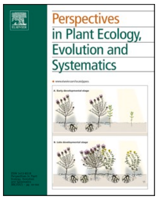
Perspectives in Plant Ecology, Evolution and Systematics 71 (2026) 125931

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Genetic diversity suggests two rather than three larch (*Larix* spp.) species across Siberia

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ARTICLE INFO

Keywords:
Genetic diversity
Hybridization
Microsatellites
Taxonomy

ABSTRACT

Although larch (*Larix* spp.) trees dominate the Siberian boreal forest, the species' genetic structure within the world's largest forest biome is still poorly understood. Here, we compile and analyze genetic data from six boreal populations of three putative larch species (*Larix sibirica* Ledeb., *Larix gmelinii* (Rupr.) Rupr., and *Larix cajanderi* Mayr) from disjunct sites distributed across much of the Russian northern taiga between 60 and 170°E. Using nine nuclear microsatellite markers (nSSR), we find high genetic diversity (mean $H_E = 0.757$) and allelic richness (mean $A_R = 9.289$) within all populations. Our analyses reveal two main genetic lineages: a western lineage corresponding to *L. sibirica* and an eastern lineage comprising *L. gmelinii* and *L. cajanderi*. Active hybridization connects these lineages across their contact zone. Our findings not only provide insights into the biogeographic structure and evolution of Eurasia's boreal forest, but also highlight the need for spatially explicit and better replicated genetic studies to resolve remaining taxonomic uncertainties.

1. Introduction

Larch (*Larix* spp.) forests dominate the Siberian boreal forest landscape (Herzschuh, 2020), providing critical ecosystem services including carbon sequestration and biodiversity maintenance under extreme environmental conditions (Schmidt, 1995). Despite their ecological importance, the taxonomy of these trees remains uncertain. Traditional classifications, based on needle and cone morphology (Barchenkov and Milyutin, 2008), recognize three main Siberian species (Abaimov, 1980; Abaimov and Koropachinsky, 1984): *Larix sibirica* Ledeb. (Siberian larch; in western Siberia), *Larix gmelinii* (Rupr.) Rupr (Dahurian larch, formerly *L. dahurica*; in central Siberia), and *Larix cajanderi* Mayr (Cajander Larch; in northeastern Siberia). Yet there is no consensus on either the total number of species or their precise geographical boundaries (Abaimov, 2010), a problem exacerbated by widespread hybridization (Abaimov, 2010; Bobrov, 1972; Dylis, 1961; Iroshnikov, 2004; Schulte et al., 2022; Semerikov et al., 2007). For instance, some sources treat *L. cajanderi* as a synonym of *L. gmelinii* (Borsch et al., 2020; The Plant List, 2025). Genetic studies provide partial clarity, with some supporting the traditional divisions (e.g.,

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https://doi.org/10.1016/j.ppees.2026.125931
Received 25 February 2025; Received in revised form 18 March 2026; Accepted 23 March 2026

Haupt et al., 2024; Larionova et al., 2010), while others reveal significant genetic overlap (Oreshkova, 2012; Semerikov and Lascoux, 1999; Zimmermann et al., 2019) that challenges clear species delineation (Gukov, 1976; Starikov, 1961; Voroshilov, 1982).

The most studied interspecific hybrid complex involves *L. sibirica* and *L. gmelinii*, yielding *L.* ^{x} *czekanowskii* Szaf. (Abaimov, 2010; Kruklis and Milyutin, 1977), where admixed populations show intermediate traits with rare heterosis (<5% of individuals; Abaimov, 2010). This system exemplifies the challenges of delineating species boundaries in *Larix*, particularly given evidence that ecological adaptation (Semerikov et al., 2013) and phenotypic plasticity (Abaimov et al., 2010) further obscure taxonomic relationships.

Clarifying species boundaries, characterizing hybridization patterns, and quantifying genetic diversity are critical for developing effective conservation strategies and forest management protocols, particularly for guiding seed sourcing and restoration efforts in the face of climate change. Microsatellite markers, or simple sequence repeats (SSRs), are widely used to study genetic diversity and population structure (Hoshino et al., 2012; Oliveira et al., 2006). These short, repetitive DNA sequences vary in length among individuals, providing high-resolution genetic fingerprints (Wang et al., 2009). Microsatellites may be selectively neutral to functionally involved in processes like chromatin organization, recombination, and gene regulation (Garrido-Ramos, 2017; Kashi and Soller, 1999; Li et al., 2004). Additionally, microsatellite loci can reflect environmental influences (Cohen et al., 2022), making them valuable for studying closely related taxa and detecting hybridization (Amyaga and Isaev, 2021; Korpelainen et al., 2010; Sánchez-Robles et al., 2012; Talve et al., 2013; Volkov and Kalko, 2021).

Here, we evaluate the genetic structure and diversity of six populations of three putative larch species (*L. sibirica*, *L. gmelinii*, and *L. cajanderi*) across Siberian boreal forest (two populations per species). We combine classical dendrochronological techniques to determine tree ages and structure of forest stand with nine nuclear microsatellite markers to assess genetic relationships and detect potential hybridization. Specifically, we address the following questions: (*i*) What is the current level of genetic diversity and differentiation within and among the studied larch populations? (*ii*) What evidence of hybridization exists among the studied larch populations? (*iii*) Does the population structure support the taxonomic status of these species?

