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ORIGINAL ARTICLE

Conservation genomics of dwarf birch (*Betula nana* L.), a threatened glacial relict in Switzerland

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Abstract
Climate change following the last glaciation fragmented habitats of cold-adapted plant species, reducing genetic diversity and potentially limiting their ability to persist. *Betula nana*, a dwarf shrub and classical glacial relict, remains widespread across the Arctic but survives only in scattered temperate and montane refugia in Europe. In Switzerland, it is well represented in the Jura Mountains yet persists with only a few small populations in the Alps. We performed whole-genome resequencing on 82 *B. nana* individuals from 12 Swiss populations, capturing all known regional occurrences and identifying 5,294,454 SNPs. Population structure analyses revealed four genetic clusters. Jura populations were closely related and clearly distinct from the alpine groups. The alpine population of Rothenthurm showed extreme genetic isolation. In contrast, the highly divergent Wachseldornmoos population proved to be introduced from North American *B. glandulosa*. The Appenzell alpine population also represented a human-mediated introduction from the Jura. Demographic reconstructions indicated that effective population sizes were relatively large during the Last Glacial Maximum but declined sharply in recent times, including in the Jura, and that historical gene flow among Swiss populations was limited. Our findings highlight an urgent conservation concern: the original alpine genetic lineage of *B. nana* in Switzerland is nearly extinct and may persist only in the Rothenthurm population. Conservation efforts should therefore prioritize safeguarding and potentially restoring genetically authentic material.

Keywords Demographic history · Ecological genetics · Genetic load · Genome evolution · Inbreeding · Introgression

Introduction

The alternation of glacial and interglacial phases is a recurrent feature of the Earth's Quaternary climate system, characterized by long glacial periods interrupted by comparatively brief warm intervals (Huybers 2007). During the current interglacial stage, anthropogenic greenhouse-gas emissions have caused global warming (Huybers 2007; Stroeve et al. 2025). When the velocity of climate change surpasses the capacity of species to acclimate, migrate, or adapt genetically, extinction risk increases sharply (Waldvogel et al. 2020; Garcia-Costoya et al. 2023; Wang et al. 2023). Plants with weaker mobility track suitable climatic niches less readily, thus some species only persist in small and climatically buffered microrefugia (climate relicts) (Hampe and Jump 2011). Owing to their long-term isolation, these populations typically experience reduced gene flow, which increases genetic isolation and inbreeding while reducing genetic diversity. Together with stronger genetic drift in small populations, these processes can increase the frequency and homozygous expression of deleterious alleles, potentially resulting in inbreeding depression (Abascal et al. 2016; De Kort et al. 2021; Bertorelle et al. 2022). Consequently, climate-relict populations may represent important conservation priorities because they can harbor unique and highly differentiated genetic variation, reflecting their distinct evolutionary histories and potential local adaptation (Hampe and Petit 2005). Preserving these populations is therefore essential to prevent further genetic erosion and habitat loss while maintaining the evolutionary

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potential of species to respond to future environmental change (Lamoreux et al. 2006; Hoffmann and Willi 2008). Examples of such cases in the Swiss Alps include *Eritrichium nanum* (Stehlik et al. 2002), *Clematis alpina* (Stefani et al. 2025), and *Nuphar pumila* (Bétrisey et al. 2020), illustrating the genetic and evolutionary distinctiveness that can arise among geographically isolated alpine populations.

The Alps and the surrounding mountain systems have long shaped European biogeographical patterns, functioning as major refugia for diverse taxa during repeated Pleistocene glaciation cycles (Taberlet et al. 1998; Brochmann et al. 2003; Tribsch and Schönswetter 2003; Holderegger and Thiel-Egenter 2009; Windmaisser et al. 2016). Intensive research over recent decades has clarified the glacial and postglacial histories of many arctic–alpine and boreal–alpine plant species (e.g., Stehlik et al. 2002; Stehlik 2003; Paun et al. 2008; Ronikier et al. 2012; Winkler et al. 2012; Eidesen et al. 2013; Arrigo et al. 2016; Bétrisey et al. 2020; Pittet et al. 2020; Brochmann et al. 2025). Nevertheless, numerous alpine relict taxa remain insufficiently investigated, particularly regarding the origin, persistence, and genetic differentiation of their contemporary populations. Consequently, for many geographically restricted alpine lineages, the extent to which they represent distinct evolutionary units remains unresolved (Borrell et al. 2018).

Betula nana L. (Betulaceae) frequently occurs in fossil pollen records during past glacial periods and is one of the most emblematic Quaternary glacial relicts of European flora (Walter and Straka 1970; Hegi 1981; Birks 2008). *Betula nana* has a circumpolar distribution, extending across Arctic, subarctic, and boreal regions of Europe, northern Asia, and North America, while also persisting as isolated relict populations farther south in mountainous regions, where it is largely confined to climatically buffered peatland habitats, particularly raised bogs (Panarctic Flora 2025; FCAA 2025). It is traditionally divided into two subspecies: subsp. *nana* (Central Europe, European Arctic, western Siberia, and eastern Canada) and subsp. *exilis* (eastern Siberia and western North America) (Hultén et al. 1986; Elven et al. 2011; FNA 2025; FCAA 2025). Its closest relatives are dwarf birches, *B. glandulosa* (a North American taxon) and *B. middendorffii*, a tetraploid species from northeast China (Dun et al. 2025). Interestingly, other morphologically similar dwarf birches (e.g., *B. michauxii*) are not closely related to *B. nana*, reflecting convergent evolution in response to similar microclimates and habitat types (Wang et al. 2016, 2021).

The southern distributional limit of *B. nana* in Europe extends into high-elevation mountain systems, where it persists in cold, humid, and oligotrophic microhabitats that resemble its boreal, subarctic or Arctic niche (De Groot et al. 1997). Across its range, *B. nana* plays a crucial ecological role in peatland functioning, contributing to soil stabilization, hydrological regulation, and carbon storage (Hollesen et al. 2015), and it is a key component of the "greening of the Arctic," responding to ongoing climate-driven changes (Büntgen et al. 2015; Mekonnen et al. 2021; Buchwal et al. 2023).

Despite its wide circumpolar range, *B. nana* is experiencing significant range contraction at its southern and low-elevation margins due to habitat loss, wetland degradation, and rapid climate warming (Schwarz and Poschlod 2015). Across much of temperate Europe, the species is considered threatened or endangered (Ejankowski et al. 2010; Schwarz and Poschlod 2015; Bornand et al. 2016; Borrell et al. 2018; Borbély and Indreica 2019).

In Switzerland, the species reaches one of the southernmost known outposts of its global distribution. Swiss populations typically occur between 800 and 1,300 m a.s.l., mainly in the Jura Mountains and parts of the Alps (Info Flora 2025). The species is rare, with small, scattered, and highly fragmented populations confined to peat bogs, fens, and transitional mires. *Betula nana* was first recorded in the Swiss flora in the mid-eighteenth century (Gagnebin 1751). Today, the largest concentration of Swiss populations is still found in the Jura Mountains, in the cantons of Neuchâtel, Vaud, Bern, and Jura (Info Flora 2025). In the alpine regions of Switzerland, the species is on the brink of extinction (Bornand et al. 2016), with only a few populations or even single individuals recently confirmed in the cantons of Bern, Schwyz, and Appenzell Ausserrhoden. Interestingly, several of these Alpine populations (e.g., Schwyz and Appenzell) were preserved in ex situ collections as a conservation measure, in some cases for extended periods, and were subsequently reintroduced over the past decades. However, the origin and genetic provenance of the reintroduced individuals were not always adequately documented and have so far not been genetically investigated (Schuler 2020, unpublished action plan; Info Flora 2025).

Whole-genome sequencing (WGS), a form of high-throughput next-generation sequencing, enables the identification of single-nucleotide polymorphisms (SNPs) and other genomic variants across the entire genome (Fuentes-Pardo and Ruzzante 2017). Applying WGS-based approaches in threatened or declining species provides critical insights for evidence-based conservation management, including identifying genetically depauperate populations, inferring connectivity, and assessing extinction risk associated with reduced adaptive potential (Palkopoulou et al. 2015). In this way, whole-genome data contribute directly to molecular-level strategies aimed at safeguarding vulnerable populations and preventing further biodiversity loss.

A large number of genetic studies from Northern Europe and the Arctic have focused on *B. nana* and closely related

taxa (*B. glandulosa* and *B. pubescens*), using a wide array of molecular methods ranging from AFLP to RADseq, but only rarely employing whole-genome sequencing. In addition to the recent pan-Arctic studies and syntheses by Dance et al. (2025) and Eidesen et al. (2015), numerous genetic investigations of dwarf birch have been conducted in regions such as North America (Touchette et al. 2023), Svalbard (Alsos et al. 2002; Eidesen et al. 2013), Iceland (Pálsson et al. 2023), Russia (Cherepanova et al. 2024), the United Kingdom (Wang et al. 2013; Borrell et al. 2018, 2020), and Poland (Dabrowska et al. 2006; Jadwiszczak et al. 2013, 2017). In contrast, there are no genetic studies focusing on the most isolated and threatened European populations at the southernmost limit of the species' distribution (e.g., in Switzerland, France, Germany, or Austria).

By focusing on Switzerland, this study aims to contribute to filling this knowledge gap for one Alpine country. Although the restriction to administrative boundaries does not reflect biogeographical units and represents a limitation in this regard, it provides a clearly defined conservation and management framework. This approach facilitates the translation of scientific findings into targeted and actionable measures within the study region.

Within this framework, we investigate population structure, genetic differentiation, and the spatial distribution of genetic diversity, while addressing the following questions: (1) What is the distribution of genetic diversity within and among *Betula nana* populations in Switzerland? (2) What is the phylogenetic differentiation between the remnant alpine populations and those in the Jura Mountains? (3) How did Quaternary climate fluctuations (particularly after the Last Glacial Maximum) affect population-history dynamics? (4) Can translocation events be detected, and if so, what were the effects of ex situ multiplication and introductions on genetic patterns? Finally, based on our results, we propose an optimal conservation strategy for the remaining relict populations of *B. nana* in the Swiss Alps and the Jura Mountains. This study provides a foundation for the protection of the species in Switzerland.

