S2). We identified a total of 13,131,713 SNPs across autosomes and chrX in the low-coverage dataset (Table S1). ngsParalog detected 2.88% of SNPs on autosomes and 13.35% on chrX as deviating from expected patterns of heterozygosity and allelic balance. For SFS based analyses, we masked low-confidence genomic regions within 75 bp of those deviant SNPs, which accounted for a total of 0.45% of autosome length (1.02% of chrX). By

using NGSrelate on the LD-pruned autosome low-coverage dataset (820,568 SNPs), we found one pair of samples with KING-robust relatedness coherent with full-siblings or parent-offspring relationship (> 0.13), and five pairs with KING between 0.09 and 0.13.

PCA and admixture analyses confirmed clear genetic separation between migratory and boreal ecotypes (Fig. 1b), with admixture apparent in boreal populations of the Caniapiscou and Nord-du-Québec region (Fig. 2a). Among the boreal populations, substructure was evident in both the PCA (Fig. 1b) and admixture at $K=4$ (Fig. 2a), broadly dividing into western, central, and eastern groups, with individuals at lower latitudes showing purer ancestry than those at the northern edge of the range (Fig. 2B).

Demographic inference of the divergence of ecotypes

Among the four demographic models for the divergence of the migratory and boreal ecotypes tested in fastsimcoal, the secondary contact model (SC) provided the best fit to the observed 2D-SFS (Fig. 3a), receiving the lowest AIC score across replicates (Fig. 3f). We considered isolation with migration (IM) as an alternative model as it showed the second lowest AIC value. For their run with the lowest AIC, both the IM and SC models showed simulated allele frequencies (Fig. 3b-c) similar to the observed 2D-SFS, with discrepancies more pronounced in the outer cells of the SFS (Fig. 3d-e). Adding growth factors to either or both populations did not improve the fit of the IM or SC model (Fig. S3), and as such we interpreted models with constant

effective population sizes (Fig. 3g). Both models showed similar divergence time and N_e , with migratory N_e more than twice the boreal N_e (Table 1). The models mainly differed in the timing of migration: while IM included constant and low gene flow from divergence to present, SC was characterized by a period of isolation after divergence, followed by subsequent (95% CI: 118 – 844 generations ago) gene flow with migration rates slightly higher than those inferred from IM (Table 1).

Both models inferred migration rates that were approximately twofold higher from migratory to boreal population than in the reverse direction (Table 1). After converting migration rates to biologically intuitive forward-in-time migrants per generation, estimated gene flow was slightly higher from migratory to boreal than from boreal to migratory populations. Nevertheless, the substantial overlap between the 95% confidence intervals suggests limited support for asymmetry in gene flow between ecotypes since divergence.

Imputation of low-coverage data and validation

We called genotypes using the high-coverage data ($n = 16$, including 9 females, mean depth of coverage = 36.8X, $sd = 4.66$) on 29,466,817 sites across autosomes and 858,120 on chrX to build a phased reference for imputation of the low-coverage genotype likelihood. After imputation, we retained 9,824,284 and 156,455 SNPs on autosomes and chrX respectively with good imputation quality and $MAF > 0.05$. By comparing genotypes called from high-coverage data and imputed from subsampled reads for the same 19 samples across all populations studied, we found that samples

displayed between 98.6 and 99.2% of genotypes in concordance across all polymorphic SNPs (MAF > 1% in high-coverage samples). This percentage of concordance increased to 99.9% on SNPs with low MAF (1 – 5%) and reached 97.9% at higher MAF (40 – 50%). Migratory and boreal samples had similar genotype concordance after imputation (Fig. S4)

Detection of divergent selection between the boreal and migratory ecotypes

Autosome-wide F_{ST} between migratory and boreal populations ranged between 0.021 and 0.026, while chrX had an average F_{ST} of 0.036 (Fig. S5). Mean permuted F_{ST} across 10 replicates averaged at 0.006 (0.009 on chrX) with little variation across 50kb windows (Fig. S5), leading to windowed F_{ST} and bF_{ST} (bootstrapped $F_{ST} = F_{ST} - \text{mean permuted } F_{ST}$) values that were highly correlated ($r_{\text{Pearson}} = 0.994$, Fig. S6). Across autosomes and chrX, 3,378 windows (1.41%) showed a mean normalized XP-nSL above 2 (longer haplotypes in migratory than boreal), while 3,555 windows (1.48%) had a mean normalized XP-nSL below -2 (longer haplotypes in boreal than migratory), suggesting that positive selection acted on both ecotype to a comparable extent, although targeting different genomic regions and genes. bF_{ST} and absolute normalized XP-nSL showed a Pearson correlation of $r^2 = 0.41$.

The windows displaying the top 0.2% bF_{ST} ($n = 479$, $bF_{ST} > 0.090$ on autosomes, $bF_{ST} > 0.174$ on chrX) were arranged in 107 non-overlapping peaks across the genome, 48 of which overlapped windows with $|XP-nSL| > 2$. The top bF_{ST} windows on

315 autosomes had a median absolute normalized XP-nSL of 1.60 (Fig. 4b), compared to
316 an expected median of 0.43 (sd = 0.05) under block bootstrapping of the autosomal
317 genome, which represent a large effect size (Cliff δ = 0.65, Table S3). Among known
318 CNVs with adaptive potential in migratory or boreal caribou (Prunier et al., 2022),
319 three overlapped the top 0.2% bF_{ST} windows.

320 The windows displaying the top 0.2% absolute normalized XP-nSL ($n = 478$,
321 $|XP-nSL| > 3.34$ on autosomes, $|XP-nSL| > 4.13$ on chrX) showed 51 distinct peaks with
322 $XP-nSL > 0$ and 68 distinct peaks with $XP-nSL < 0$. The top $|XP-nSL|$ windows on
323 autosomes had a median bF_{ST} of 0.064, compared to an expected median of 0.015
324 (sd = 0.001), which represented a very large effect size (Cliff δ = 0.95). The top 0.2%
325 bF_{ST} and top 0.2% $|XP-nSL|$ had 62 windows (22 distinct peaks) in common, and
326 relaxing thresholds to the top 1% identified 484 windows (129 distinct peaks) in
327 overlap.

328 bF_{ST} and $|XP-nSL|$ were both poorly correlated to d_{xy} and θ metrics, with the
329 strongest correlation being between $|XP-nSL|$ and minimum θ_{π} across ecotypes ($r^2 = -$
330 0.212) (Fig. S6). However, we detected a moderate effect size when comparing
331 autosomal genome-wide θ metrics to median in peaks of bF_{ST} (Cliff δ = -0.40 to -0.29,
332 Table S3, Fig. S7) and peaks of $|XP-nSL|$ (δ = -0.65 to -0.41, Fig. S8), suggesting that
333 genomic regions under putative selection showed decreased genetic diversity. We
334 also observed that absolute difference in Tajima's D between ecotype was stronger
335 in peaks of bF_{ST} (δ = 0.482) and even more pronounced in peaks of $|XP-nSL|$ (δ = 0.765),

where the ecotype on which positive selection was inferred (based on the sign of XP-nSL) consistently showed the lowest Tajima's D (Fig. 5).

Gene ontology enrichment

We confidently annotated by homology the function of 18,444 genes across chromosomes. We build three gene lists (Table S4) to reveal Gene Ontology (GO) terms that were more frequent than expected: genes overlapping 1) top 0.2% bFST windows (169 genes); 2) top 0.2% |XP-nSL| windows (136 genes); and 3) both top 1% bFST and top 1% |XP-nSL| windows (178 genes). The second list included 85 genes with XP-nSL > 0 (inferred positive selection in the migratory ecotype) and 51 with XP-nSL < 0 (positive selection in the boreal ecotype). Analyses revealed many enriched GO terms (p-value < 0.05, Table S5), with notable mentions including cuticle development, regulation of ossification, actin filament polymerization, hair follicle development, locomotory exploration behavior, and visual perception.

Discussion

Leveraging low-coverage whole-genome sequencing across 121 migratory and boreal caribou from Quebec and Labrador, we found weak population structure between the ecotypes (genome-wide $F_{ST} = 0.02$), consistent with recent split and gene flow rather than long-standing isolation. Our demographic modelling suggest that the migratory and boreal ecotypes diverged around the onset of the Holocene, through an initial period of allopatry followed by gene flow. Despite the recent divergence, we found

numerous distinct peaks of differentiation that coincided with longer haplotypes in one ecotype than the other, which suggest that positive selection has shaped differentiation at specific loci. The moderate magnitude of these peaks ($F_{ST} < 0.2$) and only modest reductions in diversity within them point to recent, incomplete soft sweeps acting on standing genetic variation, rather than hard sweeps on new mutations. Such signals would likely have been harder to detect from differentiation-based metrics alone (Zheng & Wiehe, 2019), underscoring the value of haplotype-based statistics in a system this young.

Post-glacial divergence of caribou ecotypes

Our demographic modeling of the evolutionary trajectories of the migratory and boreal ecotypes of caribou in Quebec and Labrador points toward their recent divergence through initial allopatry followed by gene flow, with an estimated time since population split of 993 – 1,670 generations (IC 95%). Assuming a generation time of 7 years (COSEWIC, 2017), this translates to 6,951 to 11,690 years ago. While the Laurentide ice sheet that covered most of North America above the 45th parallel started melting 18,000 years ago, the current range of the populations studied here were among the last landscapes to remain glaciated, until roughly 6,000 years ago (Dalton et al., 2020). As such, our estimates are consistent with the initiation of reproduction isolation between ecotypes during the deglaciation period. Pollen evidence suggest that, at the height of glaciation, tundra was mostly absent from the eastern regions of North America outside a thin strip along the ice margin (Overpeck et al., 1992; Williams et al., 2000; Li et al., 2024a). There is, however, evidence for

multiple geographically distinct glacial refugia for caribou further south (Klüttsch et al., 2012), the easternmost candidate being the Appalachian Mountains, which likely supported a common gene pool rather than the alternative migratory strategies observed today.

Based on early Holocene fossil and pollen records, Bergerud et al. (2008) suggested two concurrent routes for the northward expansion of this ancestral caribou population, starting 13,000 – 11,000 years ago: 1) toward the forested Great Lakes, then following the advance of the boreal forest to higher latitude, and 2) toward the Canadian Maritimes, St-Lawrence River coast, then Labrador, where a taiga-tundra complex followed the retreat of the ice sheet (Payette et al., 2002). Our demographic modelling lends support to a similar scenario of two potential routes, where allopatry between alternate recolonization routes displaying different habitats could have favored the adaptation of populations through diverging ecotypes, before their secondary contact after the end of deglaciation (826 – 5,908 years ago in our model). We note, however, that failure to account for N_e fluctuations can bias support toward secondary contact models (Momigliano et al., 2021). We therefore treat the SC/IM distinction as tentative considering the wide variation of population size in migratory herds (Morneau & Payette, 2000). We also emphasize that N_e values estimated here should be interpreted as long-term historical effective population sizes, providing insight in the evolutionary history of ecotypes rather than reflecting recent declines in population N_e , as inferred in Dedato et al. (2022).

A recent genomic comparison of ecotypes in Quebec and Ontario found boreal populations to be genetically connected across provinces, while migratory herds on either side of James Bay showed limited genetic similarity (Delgado et al., 2026). This pattern is consistent with the possibility that the migratory ecotype evolved independently in the two regions, rather than originating from a single ancestral migratory population. In Ontario, it has been proposed that the migratory ecotype could be derived from introgression from the Beringian lineage (Klüttsch et al., 2016). However, the traces of this introgression are minimal in Quebec-Labrador populations (Yannic et al., 2018). As such, we argue that repeated ecotype formation in caribou could stem from the underlying behavioural plasticity between migratory and sedentary strategies documented across populations (Theoret et al., 2022), followed by adaptation to local environmental conditions.