Materials and methods

Sampling and sequencing

We sampled 82 individuals in 12 populations of *B. nana* in Switzerland (Figs. 1 and S1, Table 1), in all regions where the species was observed in the last years. Individuals in each population were sampled at least 10 m away from each other. Additionally, samples of two closely related taxa, 3 individuals of *B. glandulosa* from the Rocky Mountains (Og Lake, 50.9516° N 115.6349° W) and 3 individuals of *B. nana* subsp. *exilis* from Siberian Arctic tundra (Krutaya Drisva, 69.3452°N 161.5314°E), were obtained from Dance et al. (2025) (populations BN46 and BN32 in that study, respectively). Fresh leaves for all sampled individuals were dried using silica gel, and DNA was extracted from the dried leaf tissue using a modified CTAB method. High-quality genomic DNA was extracted from leaf tissue using the TIANGEN Plant Genome Kit. DNA quality was

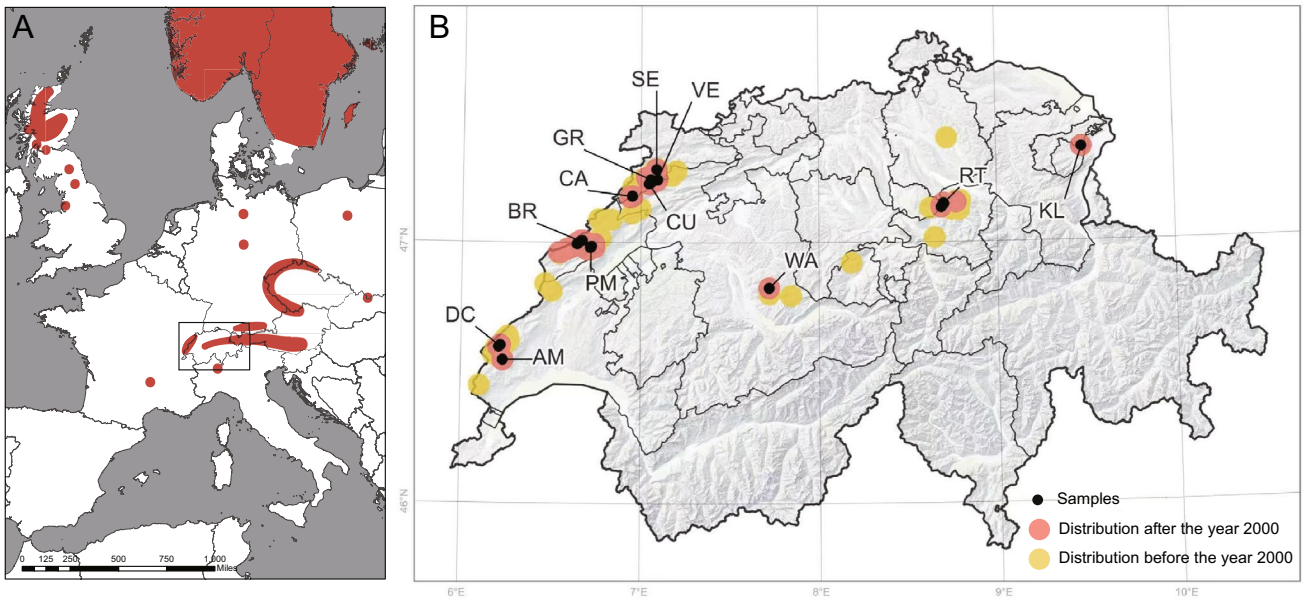

Fig. 1 **A.** Natural distribution area of *Betula nana* in Europe (red surfaces) with the position of the study site (rectangle). **B.** Study area showing the collection sites (black dots), historical (yellow circles, occurrences known before the year 2000) and recent (red circles, occurrences known after the year 2000) distribution of *Betula nana* in Switzerland. See Table 1 for population abbreviations

Table 1 General characteristics and statistics for the 12 Swiss populations of *Betula* investigated in this study

Species	Population ID	Mountain range	Locality (Canton)	Lat.(N)	Long.(E)	Alt. (m a.s.l.)	No of samples	H_o	H_o stdev	π	Tajima's D	Averaged F_{IS}	Averaged F_{IS} stdev
B. nana	AM	Jura	Ambumex (VD)	46.605	6.220	1066	8	0.283	0.018	0.0023	1.5167	−0.04	0.07
	DC	Jura	Derrière-la-Côte (VD)	46.549	6.233	1305	6	0.259	0.011	0.0025	1.0951	0.05	0.04
	BR	Jura	Brévine (NE)	47.007	6.673	1049	7	0.261	0.002	0.0030	0.2005	0.04	0.01
	PM	Jura	Ponts-de-Martel (NE)	46.985	6.725	999	7	0.260	0.004	0.0029	0.2560	0.05	0.01
	CA	Jura	Chaux-d'Abel (BE)	47.178	6.952	1005	8	0.256	0.008	0.0028	0.4893	0.06	0.03
	CU	Jura	Chaux (BE)	47.229	7.055	986	8	0.250	0.031	0.0027	0.9737	0.08	0.11
	GR	Jura	Gruère (JU)	47.241	7.056	1008	8	0.266	0.006	0.0029	0.4401	0.02	0.02
	SE	Jura	Plain de Seigne (JU)	47.281	7.088	856	2	0.269	0.003	0.0031	0.0795	0.01	0.01
	VE	Jura	Veaux (JU)	47.241	7.093	1015	8	0.265	0.017	0.0029	0.6288	0.03	0.06
	RT	Alps	Rothenthurm (SZ)	47.145	8.702	906	13	0.327	0.000	0.0020	3.3973	−0.20	0.00
	KL	Alps	Kleckelmoos (AR)	47.358	9.482	964	2	0.227	0.001	0.0018	2.0581	0.17	0.00
B. glandulosa	WA	Alps	Wachseldornmoos (BE)	46.826	7.719	992	5	0.158	0.000	0.0010	2.4377	0.42	0.00
	Total						82	0.266	0.009	0.0025	1.1311	0.03	0.03

AR Appenzell Ausserrhoden, *BE* Bern, *JU* Jura, *NE* Neuchâtel, *VD* Vaud, *SZ* Schwyz

assessed by agarose gel electrophoresis, spectrophotometry, and fluorometric quantification. Sequencing libraries were prepared by Benagen (Wuhan, China) and sequenced on the DNBSEQ-T7 platform, a high-throughput next-generation sequencing platform based on DNA nanoball (DNB) technology (Kim et al. 2021).

Data filtering, comparison, and SNP variation identification

Outgroup sequences were downloaded from NCBI (https://www.ncbi.nlm.nih.gov/sra/) and included ERR13996197 (*Betula pubescens*), SRR19939340 (*B. platyphylla*) (Chen et al. 2021), SRR24304953 (*B. pendula*), and SRR17214828 (*Alnus glutinosa*). Together with the 3 individuals of *B. glandulosa* and 3 individuals of *B. nana* subsp. *exilis*, we included six outgroup taxa, represented by a total of ten outgroup individuals (Fig. S2). Every SRA (Sequence Read Archive) paired-end sequencing dataset was converted into two FASTQ files using the –split-3 parameter of SRA Toolkit v3.0.10 for subsequent analysis. We used fastp v0.23.4, with parameters: −3 −5 -e 20 −l 50 –detect_adapter_for_pe (Table S1).

Betula platyphylla (white birch) was used as the reference genome, and all sequenced samples, together with the outgroup FASTQ files, were aligned using BWA v0.7.17 (Li & Durbin 2009). Alignment results in SAM format were converted into sorted BAM files using the sort command of samtools. PCR duplicates were removed from the sorted BAM files using Picard v2.27.5 (MarkDuplicates, REMOVE_DUPLICATES=True) (https://github.com/broadinstitute/picard). We used GATK v4.3.0.0 (De Summa et al. 2017) with the HaplotypeCaller, CombineGVCFs, GenotypeGVCFs and SelectVariants tools. To generate two datasets, we used the GATK GenotypeGVCFs tool with the -includeNonVariantSites parameter to call variants and generate two datasets: one including nonvariant and variant sites, and the other containing variant sites only. For the dataset that included nonvariant sites, filtering was performed using VCFtools v0.1.13 (Danecek et al. 2011), retaining only biallelic sites with a minimum sequencing depth of 5 (–minDP 5) and a maximum missing rate of 10% (–max-missing 0.9), resulting in Dataset 3 (Fig. S2). For the dataset excluding nonvariant sites, variant filtering was performed using the VariantFiltration tool with the following criteria: QD < 2.0 || FS > 60.0 || QUAL < 30.0 || SOR > 3.0 || MQ < 40.0 || MQRankSum < −12.5 || ReadPosRankSum < −8.0, to filter the identified SNPs (Ma et al. 2021; Wang et al. 2026).We further filtered the SNPs with the parameters: "–minDP 5 –minQ 30 –max-missing 0.9 –maf 0.05 –hwe 0.001 –minGQ 30 –min-meanDP 5 –max-meanDP 120 –recode" (Dataset 1, Fig. S2).

Population structure

We performed LD (Linkage Disequilibrium) pruning on Dataset 1, using PLINK v1.9 (Purcell et al. 2007), parameters "-indep-pairwise 50 10 0.2", resulting in Dataset 2, contained 537,284 SNP loci. The same parameters were applied to the dataset included 82 *B. nana* and 10 outgroup individuals, resulting in Dataset 4 which contained 500,744 SNP loci (Fig. S2). The vcf format file was converted to bed or ped format.

Admixture v1.3.0 (Alexander et al. 2009) estimates the probabilities of observed genotypes based on ancestral proportions and population allele frequencies. The range of K for the ancestral populations varied from 1 to 10, and the 10-fold cross-validation error (CV) value was used to determine the optimal clustering number (Fig. S3). Results were generated using R. Principal Component Analysis (PCA) (Jombart et al. 2010) was performed on Dataset 2 using PLINK, and results for the first two principal components were visualized using R.

A Python script (https://github.com/edgardomortiz/vcf2phylip) was used to convert VCF files to PHYLIP format, with heterozygous sites coded as IUPAC degenerate bases. Using ModelFinder (Kalyaanamoorthy et al. 2017), we selected the optimal nucleotide substitution model ("TVM+F+R3") from 352 candidates based on the Bayesian Information Criterion. IQ-TREE v1.6.12 (Nguyen et al. 2015) was used to construct the maximum likelihood (ML) phylogenetic trees based on concatenated SNPs for Dataset 4. We also converted Dataset 4 into NEXUS format using vcf2phylip.py, to construct the SVDquartets tree with PAUP (Chifman and Kubatko 2015), with the following parameters: "svdquartets nquartets=20,000 speciesTree bootstrap nreps=100". The trees were visualized using iTOL (https://itol.embl.de/).

We assessed the influence of spatial factors on the genetic differentiation between 12 populations and between 11 populations (without KL) separately using Mantel tests. Pairwise F_{ST} values were calculated using VCFtools and transformed to genetic distances with the formula $F_{ST}/(1 - F_{ST})$ using the vegan R package (Diniz-Filho et al. 2013). Geographic distance matrices were generated using the stats and geosphere packages in R, and Mantel tests were performed with 9,999 permutations using the vegan R package (Diniz-Filho et al. 2013).

Genetic diversity

Using Dataset 1, with VCFtools v0.1.13 (Danecek et al. 2011), the genetic differentiation index F_{ST} between each pair of clusters was calculated using the sliding window method (with a window size of 100 kb and a sliding window size of 100 kb), as well as the genetic diversity π, Tajima's D value, Observed Heterozygosity (H_o) and Expected Heterozygosity (H_e) for each population. The Tamhane's and Kruskal–Wallis tests were employed for post hoc pairwise comparisons. Linkage disequilibrium decay analysis of the populations was conducted using PopLDdecay v3.4.0 (Zhang et al. 2019). The maximum distance was set at 300 kb. The plotting parameters were "output all -bin1 100 -bin2 5000" to generate an LD decay graph.

Population history

SMC++ (Terhorst et al. 2017) was used to infer the population demography. The mutation rate was adopted from *B. pendula*, 9.5e−9 per site per generation (Salojärvi et al. 2017). A generation time of 10 years was assumed, following the estimate of Borrell et al. (2018). For each population and chromosome, the "vcf2smc" script was used to convert Dataset 2 into SMC++ input format. Demographic histories were then estimated using parameter: "smc++ estimate –spline cubic".

We inferred the demographic history of *B. nana* using multidimensional folded site frequency spectra (SFS). Folded SFSs were generated for each cluster in ANGSD v. 0.921 using the doSaf and realSFS functions (Korneliussen et al. 2014). Demographic parameters, including effective population size (N_e), divergence time and migration rates, were estimated using coalescent simulations in FASTSIMCOAL2 v. 2.6.1 (Excoffier and Foll 2011; Excoffier et al. 2013). We evaluated nine candidate demographic scenarios representing alternative divergence histories and patterns of gene flow among the four clusters and their ancestral lineages (Fig. S15), based on population relationships inferred from population genomic analyses. The same mutation rate and generation time as above were used to scale demographic estimates.

Each demographic scenario was independently run 100 times, with 100,000 coalescent simulations used to estimate the expected SFS and composite likelihood in each run. For each scenario, the replicate with the highest maximum composite likelihood was retained. Model fit was compared using the Akaike information criterion (AIC), and Akaike weights were calculated to quantify the relative support for each demographic scenario (Abascal et al. 2016; Thomé and Carstens 2016). The model with the highest Akaike weight was selected as the best-fitting scenario. For the optimal model, 95% confidence intervals (CIs) of demographic parameter estimates were obtained from 100 parametric bootstrap replicates.

Inbreeding and deleterious mutations

We used the SIFT algorithm (Sim et al. 2012) to predict harmful mutations in *B. nana* based on the reference genome and Dataset 5 (Fig. S2). For this purpose, we used TrEMBL plant database (Boeckmann et al. 2003) to search for orthologous genes. The scoring database of *B. nana* was constructed using the make-SIFT-DB-all.pl script, with the reference genome (.fa), the gene annotation file (gtf.gz), and the reference genome protein file as inputs. The protein-coding variants were classified using SIFT4G (Bortoluzzi et al. 2020) as non-synonymous harmful (SIFT score < 0.05), non-synonymous tolerant (SIFT score ≥ 0.05), or synonymous variants. The 'NA' sites and low-confidence sites were removed. We set 4 outgroups in the treefile (ERR13996197 (*Betula pubescens*), SRR19939340 (*B. platyphylla*), SRR24304953 (*B. pendula*), and SRR17214828 (*Alnus glutinosa*)), using the "-asr" option in IQ-TREE. Only sites with a posterior probability greater than 0.95 and supported by at least two sequences were retained (Ma et al. 2021). Moreover, the mutations of heterozygous, homozygous, and derived alleles were distinguished.

Dataset 6 was a dataset that re-filtered using VCFtools v0.1.13 without performing MAF, HWE and LD filtering (Fig. S2). SNPs with a genotype missing rate exceeding 5% were removed using Plink v1.9, resulting in a dataset containing 13,065,514 SNP loci. ROH (Runs of homozygosity) was calculated using the sliding window analysis method, where only ROH with lengths greater than 100 and more than 50 SNPs were detected. The window size was 50 SNPs, and ROH was calculated. The total length of ROH was divided by the total length of the reference genome to calculate F_{ROH}. The results were visualized using R v4.4.1. The Tamhane's and Kruskal–Wallis tests were employed for post hoc pairwise comparisons.

We obtained 0-fold and 4-fold degenerate sites based on the reference genome annotations, using degenotate (Mirchandani et al. 2024). Using Dataset 3, we calculated nucleotide diversity (π) at zero-fold and four-fold degenerate sites, as well as the π_N/π_S ratio, with PIXY v1.2.7 (Korunes and Samuk 2021) in 10 kb sliding windows.

Results

Sample collection and sequencing

We sequenced 82 individuals of *B. nana* from 12 Swiss populations (Figs. 1 and S2), generating 2660.79 Gb of raw data using DNBSEQ platform, and sequencing depth was 40.30× −81.65×, averaged 64.02× (Table S1). After fastp filtering, we have got 2,548.73 GB of clean data. In addition, sequencing 3 individuals of *B. glandulosa* from North America and 3 individuals of *B. nana* subsp. *exilis* from Siberia, resulting in 113.50 GB of clean data. The average Q20 value of the filtered sequencing data was 99.14%, the average Q30 value was 96.52%, and the average GC content was 37.52% (Table S1). The data were aligned to the reference genome of *B. platyphylla* (Chen et al. 2021), with an average mapping rate of 98.28% (Table S2). SNP calling strategy of the Genome Analysis Toolkit (GATK) generated 43,496,897 SNPs for 82 individuals. Further filtering resulted in 5,294,454 high-quality SNPs in Dataset 1. We used the parameter "–indep-pairwise 50 10 0.2" to generate Dataset 2 and contained 537,284 SNPs. Dataset 4 contained 500,744 SNPs.

Population structure

We selected $K = 4$ for discussion (Fig. 2a, c). The ADMIXTURE analysis showed that the cross-validation error (CV) values were low for $K = 4$–7 (Fig. S3). In the Jura Mountains, cluster 1 includes populations from the western region, while cluster 2 includes those from the eastern region. In the Alps, RT belonged to cluster 3, and WA belonged to cluster 4. The KL population, although geographically located in the Alps, clustered with BR and PM (cluster 2), suggesting that it may have originated from the Jura Mountains. When $K = 5$, AM, which was in cluster 1 at $K = 4$, shifted from cluster 1 and grouped with the Jura populations of cluster 2. CA and CU, despite their intermediate geographic position among the Jura populations, were separated into a separate cluster (Fig. S4). At $K = 6$ and $K = 7$, the clustering patterns became more fragmented, further supporting our selection of $K = 4$ (Fig. S4). PCA also separated all individuals into four clusters, consistent with the ADMIXTURE results (Figs. 2c, d and S5).

The ML phylogenetic tree showed that WA occupied the most basal position, RT was the next lineage to diverge, and the remaining populations formed a single clade. (Figs. 2b and S6). WA did not cluster with the other populations (including *B. nana* subsp. *exilis*), but clustered with *B. glandulosa*, indicating that WA belongs to *B. glandulosa* rather than *B. nana*. In the SVDquartets tree, WA also clustered with *B. glandulosa* (Fig. S7). Similarly, in both trees, RT clustered with the other *B. nana* populations, indicating that RT is *B. nana*. Additionally, the within-population branch lengths of both WA and RT are extremely short, consistent with these populations being clonal or consisting of closely related individuals (Fig. 2b).

The Mantel test revealed a significant correlation between genetic and geographic distances (isolation by distance, IBD) in the 11 populations excluding KL ($r = 0.57$, $p = 0.017$; Fig. S8a). However, no significant correlation was

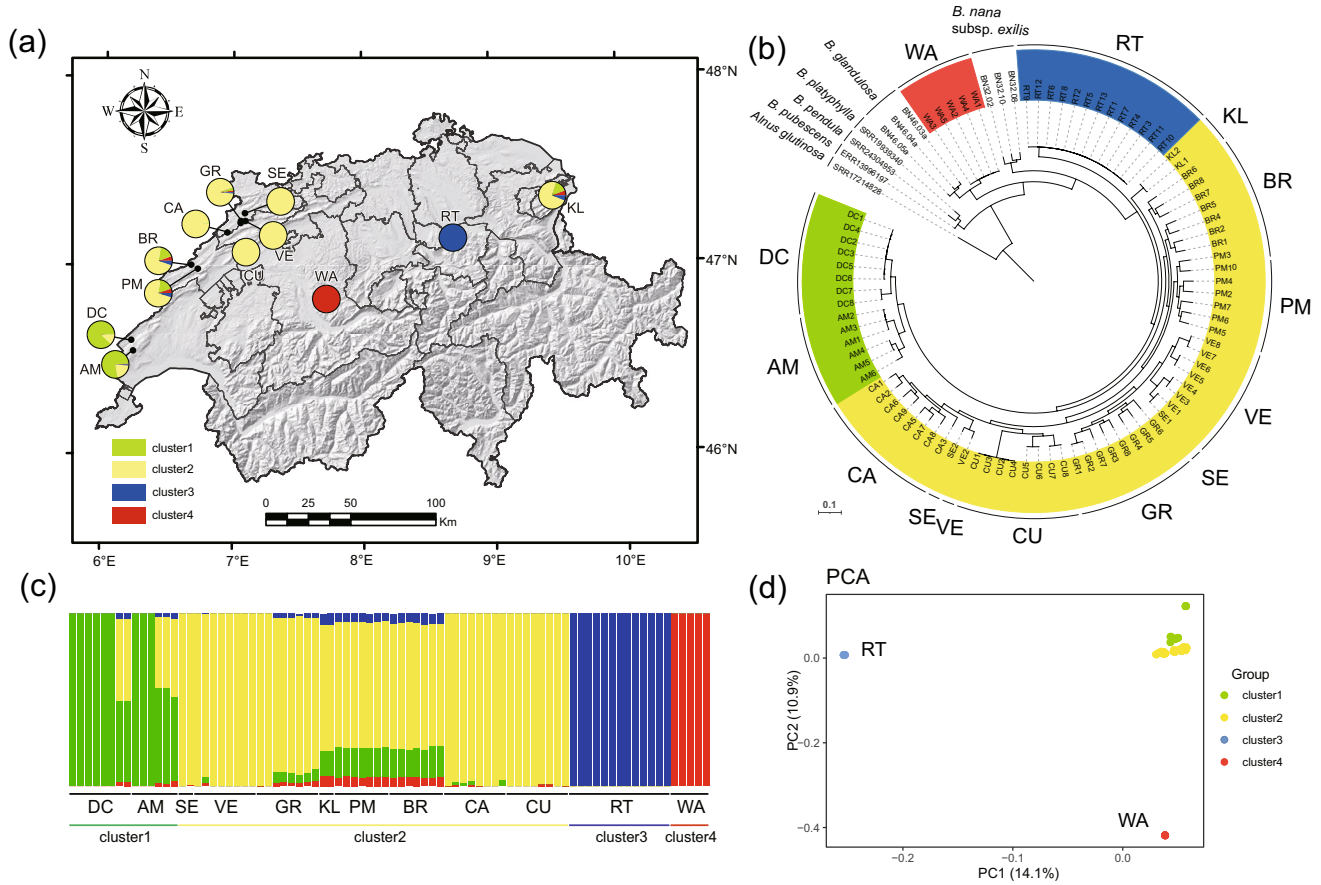

Fig. 2 **a** Map showing the geographic distribution and genetic structure of sampling locations of *Betula nana* in Switzerland. **b** Maximum-likelihood phylogenetic tree including outgroups. Colors show the four clusters of *B. nana* presented in **c**. **c** ADMIXTURE result of genetic structure of *B. nana* with K=4. **d** PCA result of the first two components. See Table 1 for population abbreviations

observed when all 12 populations were included ($r = 0.283$, $p = 0.131$; Fig. S8b).