Soft selective sweeps across the genome

Despite the recent divergence of ecotypes and the contemporary gene flow, we found patterns consistent with divergent selection. Signals of F_{ST} and XP-nSL were only partly congruent, with roughly half of differentiation peaks also showing differences in haplotype length between ecotypes. This partial overlap could reflect false positives but also different sensitivities between methods: XP-nSL can detect younger, in-progress sweeps before allele frequencies diverge enough to elevate F_{ST} , and this time lag between haplotype- and frequency-based methods is well documented (Nielsen, 2005; Sabeti et al., 2006). Tajima's D was consistently reduced, although not necessarily negative, for the ecotype under inferred selection

at XP-nSL peaks, and d_{xy} remained higher than expected from its genome-wide relationship with θ_{π} . Both patterns are pointing to a recent, ecotype-specific reduction in diversity rather than the long-standing effect of low recombination (Cruickshank & Hahn, 2014). Together, these metrics converge most clearly on XP-nSL peaks, and their combined signature (modest θ reduction, moderate bF_{ST} , and a relative enrichment in rare alleles) is consistent with ongoing, incomplete sweeps rather than fixed, hard sweeps. This underscores the added value of multiple, complementary metrics to detect selection in young and diverging lineages.

This selective signature of divergence contrasts with the case of the Svalbard reindeer ecotype, whose colonisation of the Eurasian Arctic archipelagos appears to have occurred during the early to mid-Holocene, with mitochondrial divergence among the island populations estimated at ~8,000 years ago (Hold et al., 2024). Genomic analyses revealed a selective signature characterized by pronounced drops in diversity around differentiation peaks and a large, well-resolved set of GO terms tied to cold tolerance, fat metabolism, and circadian regulation (Dusseux et al., 2025). This architecture is the result of the survival and adaptation of the Svalbard population in the face of severe bottlenecks, hostile environments, and the absence of gene flow with population outside the island. The comparison with our system highlights the importance of demography and selective strength on the shape and detectability of genomic footprints of local adaptation. Nonetheless, the convergence of multiple genomic signals allowed us to confidently identify targets of divergent selection in the ecotype pair in Quebec and Labrador, where divergence is

recent and gene flow ongoing, conditions under which selection signatures are expected to be faint and easily missed by any single method.

Local adaptation through complex traits

The genomic architecture of local adaptation we revealed here can be qualified as highly polygenic, involving genes with diverse functions, as can be expected given the diversity of traits that underlie the ecotypic differences between boreal and migratory caribou. Because these ecotypes occupy different habitats for most of the year, they are exposed to differences in abundance and variety of food sources (Webber et al., 2022), exposure to parasites (Witter et al., 2012; Raponi et al., 2018) and predators (Leblond et al., 2016; Michelot et al., 2024), and energetic demands linked to movement across the landscape. Boreal caribou populations also occur at lower densities (Callaghan et al., 2010) than migratory herds, which can aggregate by the tens of thousands during spring and summer. These ecological differences may generate trade-offs and adaptive pressures, which could be reflected in the elevated differentiation and signatures of selective sweeps we detected at candidate genes. Circadian clock genes have repeatedly been associated with migration propensity or timing in salmonids (O'Malley et al., 2010), birds (Bossu et al., 2022), and even caribou (Cavedon et al., 2022), but here we did not find any such genes in the candidate windows under selection. This supports the idea that the mutations driving the genomic patterns investigated are linked to local adaptation following the divergence in migratory strategy, rather than reflecting the causal mechanisms leading to the migratory behaviour.

Among the outlier loci, several candidate genes point to plausible axes of ecotypic divergence. A group of genes involved in bone and connective tissue development stood out, including osteocalcin, a key regulator of bone mineralization. DKK1, an antagonist of canonical Wnt/ β -catenin signaling (Chen et al., 2008), and SMAD2, a mediator of TGF- β signaling (Matsumoto et al., 2012), were also detected as outliers. Both these signaling pathways and osteocalcin are directly involved in antler growth in cervids (Baxter et al., 1999; Mount et al., 2006; Li et al., 2024b). This convergence of independently detected candidate genes on antler-relevant pathways suggests that this group of candidates may reflect selection on antler-related traits. Antlers are linked to both male and female caribou fitness through access to winter forage, intra and inter-sexual competition, and defense against predators (Schaefer & Mahoney, 2001), but also represent high energetic costs (Moen & Pastor, 1998). As such, they provide a prime target for adaptive trade-offs in the varying environments occupied by ecotypes. However, we note that these genes are broadly pleiotropic and could equally underlie other aspects of growth or bone turnover unrelated to antlers.

A further set of outliers, although not supported by formal GO enrichment analyses, is loosely associated with mitochondrial structure and energy metabolism. These include several components of the mitochondrial respiratory chain and its assembly machinery (COX6C, UQCC4, PDSS2), mitochondrial structure (MIC10, MIC27, TIMM50, TOMM6), or mitochondrial energy production (ECI1, BCKDHB). This pattern is noteworthy given the strong contrast in locomotor demands between

migratory and boreal caribou. Long-distance migration requires sustained aerobic energy production, and comparative studies in migratory birds have shown that migration is associated with increased mitochondrial abundance and oxidative capacity in flight muscle (Coulson et al., 2024; Rhodes et al., 2024). Similar seasonal increases in mitochondrial oxidative enzymes and lipid metabolism have also been documented in migratory bats (McGuire et al., 2013). Although our data do not establish a direct functional link between these candidate genes and aerobic performance, their involvement in mitochondrial structure and energy metabolism provides a plausible functional context for their association with the migratory ecotype.

Interestingly, three of the SNP-based peaks of differentiation were overlapping copy-number variants previously identified as potentially involved in the local adaptation of migratory and boreal caribou in Quebec and Labrador by Prunier et al. (2022). In these cases (e.g. Fig. 4b), the SNPs and CNV are most likely in physical linkage disequilibrium, and while we cannot confidently identify the mutation creating gains in fitness behind the inferred selection, we can safely assume the CNV has more potential to create phenotypic effects than single SNPs, through changes in gene dosage, expression, or the deletion or duplication of coding regions (Ohno, 1970; Iskow et al., 2012). While we did not test for their presence, chromosomal inversions might be another type of structural variants that underly the differentiation in SNPs observed between ecotypes, for example in large regions of consecutive top candidate F_{ST} windows such as on chromosome 33 (~350 Mb, Fig. 4b).

509 Conclusion

510 While the genomic study of speciation has often focussed on lineages that are
511 already advanced on the path toward reproductive isolation, the study of ecotypes
512 can inform on the early establishment of such isolation. Our study adds evolutionary
513 context for the mosaic of ecotypes observed around the globe in *Rangifer tarandus*.
514 Our results support the view that the migratory and sedentary ecotypes are not fixed
515 evolutionary endpoints but a dichotomy that can re-emerge from standing genetic
516 variation whenever the opportunity arise through glacial cycles. This process is closer
517 to repeated ecological sorting than to the fixation of a conserved genomic basis for
518 movement strategy. In the present case, the complex and shifting landscapes of the
519 deglaciation period may have allowed a period of allopatry that led to the adoption of
520 distinct life-history traits and initiated the process of local adaptation that we observe
521 through the footprint of divergent selection across the genome.

522 Caribou ecotypes face mounting challenges, amongst which are the loss of
523 safe, effective migration corridors (Joly et al., 2025) and the shrinking of large,
524 undisturbed landscapes (Mackey et al., 2023) needed to avoid predation (Dickie et
525 al., 2023). Preserving genetic diversity within both ecotypes should help support the
526 species' capacity to adapt to an increasingly fragmented landscape and a warming
527 climate. Because no genetic variants appear to act deterministically on ecotype,
528 gene flow between migratory and boreal caribou is unlikely to erode either strategy
529 and may instead help maintain diversity, or even supplement demographically
530 declining local populations. Clarifying how, when, and where this connectivity is

531 maintained, and quantifying the impact of immigration on the size of smaller
532 populations, will be important next steps in translating our results into management
533 considerations.

534

535 Acknowledgements

536 [REDACTED]

537 Authors contribution

538 [REDACTED]

539 Competing Interests

540 The authors do not declare any competing interests.

541 Data Archiving

542 The bioinformatic pipeline for the analyses of low-coverage data can be found at
543 [REDACTED]. All raw sequencing data analysed in this study are available on Short
544 Read Archive in Bioprojects PRJNA843030 (high coverage, Prunier et al., 2022) and
545 PRJNA846266 (low coverage, Carrier et al., 2022). Capture site information was
546 anonymized to avoid the disclosure of potentially sensitive information on the
547 geographic distribution of sampled caribou. Access requests for metadata can be
548 directed to [REDACTED].

549 Research Ethics Statement

550 Live capture and sample collection followed the Canadian Council on Animal Care
551 guidelines, and all procedures were approved by Animal Care Committees
552 ([REDACTED]).

554 References

- 555 Alexa, A. R., & Rahnenführer, J. (2017). *topGO* [Computer software]. Bioconductor.
 556 <https://doi.org/10.18129/B9.BIOC.TOPGO>
- 557 Backenstose, N. J. C., MacGuigan, D. J., Osborne, C. A., Bernal, M. A., Thomas, E. K.,
 558 Normandeau, E., Yule, D. L., Stott, W., Ackiss, A. S., Albert, V. A., Bernatchez,
 559 L., & Krabbenhoft, T. J. (2024). Origin of the Laurentian Great Lakes fish fauna
 560 through upward adaptive radiation cascade prior to the Last Glacial
 561 Maximum. *Communications Biology*, 7(1), 978.
 562 <https://doi.org/10.1038/s42003-024-06503-z>
- 563 Baxter, B. J., Andrews, R. N., & Barrell, G. K. (1999). Bone turnover associated with
 564 antler growth in red deer (*Cervus elaphus*). *The Anatomical Record*, 256(1),
 565 14–19. [https://doi.org/10.1002/\(SICI\)1097-](https://doi.org/10.1002/(SICI)1097-0185(19990901)256:1%3C14::AID-AR3%3E3.0.CO;2-A)
 566 [0185\(19990901\)256:1%3C14::AID-AR3%3E3.0.CO;2-A](https://doi.org/10.1002/(SICI)1097-0185(19990901)256:1%3C14::AID-AR3%3E3.0.CO;2-A)
- 567 Bergerud, A. T., Luttich, S. N., & Camps, L. (2008). *The Return of Caribou to Ungava*.
 568 McGill-Queen's University Press.
- 569 Bolnick, D. I., & Fitzpatrick, B. M. (2007). Sympatric Speciation: Models and
 570 Empirical Evidence. *Annual Review of Ecology, Evolution, and Systematics*,
 571 38(1), 459–487. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095804>
- 572 Bossu, C. M., Heath, J. A., Kaltenecker, G. S., Helm, B., & Ruegg, K. C. (2022). Clock-
 573 linked genes underlie seasonal migratory timing in a diurnal raptor.
 574 *Proceedings of the Royal Society B: Biological Sciences*, 289(1974),
 575 20212507. <https://doi.org/10.1098/rspb.2021.2507>
- 576 Boulet, M., Couturier, S., Côté, S. D., Otto, R. D., & Bernatchez, L. (2007). Integrative
 577 use of spatial, genetic, and demographic analyses for investigating genetic
 578 connectivity between migratory, montane, and sedentary caribou herds.
 579 *Molecular Ecology*, 16(20), 4223–4240. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-294X.2007.03476.x)
 580 [294X.2007.03476.x](https://doi.org/10.1111/j.1365-294X.2007.03476.x)
- 581 Butlin, R. K., Saura, M., Charrier, G., Jackson, B., André, C., Caballero, A., Coyne, J.
 582 A., Galindo, J., Grahame, J. W., Hollander, J., Kemppainen, P., Martínez-
 583 Fernández, M., Panova, M., Quesada, H., Johannesson, K., & Rolán-Alvarez,
 584 E. (2014). PARALLEL EVOLUTION OF LOCAL ADAPTATION AND
 585 REPRODUCTIVE ISOLATION IN THE FACE OF GENE FLOW: PARALLEL LOCAL
 586 ADAPTATION. *Evolution*, 68(4), 935–949. <https://doi.org/10.1111/evo.12329>
- 587 Callaghan, C., Viric, S., & Duffe, J. (2010). *Woodland caribou, boreal population,*
 588 *trends in Canada* (No. 11; Canadian Biodiversity: Ecosystem Status and
 589 Trends 2010, p. 36). Canadian Councils of Resource Ministers.
 590 <https://doi.org/10.5203/LWBIN.EC.2010.4>
- 591 Carrier, A., Prunier, J., Poisson, W., Trottier-Lavoie, M., Gilbert, I., Cavedon, M.,
 592 Pokharel, K., Kantanen, J., Musiani, M., Côté, S. D., Albert, V., Taillon, J.,
 593 Bourret, V., Droit, A., & Robert, C. (2022). Design and validation of a 63K
 594 genome-wide SNP-genotyping platform for caribou/reindeer (*Rangifer*

- tarandus). *BMC Genomics*, 23(1), 687. <https://doi.org/10.1186/s12864-022-08899-6>
- Castillo, D. G., Barton, N., Faria, R., Larsson, J., Stankowski, S., Butlin, R., Johannesson, K., & Westram, A. M. (2024). Predicting rapid adaptation in time from adaptation in space: A 30-year field experiment in marine snails. *SCienCe AdvAnCeS*.
- Cavedon, M., vonHoldt, B., Hebblewhite, M., Hegel, T., Heppenheimer, E., Hervieux, D., Mariani, S., Schwantje, H., Steenweg, R., Theoret, J., Watters, M., & Musiani, M. (2022). Genomic legacy of migration in endangered caribou. *PLOS Genetics*, 18(2), e1009974. <https://doi.org/10.1371/journal.pgen.1009974>
- Chen, L., Wang, K., Shao, Y., Huang, J., Li, X., Shan, J., Wu, D., & Zheng, J. J. (2008). Structural Insight into the Mechanisms of Wnt Signaling Antagonism by Dkk. *Journal of Biological Chemistry*, 283(34), 23364–23370. <https://doi.org/10.1074/jbc.M802375200>
- Chen, S., Zhou, Y., Chen, Y., & Gu, J. (2018). fastp: an ultra-fast all-in-one FASTQ preprocessor. *Bioinformatics*, 34(17), i884–i890. <https://doi.org/10.1093/bioinformatics/bty560>
- Coates, S. E. R., Comeault, A. A., Wood, D. P., Fay, M. F., Creer, S., Osborne, O. G., Dunning, L. T., & Papadopoulos, A. S. T. (2025). Plastic responses to past environments shape adaptation to novel selection pressures. *Proceedings of the National Academy of Sciences*, 122(5), e2409541122. <https://doi.org/10.1073/pnas.2409541122>
- COSEWIC. (2011). *Designatable Units for Caribou (Rangifer tarandus) in Canada* (p. 88). Committee on the Status of Endangered Wildlife in Canada.
- Coulson, S. Z., Guglielmo, C. G., & Staples, J. F. (2024). Migration increases mitochondrial oxidative capacity without increasing reactive oxygen species emission in a songbird. *Journal of Experimental Biology*, 227(9), jeb246849. <https://doi.org/10.1242/jeb.246849>
- Cruickshank, T. E., & Hahn, M. W. (2014). Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. *Molecular Ecology*, 23(13), 3133–3157. <https://doi.org/10.1111/mec.12796>
- Dallaire, X., Bouchard, R., Hénault, P., Ulmo-Diaz, G., Normandeau, E., Mérot, C., Bernatchez, L., & Moore, J.-S. (2023). Widespread Deviant Patterns of Heterozygosity in Whole-Genome Sequencing Due to Autopolyploidy, Repeated Elements, and Duplication. *Genome Biology and Evolution*, 15(12), evad229. <https://doi.org/10.1093/gbe/evad229>
- Dalton, A. S., Margold, M., Stokes, C. R., Tarasov, L., Dyke, A. S., Adams, R. S., Allard, S., Arends, H. E., Atkinson, N., Attig, J. W., Barnett, P. J., Barnett, R. L., Batterson, M., Bernatchez, P., Borns, H. W., Breckenridge, A., Briner, J. P., Brouard, E., Campbell, J. E., ... Wright, H. E. (2020). An updated radiocarbon-based ice margin chronology for the last deglaciation of the North American Ice Sheet Complex. *Quaternary Science Reviews*, 234. <https://doi.org/10.1016/j.quascirev.2020.106223>

- Dedato, M. N., Robert, C., Taillon, J., Shafer, A. B. A., & Côté, S. D. (2022). Demographic history and conservation genomics of caribou (*Rangifer tarandus*) in Québec. *Evolutionary Applications*, 15(12), 2043–2053. <https://doi.org/10.1111/eva.13495>
- Delgado, M. L., Manseau, M., Fournier, C., Martchenko, D., Taylor, R. S., Solmundson, K., Rodgers, A. R., Jackson, J., Trim, V., Kennah, J., & Wilson, P. (2026). Genomic insights into the recent evolution of ecotypes: delineating at-risk caribou populations with high gene flow. *BMC Genomics*. <https://doi.org/10.1186/s12864-026-13006-0>
- Dickie, M., Sherman, G. G., Sutherland, G. D., McNay, R. S., & Cody, M. (2023). Evaluating the impact of caribou habitat restoration on predator and prey movement. *Conservation Biology*, 37(2), e14004. <https://doi.org/10.1111/cobi.14004>
- Dussex, N., Bieker, V. C., Sun, X., Le Moullec, M., Ersmark, E., Røed, K. H., Speakman, J. R., Loe, L. E., Dalén, L., Hansen, B. B., & Martin, M. D. (2025). The Genomic Basis of the Svalbard Reindeer's Adaptation to an Extreme Arctic Environment. *Genome Biology and Evolution*, 17(9), evaf160. <https://doi.org/10.1093/gbe/evaf160>
- Dussex, N., Tørresen, O. K., van der Valk, T., Le Moullec, M., Veiberg, V., Tooming-Klunderud, A., Skage, M., Garmann-Aarhus, B., Wood, J., Rasmussen, J. A., Pedersen, Å. Ø., Martin, S. L. F., Røed, K. H., Jakobsen, K. S., Dalén, L., Hansen, B. B., & Martin, M. D. (2023). Adaptation to the High-Arctic island environment despite long-term reduced genetic variation in Svalbard reindeer. *iScience*, 26(10), 107811. <https://doi.org/10.1016/j.isci.2023.107811>
- Endler, J. A. (1977). *Geographic Variation, Speciation and Clines. (MPB-10), Volume 10*. Princeton University Press. <https://doi.org/https://doi.org/10.2307/j.ctvx5wbdg>
- Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE : a simulation study. *Molecular Ecology*, 14(8), 2611–2620. <https://doi.org/10.1111/j.1365-294X.2005.02553.x>
- Excoffier, L., Marchi, N., Marques, D. A., Matthey-Doret, R., Gouy, A., & Sousa, V. C. (2021). *fastsimcoal2* : demographic inference under complex evolutionary scenarios. *Bioinformatics*, 37(24), 4882–4885. <https://doi.org/10.1093/bioinformatics/btab468>
- Fancy, S. G., & White, R. G. (1985). Energy expenditures by caribou while cratering in snow. *Journal of Wildlife Management*, 49(4), 987–993. <https://doi.org/10.2307/3801385>
- Ferrer-Admetlla, A., Liang, M., Korneliussen, T., & Nielsen, R. (2014). On Detecting Incomplete Soft or Hard Selective Sweeps Using Haplotype Structure. *Molecular Biology and Evolution*, 31(5), 1275–1291. <https://doi.org/10.1093/molbev/msu077>

- 682 Foote, A. D. (2018). Sympatric Speciation in the Genomic Era. *Trends in Ecology &*
683 *Evolution*, 33(2), 85–95. <https://doi.org/10.1016/j.tree.2017.11.003>
- 684 Fox, E. A., Wright, A. E., Fumagalli, M., & Vieira, F. G. (2019). ngsLD: evaluating
685 linkage disequilibrium using genotype likelihoods. *Bioinformatics*, 35(19),
686 3855–3856. <https://doi.org/10.1093/bioinformatics/btz200>
- 687 Fuhrmann, N., Prakash, C., & Kaiser, T. S. (2023). Polygenic adaptation from
688 standing genetic variation allows rapid ecotype formation. *eLife*, 12, e82824.
689 <https://doi.org/10.7554/eLife.82824>
- 690 Hager, E. R., Harringmeyer, O. S., Wooldridge, T. B., Theingi, S., Gable, J. T.,
691 McFadden, S., Neugeboren, B., Turner, K. M., Jensen, J. D., & Hoekstra, H. E.
692 (2022). A chromosomal inversion contributes to divergence in multiple traits
693 between deer mouse ecotypes. *Science*, 377(6604), 399–405.
694 <https://doi.org/10.1126/science.abg0718>
- 695 Hanghøj, K., Moltke, I., Andersen, P. A., Manica, A., & Korneliussen, T. S. (2019). Fast
696 and accurate relatedness estimation from high-throughput sequencing data
697 in the presence of inbreeding. *GigaScience*, 8(5), giz034.
698 <https://doi.org/10.1093/gigascience/giz034>
- 699 Hoban, S., Kelley, J. L., Lotterhos, K. E., Antolin, M. F., Bradburd, G., Lowry, D. B.,
700 Poss, M. L., Reed, L. K., Storfer, A., & Whitlock, M. C. (2016). Finding the
701 Genomic Basis of Local Adaptation: Pitfalls, Practical Solutions, and Future
702 Directions. *The American Naturalist*, 188(4), 379–397.
703 <https://doi.org/10.1086/688018>
- 704 Hold, K., Lord, E., Brealey, J. C., Le Moullec, M., Bieker, V. C., Ellegaard, M. R.,
705 Rasmussen, J. A., Kellner, F. L., Guschanski, K., Yannic, G., Røed, K. H.,
706 Hansen, B. B., Dalén, L., Martin, M. D., & Dussex, N. (2024). Ancient reindeer
707 mitogenomes reveal island-hopping colonisation of the Arctic archipelagos.
708 *Scientific Reports*, 14(1), 4143. <https://doi.org/10.1038/s41598-024-54296-2>
- 709 Iskow, R. C., Gokcumen, O., & Lee, C. (2012). Exploring the role of copy number
710 variants in human adaptation. *Trends in Genetics*, 28(6), 245–257.
711 <https://doi.org/10.1016/j.tig.2012.03.002>
- 712 Jiggins, C. D. (2006). Sympatric Speciation: Why the Controversy? *Current Biology*,
713 16(9), R333–R334. <https://doi.org/10.1016/j.cub.2006.03.077>
- 714 Johannesson, K., Malmqvist, G., Leder, E., & Stankowski, S. (2026). Genomic
715 insights into the origin of ecotypes. *Trends in Ecology & Evolution*, 41(3), 245–
716 260. <https://doi.org/10.1016/j.tree.2025.11.011>
- 717 Joly, K., Beaupré, C., Fullman, T. J., Cameron, M. D., Barbour, N., & Gurarie, E. (2025).
718 Barrier impermeability is associated with migratory ungulate survival rates.
719 *Scientific Reports*, 16(1), 152. <https://doi.org/10.1038/s41598-025-31911-4>
- 720 Klütsch, C. F. C., Manseau, M., Trim, V., Polfus, J., & Wilson, P. J. (2016). The eastern
721 migratory caribou: the role of genetic introgression in ecotype evolution.
722 *Royal Society Open Science*, 3(2), 150469.
723 <https://doi.org/10.1098/rsos.150469>
- 724 Klütsch, C. F. C., Manseau, M., & Wilson, P. J. (2012). Phylogeographical Analysis of
725 mtDNA Data Indicates Postglacial Expansion from Multiple Glacial Refugia in

726 Woodland Caribou (*Rangifer tarandus caribou*). *PLoS ONE*, 7(12), e52661.
 727 <https://doi.org/10.1371/journal.pone.0052661>

728 Koch, E. L., Ravinet, M., Westram, A. M., Johannesson, K., & Butlin, R. K. (2022).
 729 Genetic architecture of repeated phenotypic divergence in *Littorina saxatilis*
 730 ecotype evolution. *Evolution*, 76(10), 2332–2346.
 731 <https://doi.org/10.1111/evo.14602>

732 Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015).
 733 Clumpak: a program for identifying clustering modes and packaging
 734 population structure inferences across K. *Molecular Ecology Resources*,
 735 15(5), 1179–1191. <https://doi.org/10.1111/1755-0998.12387>

736 Leblond, M., Dussault, C., Ouellet, J., & St-Laurent, M. (2016). Caribou avoiding
 737 wolves face increased predation by bears – Caught between *Scylla* and *C*
 738 *harybdis*. *Journal of Applied Ecology*, 53(4), 1078–1087.
 739 <https://doi.org/10.1111/1365-2664.12658>