Genetic diversity and Linkage disequilibrium

Based on Dataset 1, the genetic divergence (F_{ST}), nucleotide diversity (π), and Tajima's D were calculated to estimate the genetic diversity levels of each cluster (Fig. 3a). According to Wright (1965), the pairwise F_{ST} comparisons showed that the maximum F_{ST} was between cluster 3 and cluster 4 ($F_{ST} = 0.490$). The genetic differentiation of clusters 1 and 3 ($F_{ST} = 0.257$), and clusters 1 and 4 ($F_{ST} = 0.251$) was similar. Nucleotide diversity (π) indicated that the genetic diversity of cluster 2 was the highest ($\pi = 2.93 \times 10^{-3}$, $p < 0.001$), and that of cluster 4 was the lowest ($\pi = 9.79 \times 10^{-4}$, $p < 0.001$) (Fig. S9a). For Tajima's D, cluster 1 ($D = 1.24$) and cluster 2 ($D = 1.26$, $p < 0.001$) had the smallest values among all clusters, while cluster 3 had the largest ($D = 3.40$, $p < 0.001$) (Fig. S9b). The analysis of the populations (Table 1) showed that lower π values were found in WA, KL and RT ($\pi = 0.0010$, 0.0018, and 0.0020, respectively; all $p < 0.001$), and higher Tajima's D values were found in RT, WA and KL ($D = 3.397$, 2.438, and 2.058, respectively; all $p < 0.001$), indicating that these three populations have recently passed through a bottleneck.

Genomic LD decay (r^2) revealed that among the 4 clusters (Figs. 3b and S10). The r^2 values of clusters 3 and 4 declined rapidly initially, but subsequently stabilized at approximately 0.3 and 0.4, with no further decrease.

Population history and gene introgression

SMC++ analysis was used to estimate historical effective population size (Fig. 3c). The trends in effective population size (N_e) were similar between clusters 1 and 2. From 100,000 to 10,000 years ago, the N_e of clusters 1–3 remained relatively stable, N_e of cluster 4 decreased slightly and then recovered (Fig. S11). During the period from 10,000 years ago to 100 years ago, the N_e of all clusters continued to decrease. Similar results were obtained using other mutation rates (Fig. S11).

FASTSIMCOAL2 analyses strongly supported Model 9 as the best-fitting demographic scenario (Akaike weight =1; Fig. 3d; Table S7). Under this model, cluster 4 (WA)

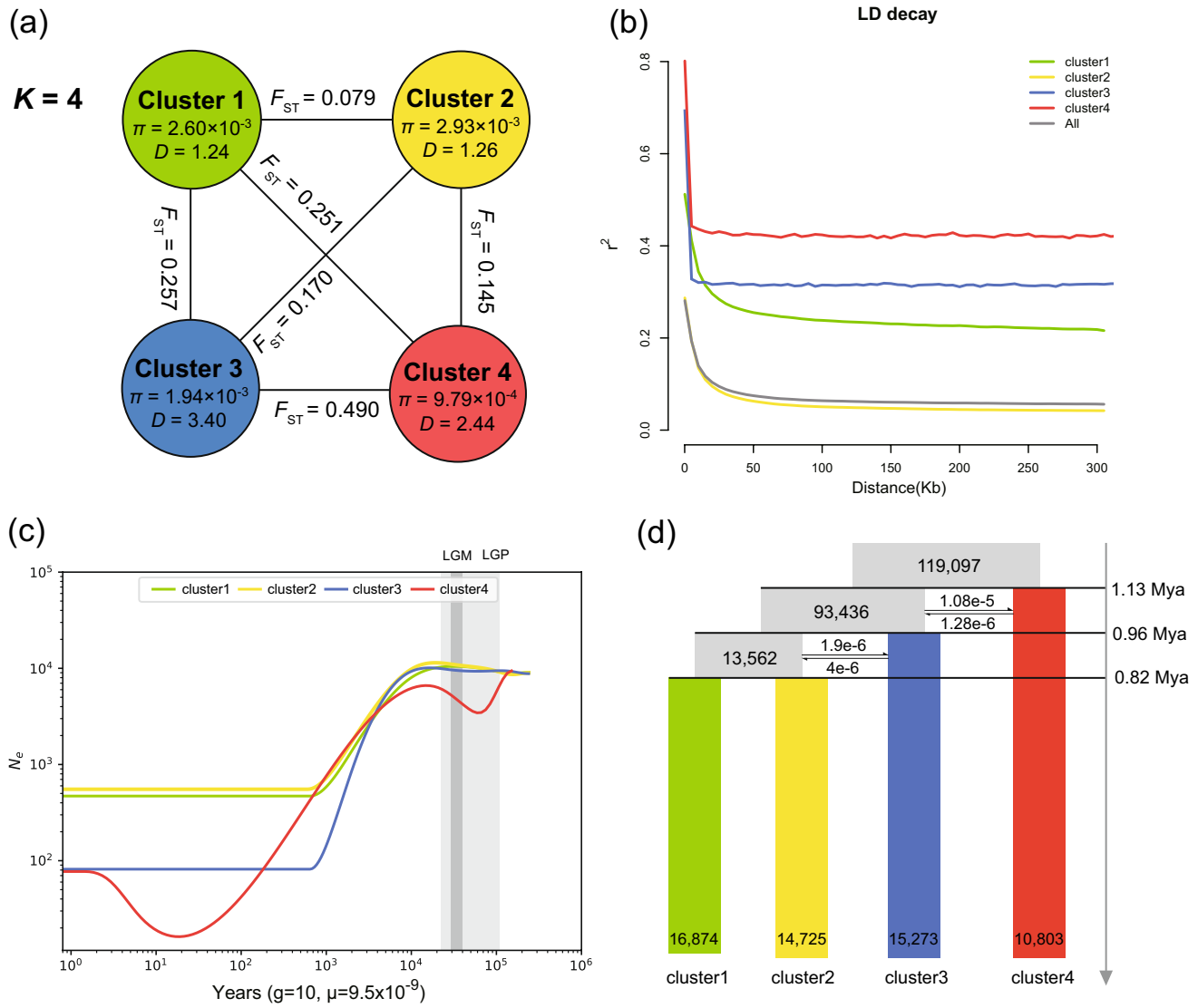

Fig. 3 **a** Nucleotide diversity (π) and Tajima's D (D) of four clusters of *Betula nana* detected in Switzerland (as defined in Fig. 2c) and genetic divergence (F_{ST}) between each cluster. **b** Linkage disequilibrium (LD) decay of four clusters. **c** SMC++ analysis for population history. Mutation rate (μ) = 9.5e−9 and generation time (g) = 10 years. Grey areas show glaciation events (LGP, Last Glacial Period; LGM, Last Glacial Maximum). **d** Schematic representation of demographic scenarios modelled for each cluster in FASTSIMCOAL2. Estimates of N_e and divergence times are indicated. The numbers next to the horizontal arrows denote the per generation migration rate between lineages

diverged from the ancestor of clusters 1–3 at approximately 1.13 Mya, followed by the divergence of cluster 3 (RT) at approximately 0.96 Mya and the subsequent divergence among clusters 1 and 2 at approximately 0.82 Mya (Fig. 3d; Table S6). Contemporary effective population sizes were broadly comparable among the four clusters, whereas ancestral population sizes varied substantially across successive divergence stages. The best-fitting model further supported historical bidirectional gene flow between cluster 3 and the ancestral lineage of clusters 1–2 and between cluster 4 and the ancestral lineage of clusters 1–3, with asymmetric migration rates in both cases.

Deleterious mutations and inbreeding

ROH (Runs of homozygosity) fragments longer than 100 kb were identified and F_{ROH} (Fraction of ROH) was calculated (Figs. 4a and S12, Table S3). The Inbreeding level of cluster 1 (6.20×10^{-6}), cluster 2 (5.56×10^{-6}) and cluster 3 (5.60×10^{-6}), are all higher than cluster 4 (3.82×10^{-6}, $p < 0.05$, Fig. 4a).

Based on the results of SIFT and functional impact of the mutations, 133,959 mutations were assigned to synonymous (72,135 loci and accounting for 53.85%), tolerated (47,097, 35.16%), and deleterious (14,727, 10.99%) respectively (Table S4). Cluster 3 has the highest deleterious/synonymous