740 Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in*
 741 *Ecology and Evolution*, 17(4), 183–189. <https://doi.org/10.1016/S0169->
 742 [5347\(02\)02497-7](https://doi.org/10.1016/S0169-5347(02)02497-7)

743 Levis, N. A., Isdaner, A. J., & Pfennig, D. W. (2018). Morphological novelty emerges
 744 from pre-existing phenotypic plasticity. *Nature Ecology & Evolution*, 2(8),
 745 1289–1297. <https://doi.org/10.1038/s41559-018-0601-8>

746 Levis, N. A., & Pfennig, D. W. (2016). Evaluating ‘Plasticity-First’ Evolution in Nature:
 747 Key Criteria and Empirical Approaches. *Trends in Ecology & Evolution*, 31(7),
 748 563–574. <https://doi.org/10.1016/j.tree.2016.03.012>

749 Li, C., Dallmeyer, A., Ni, J., Chevalier, M., Willeit, M., Andreev, A. A., Cao, X., Schild,
 750 L., Heim, B., & Herzschuh, U. (2024). *Global biome changes over the last*
 751 *21,000 years inferred from model-data comparisons*. *Vegetation*
 752 *Dynamics/Terrestrial Archives/Pleistocene*.
 753 <https://doi.org/10.5194/egusphere-2024-1862>

754 Li, C., Wang, W., Zhang, G., Ba, H., Liu, H., Wang, J., Li, W., Melino, G., & Shi, Y.
 755 (2024). Bone metabolism associated with annual antler regeneration: a deer
 756 insight into osteoporosis reversal. *Biology Direct*, 19(1), 123.
 757 <https://doi.org/10.1186/s13062-024-00561-3>

758 Li, H. (2013, March 16). *Aligning sequence reads, clone sequences and assembly*
 759 *contigs with BWA-MEM*. arXiv.Org. <https://arxiv.org/abs/1303.3997v2>

760 Li, H. (2018). Minimap2: pairwise alignment for nucleotide sequences.
 761 *Bioinformatics*, 34(18), 3094–3100.
 762 <https://doi.org/10.1093/bioinformatics/bty191>

763 Linderoth, T. (2018). *Identifying Population Histories, Adaptive Genes, and Genetic*
 764 *Duplication from Population-Scale Next Generation Sequencing*. University
 765 of California, Berkeley.

766 Lowry, D. B. (2012). Ecotypes and the controversy over stages in the formation of
 767 new species: STAGES IN SPECIATION. *Biological Journal of the Linnean*
 768 *Society*, 106(2), 241–257. <https://doi.org/10.1111/j.1095-8312.2012.01867.x>

769 Mackey, B., Campbell, C., Norman, P., Hugh, S., DellaSala, D. A., Malcolm, J. R.,
 770 Desrochers, M., & Drapeau, P. (2023). Assessing the Cumulative Impacts of
 771 Forest Management on Forest Age Structure Development and Woodland
 772 Caribou Habitat in Boreal Landscapes: A Case Study from Two Canadian
 773 Provinces. *Land*, 13(1), 6. <https://doi.org/10.3390/land13010006>
 774 Manichaikul, A., Mychaleckyj, J. C., Rich, S. S., Daly, K., Sale, M., & Chen, W.-M.
 775 (2010). Robust relationship inference in genome-wide association studies.
 776 *Bioinformatics*, 26(22), 2867–2873.
 777 <https://doi.org/10.1093/bioinformatics/btq559>
 778 Matsumoto, Y., Otsuka, F., Hino, J., Miyoshi, T., Takano, M., Miyazato, M., Makino, H.,
 779 & Kangawa, K. (2012). Bone morphogenetic protein-3b (BMP-3b) inhibits
 780 osteoblast differentiation via Smad2/3 pathway by counteracting Smad1/5/8
 781 signaling. *Molecular and Cellular Endocrinology*, 350(1), 78–86.
 782 <https://doi.org/10.1016/j.mce.2011.11.023>
 783 Maynard Smith, J., & Haigh, J. (1974). The hitch-hiking effect of a favourable gene.
 784 *Genetical Research*, 23(1), 23–35.
 785 <https://doi.org/10.1017/S0016672300014634>
 786 McGuire, L. P., Fenton, M. B., & Guglielmo, C. G. (2013). Seasonal upregulation of
 787 catabolic enzymes and fatty acid transporters in the flight muscle of
 788 migrating hoary bats, *Lasiurus cinereus*. *Comparative Biochemistry and*
 789 *Physiology Part B: Biochemistry and Molecular Biology*, 165(2), 138–143.
 790 <https://doi.org/10.1016/j.cbpb.2013.03.013>
 791 Meisner, J., & Albrechtsen, A. (2018). Inferring Population Structure and Admixture
 792 Proportions in Low-Depth NGS Data. *Genetics*, 210(2), 719–731.
 793 <https://doi.org/10.1534/genetics.118.301336>
 794 Messer, P. W., & Petrov, D. A. (2013). Population genomics of rapid adaptation by soft
 795 selective sweeps. *Trends in Ecology & Evolution*, 28(11), 659–669.
 796 <https://doi.org/10.1016/j.tree.2013.08.003>
 797 Michelot, C., Leclerc, M., Taillon, J., Dussault, C., Hénault Richard, J., & Côté, S. D.
 798 (2024). Evidence of migratory coupling between grey wolves and migratory
 799 caribou. *Oikos*, 2024(1), e10150. <https://doi.org/10.1111/oik.10150>
 800 Moen, R., & Pastor, J. (1998). Simulating antler growth and energy, nitrogen, calcium
 801 and phosphorus metabolism in caribou. *Rangifer*, 85–97.
 802 <https://doi.org/10.7557/2.18.5.1544>
 803 Momigliano, P., Florin, A.-B., & Merilä, J. (2021). Biases in demographic modelling
 804 affect our understanding of recent divergence. *Molecular Biology and*
 805 *Evolution*, msab047. <https://doi.org/10.1093/molbev/msab047>
 806 Morneau, C., & Payette, S. (2000). *Long-term fluctuations of a caribou population*
 807 *revealed by tree-ring data*.
 808 Mount, J. G., Muzylak, M., Allen, S., Althnaian, T., McGonnell, I. M., & Price, J. S.
 809 (2006). Evidence that the canonical Wnt signalling pathway regulates deer
 810 antler regeneration. *Developmental Dynamics*, 235(5), 1390–1399.
 811 <https://doi.org/10.1002/dvdy.20742>
 812 Nei, M. (1987). *Molecular Evolutionary Genetics*. Columbia University Press.

- Nielsen, R. (2005). Molecular signatures of natural selection. *Annual Review of Genetics*, 39, 197–218.
<https://doi.org/10.1146/annurev.genet.39.073003.112420>
- Ohno, S. (1970). *Evolution by Gene Duplication* (Springer-Verlag).
<https://books.google.ca/books?hl=en&lr=&id=5SjqCAAAQBAJ&oi=fnd&pg=PA1&dq=ohno+1970+reference&ots=MnY3zEH-uf&sig=dm1nTKomFOSdRdd0sE5vf7Z9kVk#v=onepage&q&f=false>
- O'Malley, K. G., Ford, M. J., & Hard, J. J. (2010). Clock polymorphism in Pacific salmon: evidence for variable selection along a latitudinal gradient. *Proceedings of the Royal Society B: Biological Sciences*, 277(1701), 3703–3714. <https://doi.org/10.1098/rspb.2010.0762>
- Overpeck, J. T., Webb, R. S., & Webb lii, T. (1992). Mapping eastern North American vegetation change of the past 18 ka: No-analogs and the future. *Geology*, 20(12), 1071. [https://doi.org/10.1130/0091-7613\(1992\)020%3C1071:MENAVC%3E2.3.CO;2](https://doi.org/10.1130/0091-7613(1992)020%3C1071:MENAVC%3E2.3.CO;2)
- Payette, S., Eronen, M., & Janinski, J. J. P. (2002). The Circumboreal Tundra-Taiga Interface: Late Pleistocene and Holocene Changes. *Ambio, Special Report Number 12*, 15–22.
- Pedersen, B. S., & Quinlan, A. R. (2018). Mosdepth: quick coverage calculation for genomes and exomes. *Bioinformatics*, 34(5), 867–868.
<https://doi.org/10.1093/bioinformatics/btx699>
- Picard toolkit. (2019). In *Broad Institute, GitHub repository*. Broad Institute.
<https://broadinstitute.github.io/picard/>
- Pokharel, K., Weldenegodguad, M., Dudeck, S., Honkatukia, M., Lindeberg, H., Mazzullo, N., Paasivaara, A., Peippo, J., Soppela, P., Stammli, F., & Kantanen, J. (2023). Whole-genome sequencing provides novel insights into the evolutionary history and genetic adaptation of reindeer populations in northern Eurasia. *Scientific Reports*, 13(1), 23019.
<https://doi.org/10.1038/s41598-023-50253-7>
- Prunier, J., Carrier, A., Gilbert, I., Poisson, W., Albert, V., Taillon, J., Bourret, V., Côté, S. D., Droit, A., & Robert, C. (2022). CNVs with adaptive potential in Rangifer tarandus: genome architecture and new annotated assembly. *Life Science Alliance*, 5(3). <https://doi.org/10.26508/lsa.202101207>
- Raponi, M., Beresford, D. V., Schaefer, J. A., Thompson, I. D., Wiebe, P. A., Rodgers, A. R., & Fryxell, J. M. (2018). Biting flies and activity of caribou in the boreal forest. *The Journal of Wildlife Management*, 82(4), 833–839.
<https://doi.org/10.1002/jwmg.21427>
- Rasmussen, M. S., Garcia-Erill, G., Korneliussen, T. S., Wiuf, C., & Albrechtsen, A. (2022). Estimation of site frequency spectra from low-coverage sequencing data using stochastic EM reduces overfitting, runtime, and memory usage. *Genetics*, 222(4), iyac148. <https://doi.org/10.1093/genetics/iyac148>
- Rhodes, E. M., Yap, K. N., Hill, G. E., & Hood, W. R. (2024). A Comparison of the Mitochondrial Performance between Migratory and Sedentary Mimid

856 Thrushes. *Integrative And Comparative Biology*, 64(6), 1859–1870.
857 <https://doi.org/10.1093/icb/icae137>

858 Rougemont, Q., Gagnaire, P., Perrier, C., Genthon, C., Besnard, A., Launey, S., &
859 Evanno, G. (2017). Inferring the demographic history underlying parallel
860 genomic divergence among pairs of parasitic and nonparasitic lamprey
861 ecotypes. *Molecular Ecology*, 26(1), 142–162.
862 <https://doi.org/10.1111/mec.13664>

863 Rougeux, C., Gagnaire, P., & Bernatchez, L. (2019). Model-based demographic
864 inference of introgression history in European whitefish species pairs'.
865 *Journal of Evolutionary Biology*, 32(8), 806–817.
866 <https://doi.org/10.1111/jeb.13482>

867 Rubinacci, S., Ribeiro, D. M., Hofmeister, R. J., & Delaneau, O. (2021). Efficient
868 phasing and imputation of low-coverage sequencing data using large
869 reference panels. *Nature Genetics*, 53(1), 120–126.
870 <https://doi.org/10.1038/s41588-020-00756-0>

871 Sabeti, P. C., Schaffner, S. F., Fry, B., Lohmueller, J., Varilly, P., Shamovsky, O., Palma,
872 A., Mikkelsen, T. S., Altshuler, D., & Lander, E. S. (2006). Positive Natural
873 Selection in the Human Lineage. *Science*, 312(5780), 1614–1620.
874 <https://doi.org/10.1126/science.1124309>

875 Schaefer, J. A., & Mahoney, S. P. (2001). ANTLERS ON FEMALE CARIBOU:
876 BIOGEOGRAPHY OF THE BONES OF CONTENTION. *Ecology*, 82(12), 3556–
877 3560. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2001)082%5B3556:AOFCBO%5D2.0.CO;2)
878 [9658\(2001\)082%5B3556:AOFCBO%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082%5B3556:AOFCBO%5D2.0.CO;2)

879 Schrider, D. R., & Kern, A. D. (2017). Soft Sweeps Are the Dominant Mode of
880 Adaptation in the Human Genome. *Molecular Biology and Evolution*, 34(8),
881 1863–1877. <https://doi.org/10.1093/molbev/msx154>

882 Sharma, S., Couturier, S., & Côté, S. D. (2009). Impacts of climate change on the
883 seasonal distribution of migratory caribou. *Global Change Biology*, 15(10),
884 2549–2562. <https://doi.org/10.1111/j.1365-2486.2009.01945.x>

885 Skotte, L., Korneliussen, T. S., & Albrechtsen, A. (2013). Estimating Individual
886 Admixture Proportions from Next Generation Sequencing Data. *Genetics*,
887 195(3), 693–702. <https://doi.org/10.1534/genetics.113.154138>

888 Szpiech, Z. A., & Hernandez, R. D. (2014). selscan: An Efficient Multithreaded
889 Program to Perform EHH-Based Scans for Positive Selection. *Molecular*
890 *Biology and Evolution*, 31(10), 2824–2827.
891 <https://doi.org/10.1093/molbev/msu211>

892 Szpiech, Z. A., Novak, T. E., Bailey, N. P., & Stevison, L. S. (2021). Application of a
893 novel haplotype-based scan for local adaptation to study high-altitude
894 adaptation in rhesus macaques. *Evolution Letters*, 5(4), 408–421.
895 <https://doi.org/10.1002/evl3.232>

896 Taylor, R. S., Manseau, M., Klütsch, C. F. C., Polfus, J. L., Steedman, A., Hervieux, D.,
897 Kelly, A., Larter, N. C., Gamberg, M., Schwantje, H., & Wilson, P. J. (2021).
898 Population dynamics of caribou shaped by glacial cycles before the last

- glacial maximum. *Molecular Ecology*, 30(23), 6121–6143.
<https://doi.org/10.1111/mec.16166>
- Theoret, J., Cavedon, M., Hegel, T., Hervieux, D., Schwantje, H., Steenweg, R., Watters, M., & Musiani, M. (2022). Seasonal movements in caribou ecotypes of Western Canada. *Movement Ecology*, 10(1), 12.
<https://doi.org/10.1186/s40462-022-00312-x>
- Webber, Q. M. R., Ferraro, K. M., Hendrix, J. G., & Vander Wal, E. (2022). What do caribou eat? A review of the literature on caribou diet. *Canadian Journal of Zoology*, 100(3), 197–207. <https://doi.org/10.1139/cjz-2021-0162>
- Williams, J. W., Webb, T., Richard, P. H., & Newby, P. (2000). Late Quaternary biomes of Canada and the eastern United States. *Journal of Biogeography*, 27(3), 585–607. <https://doi.org/10.1046/j.1365-2699.2000.00428.x>
- Witter, L. A., Johnson, C. J., Croft, B., Gunn, A., & Gillingham, M. P. (2012). Behavioural trade-offs in response to external stimuli: time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. *Journal of Animal Ecology*, 81(1), 284–295. <https://doi.org/10.1111/j.1365-2656.2011.01905.x>
- Yannic, G., Ortego, J., Pellissier, L., Lecomte, N., Bernatchez, L., & Côté, S. D. (2018). Linking genetic and ecological differentiation in an ungulate with a circumpolar distribution. *Ecography*, 41(6), 922–937.
<https://doi.org/10.1111/ecog.02995>
- Yannic, G., Pellissier, L., Ortego, J., Lecomte, N., Couturier, S., Cuyler, C., Dussault, C., Hundertmark, K. J., Irvine, R. J., Jenkins, D. A., Kolpashikov, L., Mager, K., Musiani, M., Parker, K. L., Røed, K. H., Sipko, T., Pórisson, S. G., Weckworth, B. V., Guisan, A., ... Côté, S. D. (2014). Genetic diversity in caribou linked to past and future climate change. *Nature Climate Change*, 4(2), 132–137.
<https://doi.org/10.1038/nclimate2074>
- Zheng, Y., & Wiehe, T. (2019). Adaptation in structured populations and fuzzy boundaries between hard and soft sweeps. *PLOS Computational Biology*, 15(11), e1007426. <https://doi.org/10.1371/journal.pcbi.1007426>

931 Figure legends

932 Figure 1: a) Capture sites for migratory (square) and boreal (round) caribou samples
933 analysed in this study. Smaller points were sequenced at low coverage and larger
934 points at high coverage. Quebec and Labrador distribution range for the migratory
935 (orange, annual ranges, MELCCFP, 2018-2024) and boreal (green, distribution range,
936 MELCCFP, 2019) ecotypes are displayed in shaded areas, with the dashed line
937 showing the northern limit of observations for boreal caribou in Québec at the time
938 of sampling. b) First two axes of a principal component analysis for the covariance of
939 genotype likelihoods at 820,568 genome-wide SNPs.

940 Figure 2: a) Individual proportion of ancestry for $K = 2$ and 4 ancestral populations,
941 CLUMPAK-averaged over replicate runs in the major mode (out of 50 runs). Individuals
942 were grouped by population (migratory) or region (boreal) and ordered by longitude of
943 capture site within regions. b) Pie charts depicting ancestral proportion ($K = 4$) of
944 samples at their capture site. Individuals captured within 50 km had their ancestry
945 proportion averaged and grouped in pie chart of area proportional to their sample
946 size.

947 Figure 3: a) Observed two-dimensional site-frequency spectrum (2D-SFS) in
948 migratory (Rivière-aux-Feuilles) and boreal (Nord-du-Québec) populations of
949 caribou. b-c) Simulated 2D-SFS from the run with the lowest AIC for the isolation with
950 migration (IM) and secondary contact (SC) models. d-e) Ratio of observed and
951 simulated site frequency by minor allele count class. Classes with less than 10 sites

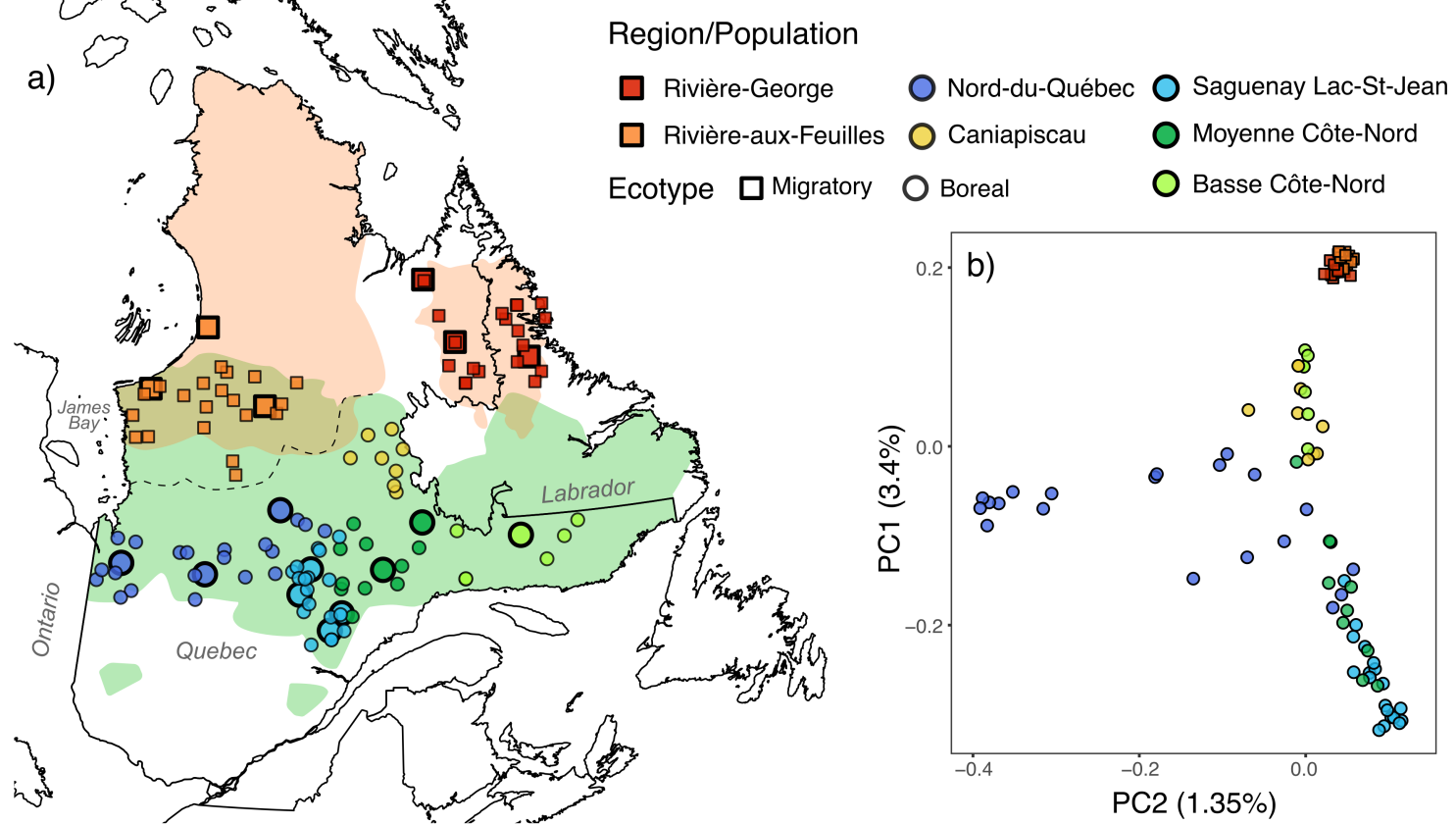
in either the observed or simulated 2d-SFS were not displayed. f) Akaike Information Criterion (AIC) for 100 runs of each competing demographic models. g) Forward-in-time representation of the IM (blue) and SC (yellow) models. Width of rectangles are proportional to N_e (range : 14,467 – 31,384) and line width of arrows is proportional to the number of migrants per generation (9.9 – 17.2).