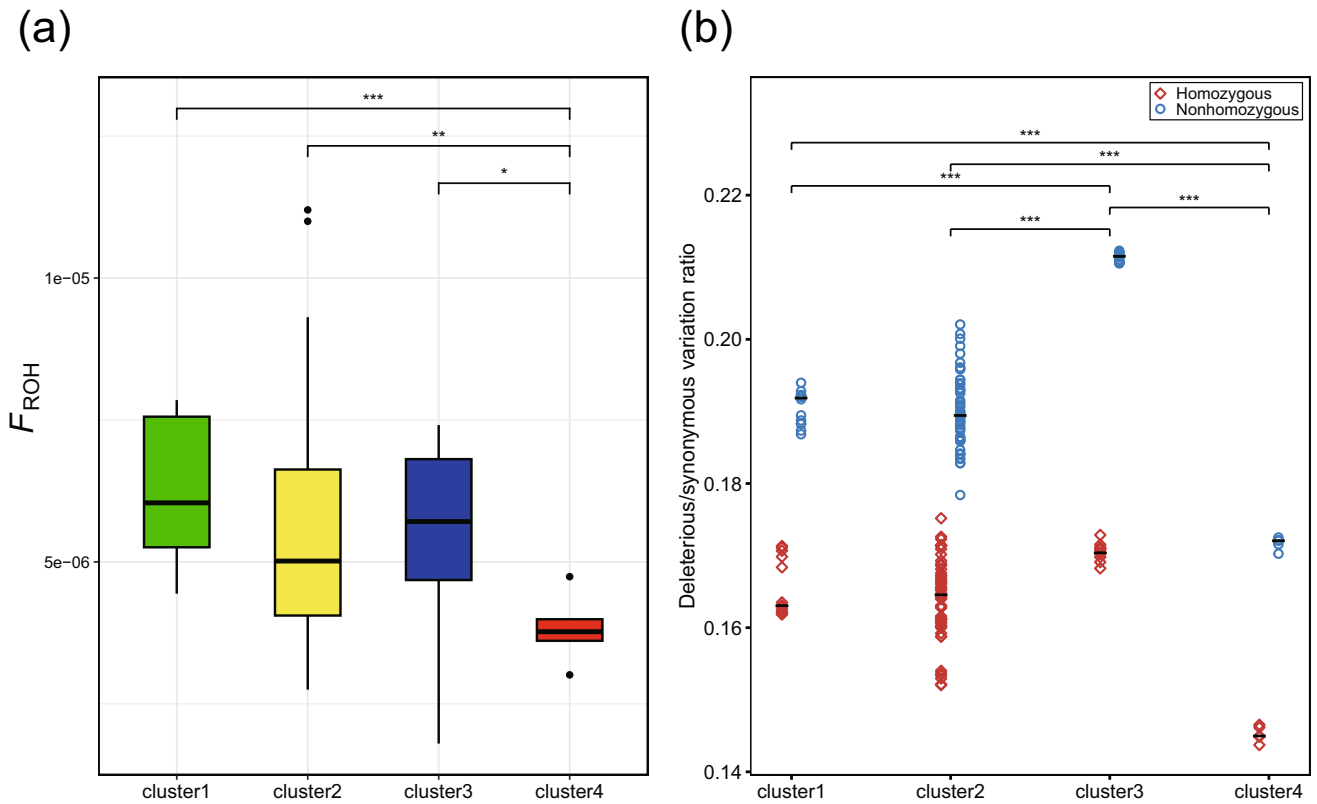

Fig. 4 **a** Inbreeding coefficient estimated from Runs of Homozygosity (F_{ROH}) for each of the four *Betula nana* clusters (See Fig. 2c for the cluster composition). **b** Ratios of homozygous derived deleterious variants to homozygous derived synonymous variants for different populations. The horizontal bars denote population means

variation ratio of homozygous (0.171, $p < 0.001$) and non-homozygous (0.211, $p < 0.001$), while lowest in cluster 4 with homozygous (0.145, $p < 0.001$) and non-homozygous (0.172, $p < 0.001$) (Figs. 4b and S13). Additionally, the π_N/π_S ratio of all populations was around 0.5, indicating that all populations have undergone purifying selection (Table S5).

Discussion and conclusions

Despite the restricted geographical scope of our study, which focused exclusively on Swiss populations of *B. nana*, our results provide important insights into the genetic status and conservation challenges of this rare glacial relict species. Through analyses of population structure, genetic diversity, and genetic load, we found that the genetic composition of Swiss alpine populations has been strongly affected by historical demographic changes and recent anthropogenic influences. In particular, one of the remaining alpine populations is characterized by very low genetic diversity, highlighting its potential vulnerability. Demographic reconstructions indicate a substantial decline in effective population size following the last glacial period. Moreover, present-day patterns of genetic diversity and population structure appear to have been further shaped by recent human-mediated introductions. Together, these findings emphasize the importance of comprehensive, genetically informed conservation strategies to safeguard the remaining *B. nana* populations in Switzerland and provide a valuable framework for future assessments of this species across the Alpine region.

Genetic diversity of *Betula nana* in Switzerland

Across Europe, *B. nana* populations show considerable variation in their levels of genetic diversity; however, comparisons among studies must be interpreted with caution because different marker systems capture genetic variation at different evolutionary scales and are not directly comparable. Microsatellite, AFLP, and RAPD studies provide valuable information on relative patterns of genetic diversity among populations, but their diversity estimates cannot be directly compared with SNP-based heterozygosity estimates.

Within this methodological context, microsatellite-based analyses have revealed relatively high levels of genetic diversity in some relict Polish populations (mean $H_o = 0.556$; Jadwiszczak et al. 2013), whereas studies based on dominant markers (AFLP and RAPD) from Poland, Belarus, and

Sweden have generally indicated reduced within-population variation (Jadwiszczak et al. 2017; Dabrowska et al. 2021). Although these estimates cannot be quantitatively compared with our SNP-based results, they provide evidence that genetic diversity in *B. nana* varies substantially among regions and populations.

More directly comparable are genomic and RAD-seq studies from the United Kingdom (Zohren et al. 2016; Borrell et al. 2018), which reported moderate levels of SNP-based genetic diversity. In comparison, the Swiss populations analyzed here show relatively low SNP-based heterozygosity, with values ranging from 0.158 in the isolated Wachseldornmoos population to 0.327 in Rothenthurm, while Jura populations showed intermediate values (H_o = 0.250–0.283). These patterns are consistent with the expectation that long-term isolation, small effective population sizes, and the marginal distribution of *B. nana* in Switzerland have contributed to genetic erosion.

Recent cpDNA studies from the Ural Mountains (Cherepanova et al. 2024; Medvedeva et al. 2025) have also documented low haplotypic diversity in northern *B. nana* populations, particularly in the Polar Urals, suggesting that genetic impoverishment occurs in several marginal populations across the species' range. Conversely, SNP-based analyses from Iceland (Pálsson et al. 2023) indicate moderate genetic variation maintained through hybridization and gene flow, illustrating the importance of regional demographic history in shaping genetic diversity.

Overall, although marker systems differ among studies and direct quantitative comparisons remain limited, the available genomic evidence suggests that Swiss populations represent genetically depauperate remnants of *B. nana* at the southern edge of its distribution. Their conservation is therefore important for preserving the remaining genetic diversity and evolutionary potential of this glacial relict species.

The distribution of genetic diversity and potential driving factors

The results of our ADMIXTURE analysis revealed that Swiss *B. nana* populations can be divided into four genetic clusters (Fig. 2). Clusters 1 and 2 showed very similar genetic structures, whereas clusters 3 and 4 differed markedly. This suggests that the Jura populations originated from different ancestral lineages compared with the populations in the Swiss Alps. The PCA analysis further underscores this pattern, showing that the alpine populations from Wachseldornmoos (WA, canton of Bern) and Rothenthurm (RT, canton of Schwyz) are clearly separated from the Jura populations – and also distinctly separated from each other. The only exception among the alpine occurrences is the extremely small group from Kleckelmoos (KL, canton of Appenzell Ausserrhoden), which comprises only two individuals and shows very short branch lengths, suggesting that they may consisting of a single clone or consisting of closely related individuals. Its genetic structure most closely resembled that of Brévine (BR) and Ponts-de-Martel (PM) in the canton of Neuchâtel, both belonging to cluster 2. The KL population, discovered in 1917, was maintained ex situ at the Botanical Garden of St. Gallen for nearly a century before its reintroduction in 2013 (pers. comm. R. Nagel; Info Flora 2025). Based on our results, it is probable that the original plant material was inadvertently replaced or mixed during ex situ cultivation with material from the genetically well-known and large BR or PM populations.

The Wachseldornmoos population (WA) was genetically the most divergent among all studied sites, raising the suspicion that it might represent an introduced taxon of dwarf birch. It diverged from the other populations at an early stage (Fig. 2b), and its observed heterozygosity (H_o) was low (Table 1), arguing against any hybridization event. Furthermore, the five individuals analyzed showed very short within-cluster branch lengths (Fig. 2b), suggesting that they may be consist of closely related individuals or originate from a single parent. Additional morphological and genetic analyses confirmed that these plants belong to the North American species *B. glandulosa* (Figs. 2b and S14). This small group was recorded for the first time only in 2017 (Info Flora 2025), and the circumstances of its introduction remain unknown. A natural occurrence of *B. glandulosa* in Europe can be excluded with high certainty.

The third alpine population, Rothenthurm (RT), is also genetically highly isolated (Table 1, Fig. 2b). In this case, however, the ex situ cultivation and subsequent reintroduction are well documented: all extant plants were propagated from individuals originating from the nearby natural population of Roblosen, which was destroyed, and were transplanted to their current site between 2006 and 2008 (Schuler 2020, unpublished action plan). Despite their low genetic diversity, these plants are of considerable conservation importance, as they likely represent the last individuals in the Swiss Alps potentially carrying an autochthonous alpine gene pool. The IBD analysis excluding KL showed significant isolation by distance among populations.

Our additional analyses corroborate the strong isolation of clusters 3 and 4. For instance, the F_{ST} estimates (Fig. 3a) reveal pronounced differentiation between clusters 1 and 4, substantial divergence of cluster 3 from all other populations, and close genetic relatedness among clusters 1 and 2. The LD pattern (Fig. 3b) also shows that cluster 3 and 4 present much higher isolation at a genome-wide scale than the others. Genome-wide Tajima's *D* values are elevated in KL, RT, and WA, and consistent with demographic contraction.

The uniformly low π values further support a history of contraction and reflect the extremely small effective sizes of these alpine groups. Taken together, these metrics confirm that all three alpine populations may derive from genetically impoverished ex situ material.

Our analysis of runs of homozygosity (ROH) provided additional insights (Fig. 4). Long ROH typically signals recent inbreeding, whereas short ROH indicates older or more diffuse inbreeding episodes (Kirin et al. 2006). All *B. nana* (cluster 1–3) have higher F_{ROH} and more deleterious mutations than WA (cluster 4) – consistent with WA representing an introduced *B. glandulosa* population. This might be because *B. glandulosa* may have a lower level of inbreeding compared to *B. nana*, and may carry fewer harmful mutations. An additional, non-exclusive explanation involves strong purifying selection, because the π_N/π_S ratio for all populations was around 0.5 (Table S5): if WA individuals are poorly adapted to their current environments, carriers of deleterious mutations may have reduced survival, further limiting the presence of such variants. In RT (cluster 3), many deleterious mutations occur in the heterozygous state. Because recessive deleterious alleles are masked in heterozygotes, they may escape purifying selection, potentially explaining why RT exhibits a weaker signal of purifying selection than WA despite carrying a high burden of harmful mutations (Fig. S13). However, inbreeding may increase the homozygosity of these alleles, exposing them to selection and potentially resulting in inbreeding depression that could contribute to population decline.