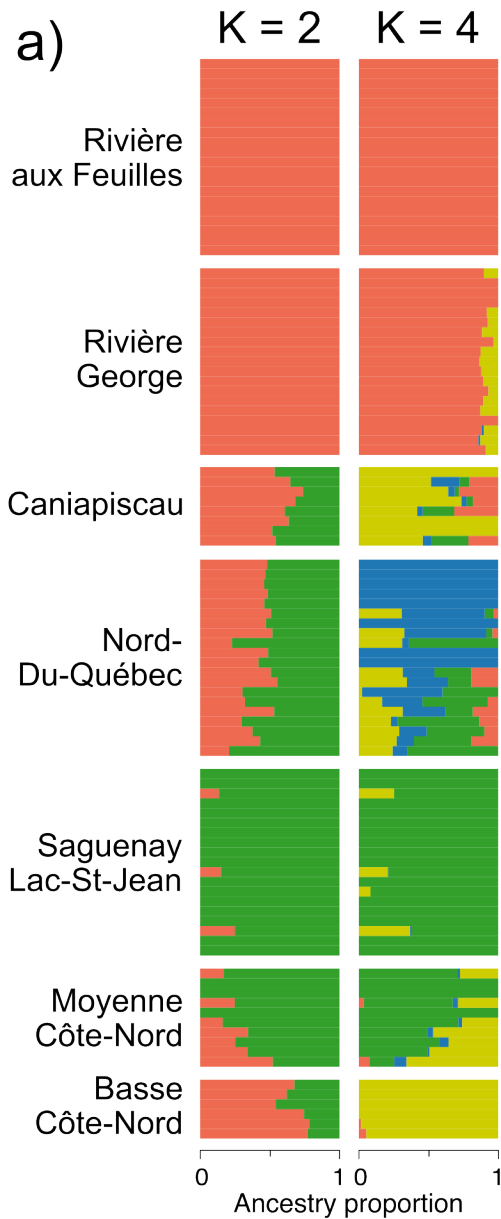
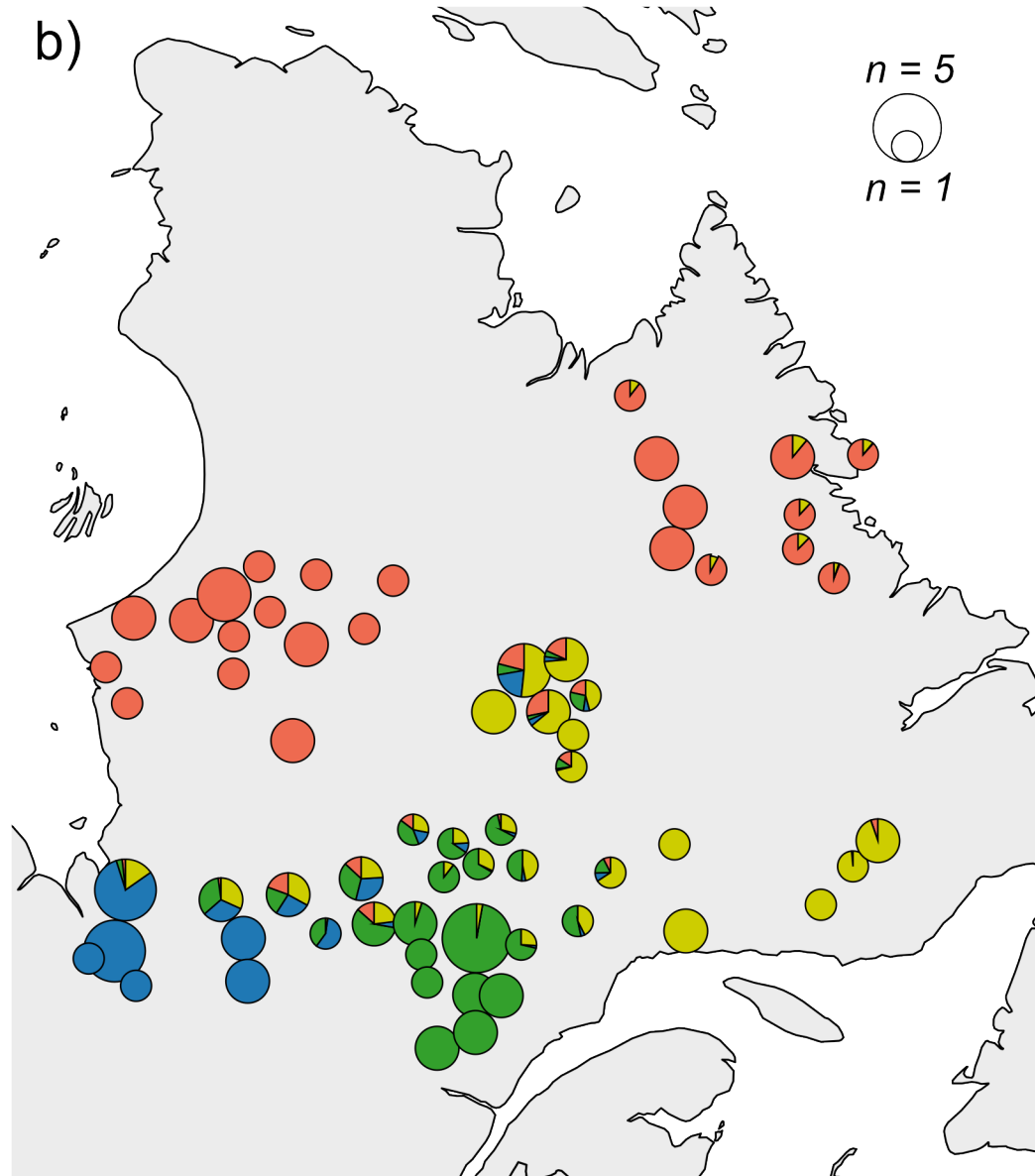
Figure 4: a-b) Genome-wide distribution of bF_{ST} between migratory and boreal populations. Lines represent bF_{ST} values in 50kb windows (window step of 10kb), while points highlight the top 0.2% of values. Points are colored to reflect the average normalized XP-nSL in top bF_{ST} windows, with darkest colors for normalized XP-nSL above 2 (orange) or below -2 (green), as displayed in panel c). The dashed horizontal line indicates the mean bF_{ST} across autosomes or chrX. Blue arrows denote the position of putatively adaptive CNVs from Prunier et al. 2022. Unannotated tick marks in panel a) denote 25 Mb increments. c) Density plot for normalized XP-nSL in windows with bF_{ST} in the top 0.2% (solid outline and colored area) or other windows (dashed outline).

Figure 5: Comparison of Tajima's D in windows of 50 kb for the boreal and migratory ecotype. Black points show the distribution across autosomes, while colored points highlight windows with a) the top 0.2% bF_{ST} in light and dark (for windows with average $|XP-nSL| > 2$) red, and b) the top 0.2% $|XP-nSL|$ in orange ($XP-nSL > 0$) and green ($XP-nSL < 0$). Violin and boxplots show the distributions of Tajima's D for genome-wide and top candidate windows along the axes.

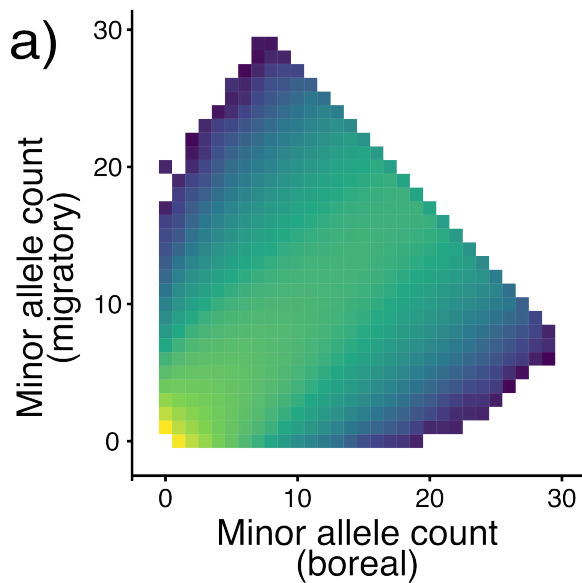
Table 1: Parameter estimates and 95% confidence intervals estimated by parametric bootstrap for effective population sizes (N_e) of caribou in Quebec and Labrador, timing of demographic events (in generations before present), migration rates and number of migrants per generation for the isolation with migration and secondary contact demographic models. Migration directionality is presented forward in time, and number of migrants per generation is a product of the migration rate and the N_e of the sink population.

Parameter	Isolation with migration		Secondary contact	
	Parameter estimate	IC 95%	Parameter estimate	IC 95%
Ancestral N_e	31,147	37,081 38,651	31,384	37,297 38,431
Migratory N_e	26,792	29,017 37,484	27,899	30,234 36,829
Boreal N_e	14,467	14,588 21,346	14,596	14,994 20,441
Divergence time	1,229	995 2,047	1,041	993 1,670
Secondary contact time	--	--	333	118 844
Boreal → migratory migration rate	3.68×10^{-4}	1.19×10^{-4} 4.63×10^{-4}	4.9×10^{-4}	2.5×10^{-4} 10.6×10^{-4}
Migratory → boreal migration rate	7.81×10^{-4}	4.16×10^{-4} 8.97×10^{-4}	11.8×10^{-4}	6.4×10^{-4} 18.8×10^{-4}
Boreal → migratory migrants/generation	9.9	4.4 13.6	13.7	8.9 34.4
Migratory → boreal migrants/generation	11.3	8.6 13.2	17.2	12.9 34.5





Observed SFS



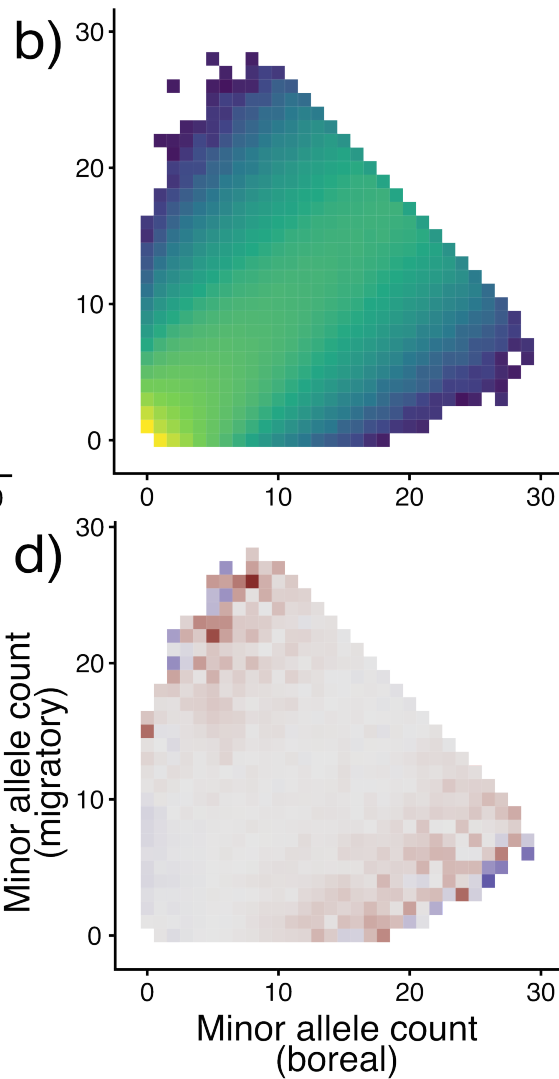
Frequency ($\log_{10}$)

-6 -5 -4 -3 -2 -1

Observed/simulated ratio ($\log_{10}$)

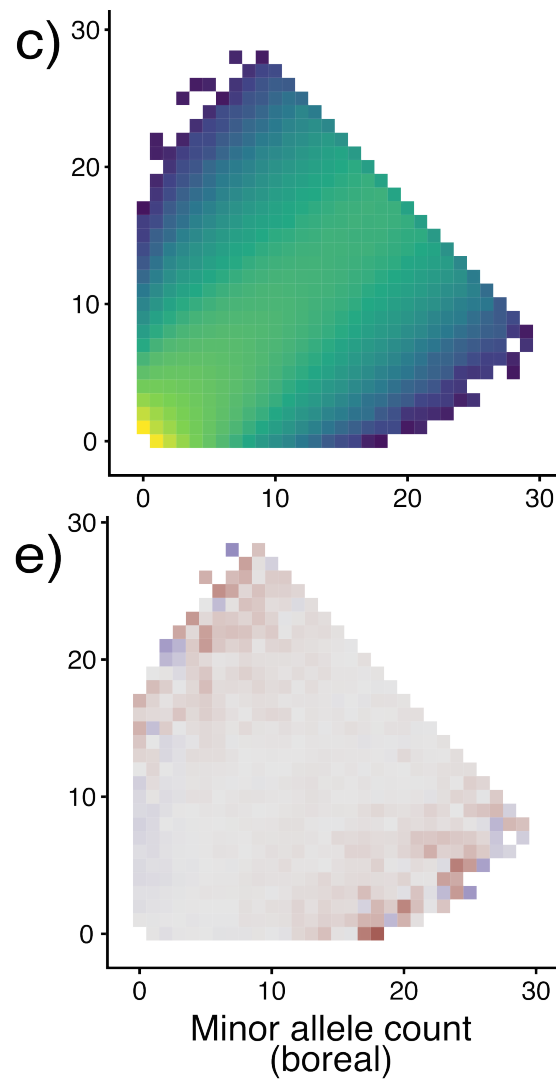
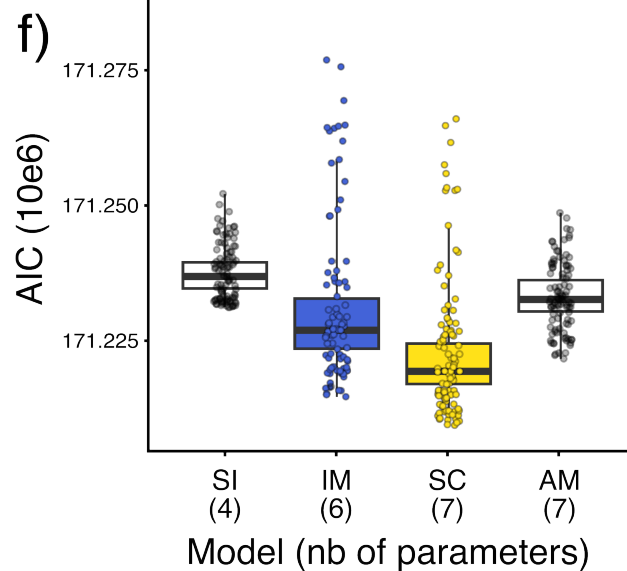
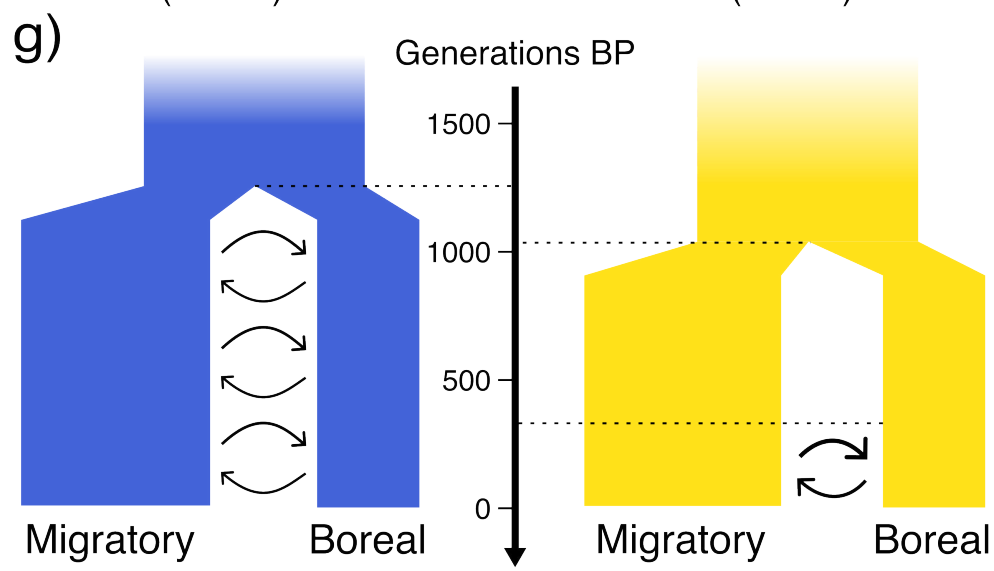
-0.8 -0.4 0.0 0.4 0.8