Paleoclimate fluctuations affected the historical dynamics of *B. nana* populations in Switzerland

Our SMC++ analysis using a mutation rate of 9.5×10^{-9} (Fig. 3c) shows that the effective population size (N_e) of all clusters remained relatively stable throughout the Last Glacial Period (LGP) and the Last Glacial Maximum (LGM). The N_e of clusters 1–3 remained relatively stable, N_e of cluster 4 decreased slightly and then recovered. These trends may reflect favorable conditions for *B. nana* during the LGP. After the end of the LGP, rapid climatic warming triggered a marked reduction in N_e across all groups, indicating that *B. nana* struggled to adapt to post-glacial conditions and experienced substantial habitat contraction. Analyses using alternative mutation rates (Fig. S11) yielded the same general pattern, with N_e peaking during the LGP. Similar conclusions were drawn by Birks (2008), who noted that *B. nana*—a typical ice-age relict – expanded southward into Central European lowlands during the LGP but retreated to Arctic and high mountain regions during the last interglacial period due to increased competition and habitat loss. In Poland, fossil records show that *B. nana* appeared in the northeast around 13,000 years ago and persisted into the early–middle Holocene before disappearing roughly 9,000 years ago as the Atlantic-period warming intensified (Drzymulska 2014).

A particularly interesting pattern concerns cluster 2, which shows the smallest post-glacial decrease in N_e. This population occupies a region that remained ice-free during the LGM (Fig. S1), and may thus remain in situ, unlike clusters 1, as well as cluster 3 (RT). Although *B. nana* is a glacial relict, it typically colonizes newly deglaciated terrain only after a substantial delay. Harning et al. (2023) demonstrated that *B. nana* often arrives more than 1,000 years after ice retreat. Crump et al. (2019) found large postglacial migration lags in dwarf birch in Baffin Island in North America. Similar patterns have been documented for *B. nana* in the United Kingdom and Iceland, where wind pollination does not translate into meaningful long-distance gene flow (Wang et al. 2016; Pálsson et al. 2023). The species' low seed viability and reliance on vegetative reproduction (Jadwiszczak et al. 2017) further restrict dispersal. Nevertheless, *B. nana* may occasionally achieve long-distance dispersal through rare stochastic events, as illustrated by its colonization of remote high-Arctic regions such as the Svalbard Archipelago (Alsos et al. 2015). Consequently, clusters 1 and 3 likely recolonized the study area considerably later – and with smaller founding populations – than cluster 2.

In the Fastsimcoal results (Fig. 3d), cluster 4 (WA) diverged from the ancestor of clusters 1–3 at approximately 1.13 Mya. This was followed by the divergence of cluster 3 (RT) at approximately 0.96 Mya and the subsequent divergence among clusters 1 and 2 at approximately 0.82 Mya. This timing is similar to the time that *B. nana* diverged with *B. glandulosa* (Dance et al. 2025). Fastsimcoal also shows gene flow between cluster 3 and the ancestral lineage of clusters 1, 2 and between cluster 4 and the ancestral lineage of clusters 1–3. The effective population sizes estimated by Fastsimcoal are larger than census population size. This may be because a very recent decline in effective population size may not be fully captured by the method (Tao et al. 2023).

Conservation implications for *Betula nana* in Switzerland

Our study paints a sobering picture of the conservation status of *B. nana* in Switzerland: although the Jura populations still maintain moderate genetic diversity, the alpine gene pool has been reduced to a critically fragile remnant and is now represented only by a few reintroduced, genetically impoverished individuals. This situation is dramatic, as the native alpine lineage has been almost entirely lost, leaving Switzerland with only small, isolated, and partly misidentified lineages. The clear genetic distinctness between Jura

and alpine groups underscores that both regions harbor distinct and historically differentiated components of the species' historical diversity. Both require targeted conservation action, although the urgency is far greater in the Alps.

A first priority must be a comprehensive, fine-scale field inventory throughout the Swiss Alps and pre-alpine wetlands to verify whether any overlooked natural populations persist. Should new occurrences be discovered, immediate genomic analyses will be essential to determine whether they represent genuinely autochthonous alpine lineages or planted/ex situ-derived material. Because past ex situ cultivation practices have repeatedly led to unintended genetic mixing—as demonstrated by the KL population, the presence of *B. glandulosa* at WA – future ex situ propagation must follow strict genetic management guidelines. This includes verified origin of plant material, separate cultivation of genetic lineages, periodic genetic screening, and long-term documentation and archiving of plant histories.

As shown in the diversity analysis, the RT population has low π, high Tajima's D, and a small population size. It has many heterozygous harmful mutations, and if inbreeding occurs, the effects could be even more severe. Thus, RT is the most threatened population and requires urgent protection.

Given the self-incompatibility of *B. nana*, the clonal structure of many small Swiss populations, and the extremely limited gene flow detected in our study, restoring functional population sizes will require active reinforcement. Current conservation frameworks across northern Europe – such as those implemented in Scotland, Norway, and Iceland – emphasize peatland restoration, grazing management, and rewetting of mires to stabilize dwarf birch populations (Aradóttir and Arnalds 2001; Scott 2001; Borrell et al. 2020; Watts et al. 2026).For the Jura Mountains, where diversity is still present but declining, conservation should focus on habitat protection, hydrological restoration of peatlands, and population enlargement using locally appropriate genetic material. In the Alps, where the native lineage has nearly disappeared, priority should be given to locating any remaining natural individuals, securing them through ex situ collections that are rigorously genetically monitored, and improving habitat conditions to maximize the survival and reproductive success of the surviving plants. At this stage, conservation efforts should concentrate on safeguarding, documenting, and managing the remaining Swiss genetic resources rather than introducing material from outside Switzerland, ensuring that the distinctiveness of the native alpine lineage is protected. Equally important is the long-term conservation of suitable habitats.

Finally, all conservation actions should be embedded in a national management plan that integrates ecological monitoring, genetic surveillance, ex situ safeguarding, and strictly controlled reintroductions. Only through coordinated, science-based action can Switzerland preserve what remains of this glacial relict – and potentially rebuild a viable alpine lineage before it disappears forever.

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Author contributions GK and Y-GS conceived and designed the study. Material preparation and data collection were performed by LC, NK, YF, GK, MD and MM-F. Data analyses and figures were performed by Y-RC, B-JW, J-LS, X-LD, NW and YF. Y-GS, GK, MD and MM-F obtained funding. The first draft of the manuscript was written by Y-RC, GK and Y-GS and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All raw sequencing data have been deposited in the National Genomics Data Center, China National Center for Bioinformation under BioProject accession number PRJCA056771.

Declarations

Competing interests The authors declare no competing interests.

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References

Abascal F, Corvelo A, Cruz F et al (2016) Extreme genomic erosion after recurrent demographic bottlenecks in the highly endangered *Iberian lynx*. Genome Biol 17:251. https://doi.org/10.1186/s13059-016-1090-1

Alexander DH, Novembre J, Lange K (2009) Fast model-based estimation of ancestry in unrelated individuals. Genome Res 19:1655–1664. https://doi.org/10.1101/gr.094052.109

Alsos IG, Engelskjøn T, Brochmann C (2002) Conservation genetics and population history of *Betula nana*, *Vaccinium uliginosum*, and *Campanula rotundifolia* in the Arctic Archipelago of Svalbard. Arct Antarct Alp Res 34:408–418. https://doi.org/10.1080/15230430.2002.12003511

Alsos IG, Ehrich D, Eidesen PB, Solstad H, Westergaard KB, Schönswetter P, Tribsch A, Birkeland S, Elven R, Brochmann C (2015) Long-distance plant dispersal to North Atlantic islands: colonization routes and founder effect. AoB PLANTS. https://doi.org/10.1093/aobpla/plv036

Aradóttir AL, Arnalds O (2001) Ecosystem degradation and restoration of birch woodlands in Iceland. In: Wielgolaski FE (ed) Nordic Mountain Birch Ecosystems. UNESCO, Paris, and Parthenon Publishing, Carnforth, pp 293–306

Arrigo N, Bétrisey S, Graf L, Bilat J, Gerber E, Kozlowski G (2016) Hybridization as a threat in climate relict *Nuphar pumila* (Nymphaeaceae). Biodivers Conserv 25:1863–1877. https://doi.org/10.1007/s10531-016-1165-z

Bertorelle G, Raffini F, Bosse M, Bortoluzzi C, Iannucci A, Trucchi E, Morales HE, van Oosterhout C (2022) Genetic load: genomic estimates and applications in non-model animals. Nat Rev Genet 23:492–503. https://doi.org/10.1038/s41576-022-00448-x

Bétrisey S, Arrigo N, Graf L, Bilat J, Gerber E, Kozlowski G (2020) Glacial relicts in the Alps: the decline and conservation strategy for *Nuphar pumila* (Nymphaeaceae). Alp Bot 130:89–99. https://doi.org/10.1007/s00035-020-00232-9

Birks HH (2008) The Late-Quaternary history of arctic and alpine plants. Plant Ecol Divers 1:135–146. https://doi.org/10.1080/17550870802328652

Boeckmann B, Bairoch A, Apweiler R, Blatter MC, Estreicher A, Gasteiger E, Martin MJ, Michoud K, O'Donovan C, Phan I, Pilbout S, Schneider M (2003) The SWISS-PROT protein knowledgebase and its supplement TrEMBL in 2003. Nucleic Acids Res 31:365–370. https://doi.org/10.1093/nar/gkg095

Borbély E, Indreica A (2019) Conservation status of the rare species *Betula nana* in the peatbog Tinovul Luci (the Harghita Mountains, Romania). Stud Univ Babes-Bolyai Biol 64:5–12. https://doi.org/10.24193/subbbiol.2019.2.01

Bornand C, Gygax A, Juillerat P, Jutzi M, Möhl A, Rometsch S, Sager L, Santiago H, Eggenberg S (2016) Rote Liste Gefässpflanzen: Gefährdete Arten der Schweiz. Bundesamt für Umwelt, Bern und Info Flora, Genf (Umwelt-Vollzug Nr. 1621). Pp 178

Borrell JS, Wang N, Nichols RA, Buggs RJA (2018) Genetic diversity maintained among fragmented populations of a tree undergoing range contraction. Heredity 121:304–318. https://doi.org/10.1038/s41437-018-0132-8

Borrell JS, Zohren J, Nichols RA, Buggs RJA (2020) Genomic assessment of local adaptation in dwarf birch to inform assisted gene flow. Evol Appl 13:161–175. https://doi.org/10.1111/eva.12883

Bortoluzzi C, Bosse M, Derks MFL et al (2020) The type of bottleneck matters: insights into the deleterious variation landscape of small managed populations. Evol Appl 13:330–341. https://doi.org/10.1111/eva.12872

Brochmann C, Gabrielsen TM, Nordal I, Landvik JY, Elven R (2003) Glacial survival or *tabula rasa*? The history of North Atlantic biota revisited. Taxon 52:417–450. https://doi.org/10.2307/3647381

Brochmann C, Elphinstone C, Birkeland S, Ikeda H, Eidesen PB, Alsos IG, Westergaard KB (2025) Phylogeography of Arctic plants: Where are we after 35 years, and where to go? Plant Ecol Divers 18:99–123. https://doi.org/10.1080/17550874.2025.2571098

Buchwal A, Syndonia Bret-Harte M, Bailey H, Welker JM (2023) From intra-plant to regional scale: June temperature and regional climates directly and indirectly control *Betula nana* growth in Arctic Alaska. Ecosystems 26:491–509. https://doi.org/10.1007/s10021-022-00771-8

Büntgen U, Hellmann L, Tegel W, Normand S, Myers-Smith I, Kirdyanov AV, Nievergelt D, Schweingruber FH (2015) Temperature-induced recruitment pulses of Arctic dwarf shrub communities. J Ecol 103:489–501. https://doi.org/10.1111/1365-2745.12361

Chen S, Wang Y, Yu L, Zheng T, Wang S, Yue Z, Jiang J, Kumari S, Zheng C, Tang H, Li J, Li Y, Chen J, Zhang W, Kuang H, Robertson JS, Zhao PX, Li H, Shu S, Yordanov YS, Huang H, Goodstein DM, Gai Y, Qi Q, Min J, Xu C, Wang S, Qu GZ, Paterson AH, Sankoff D, Wei H, Liu G, Yang C (2021) Genome sequence and evolution of *Betula platyphylla*. Hortic Res 8:37. https://doi.org/10.1038/S41438-021-00481-7

Cherepanova O, Medvedeva S, Filippov E, Skaptsov M, Ivchenko T, Teptina A (2024) Biodiversity evolution of a shrub *Betula nana* L. populations in the Urals. Int J for Res. https://doi.org/10.1155/2024/2644583

Chifman J, Kubatko L (2015) Identifiability of the unrooted species tree topology under the coalescent model with time-reversible substitution processes, site-specific rate variation, and invariable sites. J Theor Biol 374:35–47. https://doi.org/10.1016/j.jtbi.2015.03.006

Crump SE, Miller GH, Power M, Sepúlveda J, Dildar N, Coghlan M, Bunce M (2019) Arctic shrub colonization lagged peak postglacial warmth: molecular evidence in lake sediment from Arctic Canada. Glob Chang Biol 25:4244–4256. https://doi.org/10.1111/gcb.14836

Dabrowska G, Dzialuk A, Burnicka O, Ejankowski W, Gugnacka-Fiedor W, Goc A (2006) Genetic diversity of postglacial relict shrub *Betula nana* revealed by RAPD analysis. Dendrobiology 55:19–23

Dabrowska GB, Dabrowski HP, Szyp-Borowska I (2021) Genetic diversity of *Betula nana* in Sweden and conservation implications for protection of relict Polish populations. Folia for Pol A 63:225–231. https://doi.org/10.2478/ffp-2021-0023

Dance M, Saupe EE, Borrell J et al (2025) Molecular footprints of quaternary climate fluctuations in the circumpolar tundra shrub dwarf birch. Mol Ecol 34:e70082. https://doi.org/10.1111/mec.70082

Danecek P, Auton A, Abecasis G, Albers CA, Banks E, DePristo MA, Handsaker RE, Lunter G, Marth GT, Sherry ST, McVean G, Durbin R, 1000 Genomes Project Analysis Group (2011) The

variant call format and VCFtools. Bioinformatics 27:2156–2158. https://doi.org/10.1093/bioinformatics/btr330

De Groot WJ, Thomas PA, Wein RW (1997) *Betula nana* L. and *Betula glandulosa* Michx. J Ecol 85:241–264. https://doi.org/10.2307/2960655

De Kort H, Prunier JG, Ducatez S, Honnay O, Baguette M, Stevens VM, Blanchet S (2021) Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. Nat Commun 12:516. https://doi.org/10.1038/s41467-021-20958-2

De Summa S, Malerba G, Pinto R, Mori A, Mijatovic V, Tommasi S (2017) GATK hard filtering: tunable parameters to improve variant calling for next generation sequencing targeted gene panel data. BMC Bioinformatics 18:119. https://doi.org/10.1186/s12859-017-1537-8

Diniz-Filho JA, Soares TN, Lima JS et al (2013) Mantel test in population genetics. Genet Mol Biol 36:475–485. https://doi.org/10.1590/S1415-47572013000400002

Drzymulska D (2014) Postglacial occurrence and decline of *Betula nana* L. (dwarf birch) in northeastern Poland. Est J Earth Sci 63:76–87. https://doi.org/10.3176/earth.2014.07

Dun X, Ding J, Jadwiszczak KA, Zhou S, Wang Q, Nakamura K, Fan Y, Nagamitsu T, Chen D, Wang N (2025) Morphological and molecular data demonstrate the existence of *Betula fruticosa* and *B. middendorffii* and the absence of *B. ovalifolia* in northeastern China. Bot J Linn Soc 208:303–312. https://doi.org/10.1093/botlinnean/boae075

Eidesen PB, Ehrich D, Bakkestuen V, Alsos IG, Gilg O, Taberlet P, Brochmann C (2013) Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. New Phytol 200:898–910

Eidesen PB, Alsos IG, Brochmann C (2015) Comparative analyses of plastid and AFLP data suggest different colonization history and asymmetric hybridization between *Betula pubescens* and *B. nana*. Mol Ecol 24:3993–4009. https://doi.org/10.1111/mec.13289

Ejankowski W (2010) Demographic variation of dwarf birch (*Betula nana*) in communities dominated by *Ledum palustre* and *Vaccinium uliginosum*. Biologia (Bratisl) 65:248–253. https://doi.org/10.2478/s11756-010-0007-9

Elven R, Murray D, Razzhivin V, Yurtsev B (2011) Annotated Checklist of the Panarctic Flora (PAF) Vascular plants version 1.0. Checklist of the Panarctic Flora (PAF). http://panarcticflora.org/

Excoffier L, Foll M (2011) Fastsimcoal: a continuous-time coalescent simulator of genomic diversity under arbitrarily complex evolutionary scenarios. Bioinformatics 27:1332–1334. https://doi.org/10.1093/bioinformatics/btr124

Excoffier L, Dupanloup I, Huerta-Sánchez E, Sousa VC, Foll M (2013) Robust demographic inference from genomic and SNP data. PLoS Genet 9:e1003905. https://doi.org/10.1371/journal.pgen.1003905

FCAA (2025) Flora of the Canadian Arctic Archipelago. Available at: https://nature.ca/aaflora/data/www/bebena.htm. Accessed 4 December 2025

FNA (2025) Flora of North America. Available at: www.efloras.org. Accessed 4 December 2025

Fuentes-Pardo AP, Ruzzante DE (2017) Whole-genome sequencing approaches for conservation biology: advantages, limitations and practical recommendations. Mol Ecol 26:5369–5406. https://doi.org/10.1111/mec.14264

Gagnebin A (1751) Description du Bouleau nain ou petit Bouleau. Acta Helvetica 1:58–61

Garcia-Costoya G, Williams CE, Faske TM, Moorman JD, Logan ML (2023) Evolutionary constraints mediate extinction risk under climate change. Ecol Lett 26:529–539. https://doi.org/10.1111/ele.14173

Hampe A, Jump AS (2011) Climate relicts: past, present, future. Annu Rev Ecol Evol Syst 42:313–333. https://doi.org/10.1146/annurev-ecolsys-102710-145015

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecol Lett 8:461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Harning DJ, Sacco S, Anamthawat-Jónsson K, Ardenghi N, Thordarson T, Raberg JH, Sepúlveda J, Geirsdóttir Á, Shapiro B, Miller GH (2023) Delayed postglacial colonization of *Betula* in Iceland and the circum North Atlantic. Elife 12:RP87749. https://doi.org/10.7554/eLife.87749

Hegi G (1981) Illustrierte Flora von Mitteleuropa. Band III. Teil 1. Verlag Paul Parey, Berlin

Hoffmann AA, Willi Y (2008) Detecting genetic responses to environmental change. Nat Rev Genet 9:421–432. https://doi.org/10.1038/nrg2339

Holderegger R, Thiel-Egenter C (2009) A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. J Biogeogr 36:476–480. https://doi.org/10.1111/j.1365-2699.2008.02027.x

Hollesen J, Buchwal A, Rachlewicz G, Hansen BU, Hansen M, Stecher O, Elberling B (2015) Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past centuries. Glob Change Biol 21:2410–2423. https://doi.org/10.1111/gcb.12913

Hultén E, Fries M (1986) Atlas of north European vascular plants north of the Tropic of Cancer. Koeltz Scientific

Huybers P (2007) Glacial variability over the last two million years: an extended depth-derived agemodel, continuous obliquity pacing, and the Pleistocene progression. Quat Sci Rev 26:37–55. https://doi.org/10.1111/gcb.12913

Info Flora (2025) Centre national de données et d'informations sur la flore de Suisse. Available at: www.infoflora.ch. Accessed 5 December 2025

Jadwiszczak KA, Drzymulska D, Banaszek A, Jadwiszczak P (2013) Population history, genetic variation and conservation status of the endangered birch species *Betula nana* L. in Poland. Silva Fenn 46:465–477. https://doi.org/10.14214/sf.905

Jadwiszczak KA, Kłosowski S, Zalewska I, Banaszek A, Chrzanowska A (2017) Genetic diversity and sexual reproduction in relict populations of *Betula nana*. Silva Fenn 51:5643. https://doi.org/10.14214/sf.5643

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet 11:94. https://doi.org/10.1186/1471-2156-11-94

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nat Methods 14:587–589. https://doi.org/10.1038/nmeth.4285

Kim HM, Jeon S, Chung O et al (2021) Comparative analysis of 7 short-read sequencing platforms using the Korean reference genome: MGI and Illumina sequencing benchmark for whole-genome sequencing. Gigascience 10:giab014. https://doi.org/10.1093/gigascience/giab014

Kirin M, McQuillan R, Franklin CS, Campbell H, McKeigue PM, Wilson JF (2006) Genomic runs of homozygosity record population history and consanguinity. PLoS ONE 5:e13996. https://doi.org/10.1371/journal.pone.0013996

Korneliussen TS, Albrechtsen A, Nielsen R (2014) ANGSD: analysis of next generation sequencing data. BMC Bioinformatics 15:356. https://doi.org/10.1186/s12859-014-0356-4

Korunes KL, Samuk K (2021) Pixy: unbiased estimation of nucleotide diversity and divergence in the presence of missing data. Mol Ecol Resour 21:1359–1368. https://doi.org/10.1111/1755-0998.13326

Lamoreux JF, Morrison JC, Ricketts TH, Olson DM, Dinerstein E, McKnight MW, Shugart HH (2006) Global tests of biodiversity concordance and the importance of endemism. Nature 440:212–214. https://doi.org/10.1038/nature04291

Li H, Durbin R (2009) Fast and accurate short read alignment with Burrows–Wheeler transform. Bioinformatics 25:1754–1760. https://doi.org/10.1093/bioinformatics/btp324