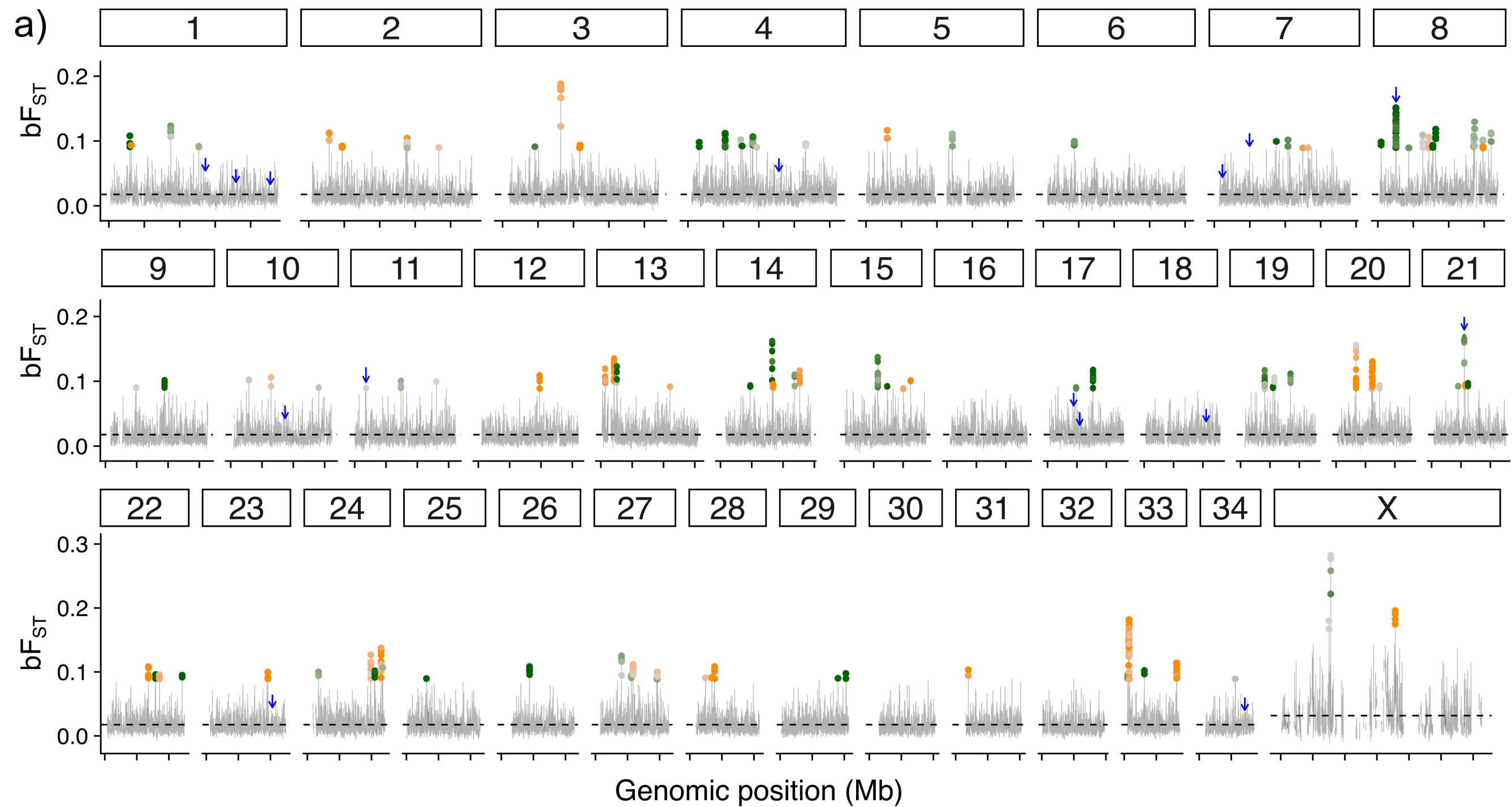
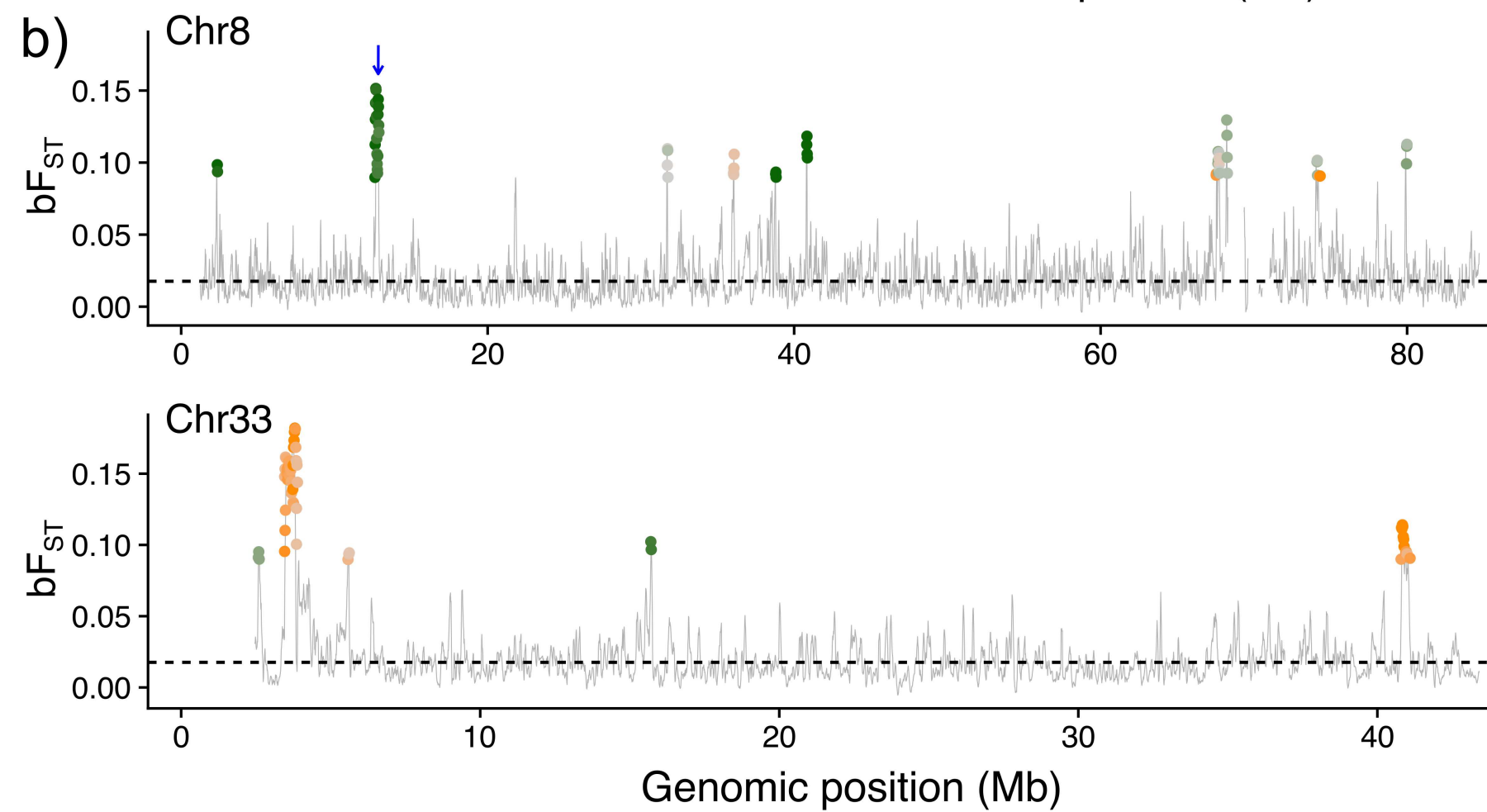
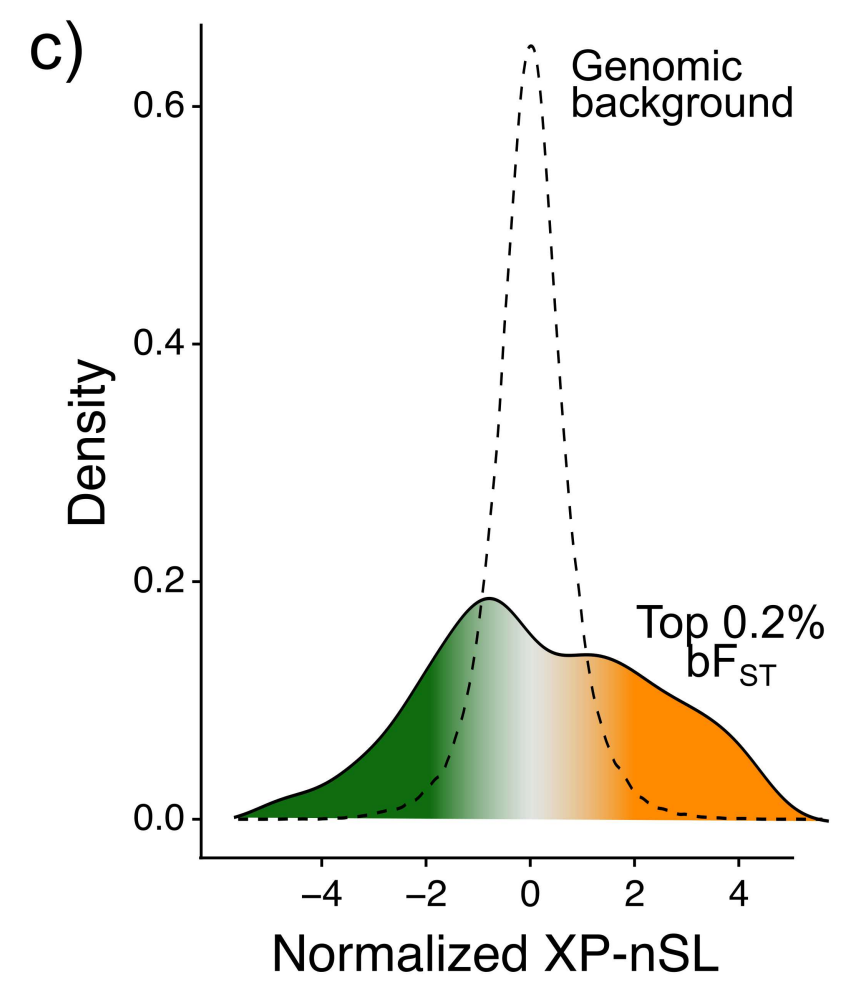
Isolation with migration



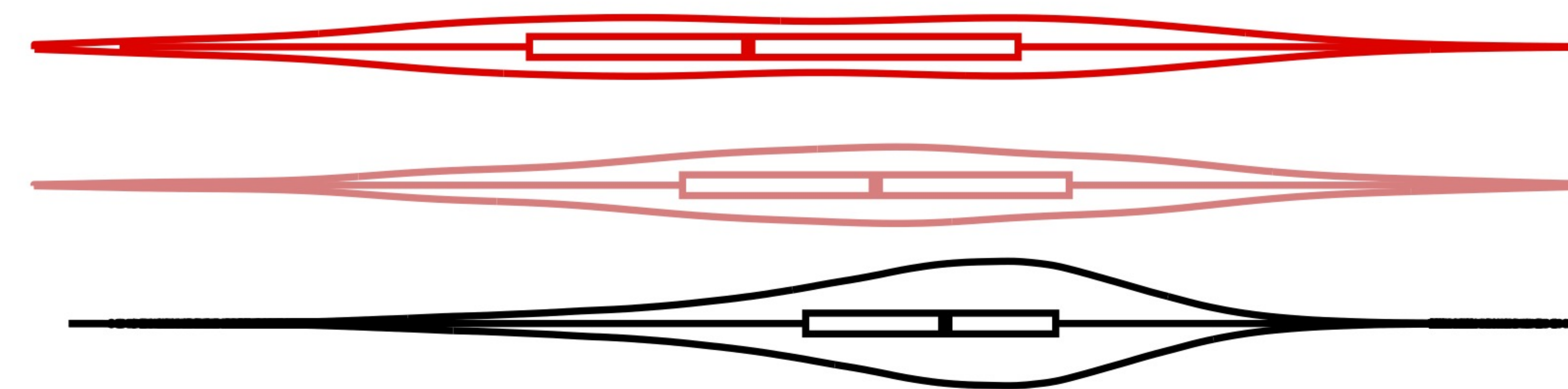
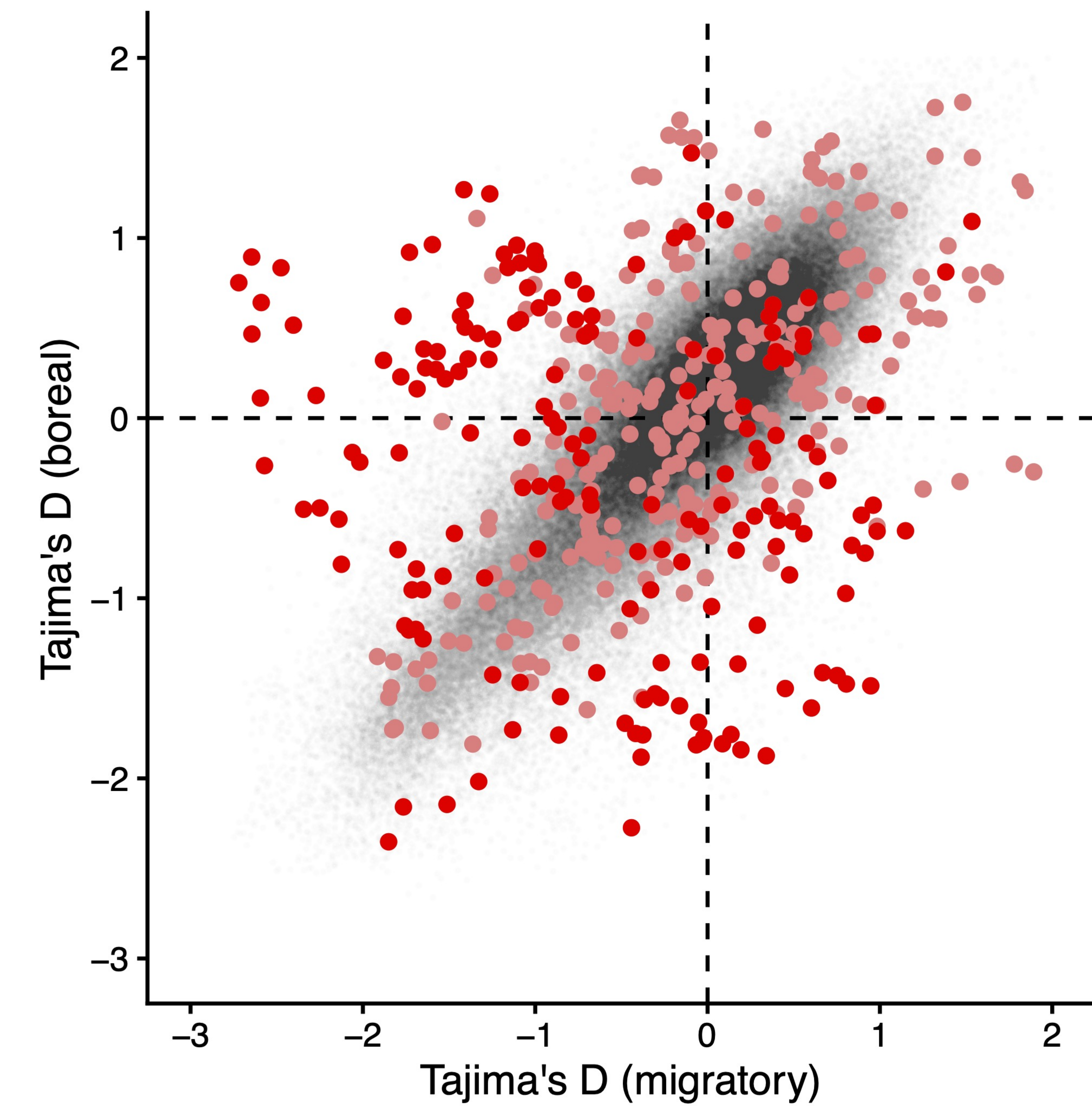
Secondary contact

Simulated SFS

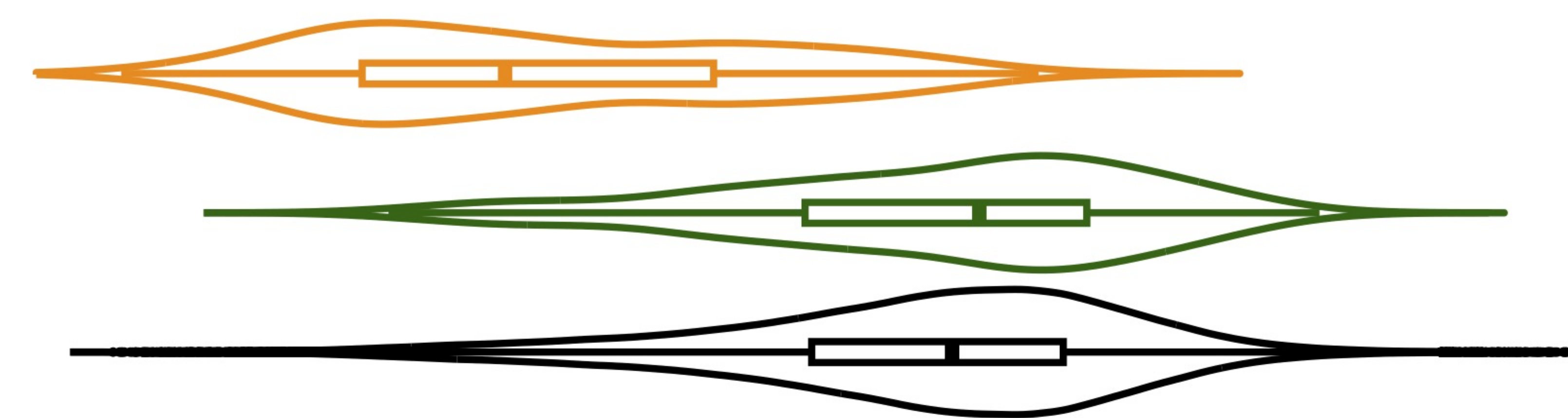
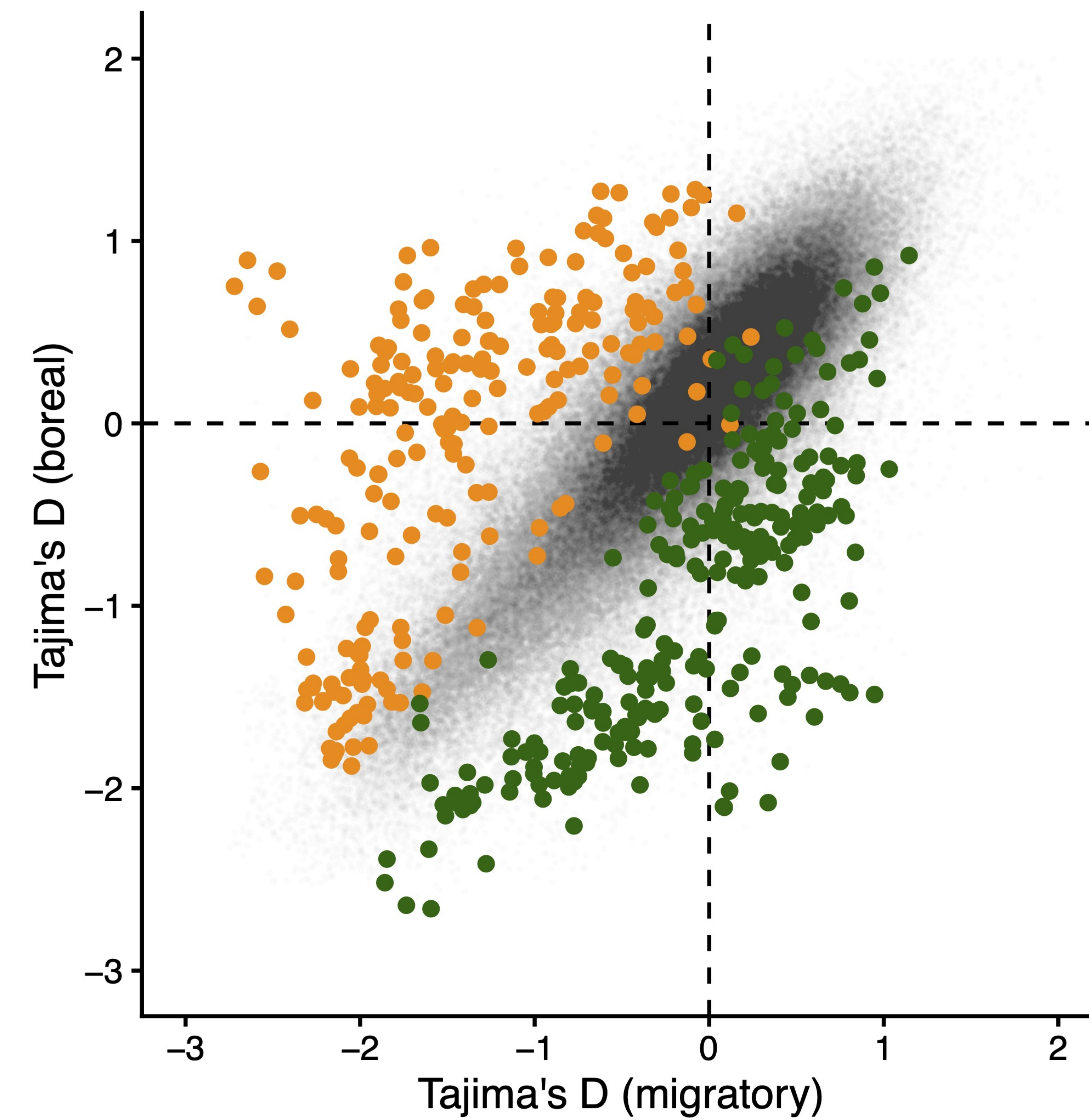




a)



b)



Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SuppTableHeredityCaribouWGS.xlsx](#)
- [SupplementaryMethodsFiguresHeredityCaribouWGS.pdf](#)