Ma H, Liu Y, Liu D, Sun W, Liu X, Wan Y, Zhang X, Zhang R, Yun Q, Wang J, Li Z, Ma Y (2021) Chromosome-level genome assembly and population genetic analysis of a critically endangered rhododendron provide insights into its conservation. Plant J 107:1533–1545. https://doi.org/10.1111/tpj.15399

Medvedeva SO, Cherepanova OE, Petrova IV, Teptina AY (2025) Detection and verification of hybrid *Betula nana* L. plants in the Urals. Dokl Biol Sci 521:107–110. https://doi.org/10.1134/S0012496624600696

Mekonnen ZA, Riley WJ, Berner LT, Bouskill NJ, Torn MS, Iwahana G, Breen AL, Myers-Smith IH, Criado MG, Liu Y, Euskirchen ES (2021) Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. Environ Res Lett 16:053001. https://doi.org/10.1088/1748-9326/abf28b

Mirchandani CD, Shultz AJ, Thomas GWC, Smith SJ, Baylis M, Arnold B, Corbett-Detig R, Enbody E, Sackton TB (2024) A fast, reproducible, high-throughput variant calling workflow for population genomics. Mol Biol Evol 41:msad270. https://doi.org/10.1093/molbev/msad270

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol Biol Evol 32:268–274. https://doi.org/10.1093/molbev/msu300

Panarctic Flora (2025) Available at: www.panarcticflora.org. Accessed 4 December 2025

Palkopoulou E, Mallick S, Skoglund P, Enk J, Rohland N, Li H, Omrak A, Vartanyan S, Poinar H, Götherström A, Reich D, Dalén L (2015) Complete genomes reveal signatures of demographic and genetic declines in the woolly mammoth. Curr Biol 25:1395–1400. https://doi.org/10.1016/j.cub.2015.04.007

Pálsson S, Wasowicz P, Heiðmarsson S, Magnússon KP (2023) Population structure and genetic variation of fragmented mountain birch forests in Iceland. J Hered 114:165–174. https://doi.org/10.1093/jhered/esac062

Paun O, Schönswetter P, Winkler M, Consortium I, Tribsch A (2008) Historical divergence vs. contemporary gene flow: Evolutionary history of the calcicole *Ranunculus alpestris* group (Ranunculaceae) in the European Alps and the Carpathians. Mol Ecol 17:4263–4275. https://doi.org/10.1111/j.1365-294x.2008.03908.x

Pittet L, Fragnière Y, Grünig S, Bétrisey S, Clément B, Gerber E, Ronikier M, Kozlowski G, Parisod C (2020) Genetic structure of the narrow endemic *Papaver occidentale* indicates complex patterns of survival and immigration in the Western Prealps. Alp Botany 130:129–140. https://doi.org/10.1007/s00035-020-00238-3

Purcell S, Neale B, Todd-Brown K, Thomas L, Ferreira MA, Bender D, Maller J, Sklar P, de Bakker PI, Daly MJ, Sham PC (2007) PLINK: a tool set for whole-genome association and population-based linkage analyses. Am J Hum Genet 81:559–575. https://doi.org/10.1086/519795

Ronikier M, Schneeweis GM, Schönswetter P (2012) The extreme disjunction between Beringia and Europe in *Ranunculus glacialis* sl. (Ranunculaceae) does not coincide with the deepest genetic split—a story of the importance of temperate mountain ranges in arctic-alpine phylogeography. Mol Ecol 21:5561–5578. https://doi.org/10.1111/mec.12030

Salojärvi J, Smolander OP, Nieminen K et al (2017) Genome sequencing and population genomic analyses provide insights into the adaptive landscape of silver birch. Nat Genet 49:904–912. https://doi.org/10.1038/ng.3862

Schuler H (2020) Aktionsplan für die Zwergbirke (*Betula nana*) im Kanton Schwyz. Internal, unpublished report, available at the Office of Forest and Nature of the Canton of Schwyz.

Schwarz BU, Poschlod P (2015) Die Letzten ihrer Artin Bayern – Das Eiszeitrelikt Zwergbirke (*Betula nana* L.). Eine Bestandsanalyse mit biologisch-ökologischen Untersuchungen. ANLiegen Natur 37:19–30. https://doi.org/10.63653/psuu5150

Scott D (2001) Recovery of a dwarf birch (*Betula nana*) population following reduction in grazing by red deer (*Cervus elaphus*). Bot J Scotl 53:155–167. https://doi.org/10.1080/03746600108685020

Sim NL, Kumar P, Hu J, Henikoff S, Schneider G, Ng PC (2012) SIFT web server: predicting effects of amino acid substitutions on proteins. Nucleic Acids Res 40:W452–W457. https://doi.org/10.1093/nar/gks539

Stefani S, Champoud L, Fazan L et al (2025) Genetic divergence of *Clematis alpina* in the Swiss Prealps: a tale of the margins. Alp Botany 135:167–185. https://doi.org/10.1007/s00035-025-00333-3

Stehlik I (2003) Resistance or emigration? Response of alpine plants to the ice ages. Taxon 52:499–510. https://doi.org/10.2307/3647448

Stehlik I, Blattner FR, Holderegger R, Bachmann K (2002) Nunatak survival of the high Alpine plant *Eritrichium nanum* (L.) Gaudin in the central Alps during the ice ages. Mol Ecol 11:2027–2036. https://doi.org/10.1046/j.1365-294x.2002.01595.x

Stroeve JC, Notz D, Dawson J, Schuur EAG, Dahl-Jensen D, Giesse C (2025) Disappearing landscapes: the Arctic at +2.7°C global warming. Science 387:616–621. https://doi.org/10.1126/science.ads1549

Taberlet P, Fumagalli L, Wust-Saucy A-G, Cosson J-F (1998) Comparative phylogeography and postglacial colonization routes in Europe. Mol Ecol 7:453–464. https://doi.org/10.1046/j.1365-294x.1998.00289.x

Tao T, Milne RI, Li J et al (2023) Conservation genomic investigation of an endangered conifer, *Thuja sutchuenensis*, reveals low genetic diversity but also low genetic load. Plant Divers 46:78–90. https://doi.org/10.1016/j.pld.2023.06.005

Terhorst J, Kamm JA, Song YS (2017) Robust and scalable inference of population history from hundreds of unphased whole genomes. Nat Genet 49:303–309. https://doi.org/10.1038/ng.3748

Thomé MT, Carstens BC (2016) Phylogeographic model selection leads to insight into the evolutionary history of four-eyed frogs. Proc Natl Acad Sci USA 113:8010–8017. https://doi.org/10.1073/pnas.1601064113

Touchette L, Godbout J, Lamothe M, Porth I, Isabel N (2023) A cryptic syngameon within *Betula* shrubs revealed: implications for conservation in changing subarctic environments. Evol Appl 17:e13689. https://doi.org/10.1111/eva.13689

Tribsch A, Schönswetter P (2003) Patterns of endemism and comparative phylogeography confirm palaeoenvironmental evidence for Pleistocene refugia in the eastern Alps. Taxon 52:477–497. https://doi.org/10.2307/3647447z

Waldvogel AM, Feldmeyer B, Rolshausen G et al (2020) Evolutionary genomics can improve prediction of species' responses to climate change. Evol Lett 4:4–18. https://doi.org/10.1002/evl3.154

Walter H, Straka H (1970) Arealkunde. Floristisch-historische Geobotanik. Verlag Eugen Ulmer, Stuttgart

Wang N, Thomson M, Bodles WJ, Crawford RM, Hunt HV, Featherstone AW, Pellicer J, Buggs RJA (2013) Genome sequence of dwarf birch (*Betula nana*) and cross-species RAD markers. Mol Ecol 22:3098–3111. https://doi.org/10.1111/mec.12131

Wang N, McAllister HA, Bartlett PR, Buggs RJA (2016) Molecular phylogeny and genome size evolution of the genus *Betula* (Betulaceae). Ann Bot 117:1023–1035. https://doi.org/10.1093/aob/mcw048

Wang N, Kelly LJ, McAllister HA, Zohren J, Buggs RJA (2021) Resolving phylogeny and polyploid parentage using genus-wide

genome-wide sequence data from birch trees. Mol Phylogenet Evol 160:107126. https://doi.org/10.1016/j.ympev.2021.107126

Wang TR, Meng HH, Wang N, Zheng SS, Jiang Y, Lin DQ, Song YG, Kozlowski G (2023) Adaptive divergence and genetic vulnerability of relict species under climate change: a case study of *Pterocarya macroptera*. Ann Bot 132:241–254. https://doi.org/10.1093/aob/mcad083

Wang SS, Wang TR, Wang LL, Huang PH, Liang SD, Zheng SS, Yang LH, Li Y, Meng HH, Zhong X, Li XC, Ge BJ, Lu ZJ, Kang YX, Yuan Q, Jin DM, Ning X, Kozlowski G, Jang YJ, Xu J, Lee JH, Song YG (2026) Spatiotemporal genomic patterns of Quercus gilva: decoupling historical isolation from contemporary environmental adaptation. For Res. https://doi.org/10.48130/forres-0026-0016

Watts SH, Warwick A, Park KJ, Barsoum N, Jump AS (2026) Thinking outside the bog: planting dwarf birch (*Betula nana*) for mountain woodland restoration beyond habitat refugia constrained by overgrazing. For Ecol Manage 605:123430. https://doi.org/10.1016/j.foreco.2025.123430

Windmaisser T, Kattari S, Heubl G, Reisch C (2016) Glacial refugia and postglacial expansion of the alpine-prealpine plant species *Polygala chamaebuxus*. Ecol Evol 6:7809–7819. https://doi.org/10.1002/ece3.2515

Winkler M, Tribsch A, Schneeweis GM, Brodbeck S, Gugerli F, Holderegger R, Abbott RJ, Schönswetter P (2012) Tales of the unexpected: phylogeography of the arctic-alpine model plant *Saxifraga oppositifolia* (Saxifragaceae) revisited. Mol Ecol 21:4618–4630. https://doi.org/10.1111/j.1365-294X.2012.05705.x

Wright S (1965) The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 1:395-420.282. https://doi.org/10.1111/j.1558-5646.1965.tb01731.x

Zhang C, Dong SS, Xu JY, He WM, Yang TL (2019) PopLDdecay: a fast and effective tool for linkage disequilibrium decay analysis based on variant call format files. Bioinformatics 35:1786–1788. https://doi.org/10.1093/bioinformatics/bty875

Zohren J, Wang N, Kardailsky I, Borrell JS, Joecker A, Nichols RA, Buggs RJ (2016) Unidirectional diploid-tetraploid introgression among British birch trees with shifting ranges shown by restriction site-associated markers. Mol Ecol 25:2413–2426. https://doi.org/10.1111/mec.13644

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