2. Methods

2.1. Description of study species

L. sibirica is primarily distributed across western Siberia, from 60º–70ºE to 110º–120ºE, where it is associated with discontinuous permafrost and relatively warmer climate conditions compared to the eastern species (Abaimov, 2010). Its cones range from 10 to 50 mm in length and width, with needles measuring 10–58 mm. The eastern boundary of *L. sibirica* overlaps with the western boundary of *L. gmelinii* (Bobrov, 1978). *L. gmelinii* is native to central Siberia, where it exhibits higher resistance to lower temperatures than *L. sibirica* and is largely restricted to continuous permafrost (Koropachinsky, 1983; Abaimov, 2010). It displays a broad conical crown, with cones ranging 5–25 mm wide and 8–35 mm long, and needles (4–42 mm) typically arranged in bundles of 10–30 (Abaimov, 2010; Zhang and Wang, 2008). Genetic and palynological evidence indicates greater hardiness in *L. gmelinii*, including persistence in northern refugia during the Last Glacial and clonal reproduction in permafrost regions (Kruse et al., 2020; Schulte et al., 2022). Its eastern range overlaps with *L. cajanderi* around 120–127ºE (Bobrov, 1972). *L. cajanderi* is found mainly in the Sakha Republic and Chukotka (northeastern Siberia), where it grows in waterlogged permafrost areas under harsh continental conditions. Compared to *L. gmelinii*, *L. cajanderi* shows further specialization for survival on permafrost, gaining an advantage in upper mountain belts (Koropachinksy and Milyutin, 2011). It is characterized by a slenderer form (10–23 m height), shorter needles (6–33 mm) arranged in bundles of 12–59, and cones ranging from 10 to 28 mm wide and 9–25 mm long (Abaimov, 2010). Its crown is typically more rounded (Rysin, 2010). The western distribution of *L. cajanderi* overlaps with *L. dahurica* ssp. *cajanderi* near 120º–123ºE (Dylis, 1961).

2.2. Study area and material collection

The study region covers Arctic and sub-Arctic areas in the forest-tundra and taiga biomes across Siberian boreal forest, ranging from the Ural Mountains in the west to Chukotka Autonomous District in the east (60–170°E). Six populations were sampled, two per species (Fig. 1): *L. sibirica* in western Siberia at the Northern Urals (**NUR**) and Yamal Peninsula (**YAM**), *L. gmelinii* in central Siberia at Tura (**TUR**) and Khatanga (**KHA**), and *L. cajanderi* in northeastern Siberia at Chokurdakh (**CHO**) and Bilibino (**BIL**). Populations in **YAM**, **KHA**, **CHO** and **BIL** are situated within the forest-tundra ecotone, while **NUR** and **TUR** are in the taiga (Table S1). The distance between conspecific populations varies from 813 to 1007 km (Table S2).

For each population, nineteen to twenty dominant trees were sampled. Wood cores were collected at breast height (1.3 m) using a 5 mm diameter increment borer for tree age determination. Needles for genetic analysis were silica-dried, stored in paper bags during field campaigns and frozen at −20 °C in the laboratory.

2.3. Tree ages within populations

Wood cores were air-dried, mounted on wooden holders, and polished with progressively finer sandpaper up to 1200 grit. Polished cores were scanned at 3200 dpi resolution using an Epson Perfection V800 flatbed scanner with Silverfast SE software (LaserSoft Imaging, USA). Tree-ring width (TRW) was measured on digitized cores using CooRecoder v. 9.3 (Cybis Elektronik & Data AB, Sweden). TRW series were visually cross-dated, with dating accuracy verified using COFECHA (Holmes, 1983). The age of each individual sampled tree was determined.

2.4. DNA isolation, amplification and sizing

Total genomic DNA was extracted from the silica-dried needles of 119 trees following the CTAB method (Doyle and Doyle, 1990). DNA quality and quantity were assessed with a Nanodrop 8000 spectrophotometer (Thermo Fisher Scientific, USA), and concentrations were adjusted to 10 ng/μl. Twelve nuclear microsatellite primers were selected (Isoda and Watanabe, 2006) and combined into three multiplex sets: Multiplex A: bcLK056, bcLK066, bcLK228, and bcLK260; Multiplex B: bcLK211, bcLK224, bcLK232, and bcLK253; Multiplex C: bcLK189, bcLK225, bcLK235, and bcLK263. Reverse primers were labeled with a fluorescent dye (Table S3).

Polymerase chain reaction (PCR) was performed in a 10 μL reaction volume using the GenPak® PCR Core Kit (Laboratory Isogen Ltd., Russia). Amplification was conducted on a BioRad T100 thermal cycler (BioRad, USA) following Kruse et al. (2018). Amplified fragments were run on an ABI PRISM 310 genetic analyzer (Applied Biosystems, USA), with the Orange−500 DNA (NimaGen, The Netherlands) size standard, and scored using GeneMapper v. 5.0 (Life Technologies Corporation, USA).

2.5. Genetic data analysis: Intra- and inter-site variability

Presence of null alleles and potential genotyping errors was assessed using Micro-Checker software (Van Oosterhout et al., 2006). Two microsatellite markers (bcLK056 and bcLK211) showed high null allele frequencies (>0.20) and were excluded from further analysis, along with bcLK263 due to unstable amplification.

Genetic diversity per population was estimated using GenAlEx v. 6.5

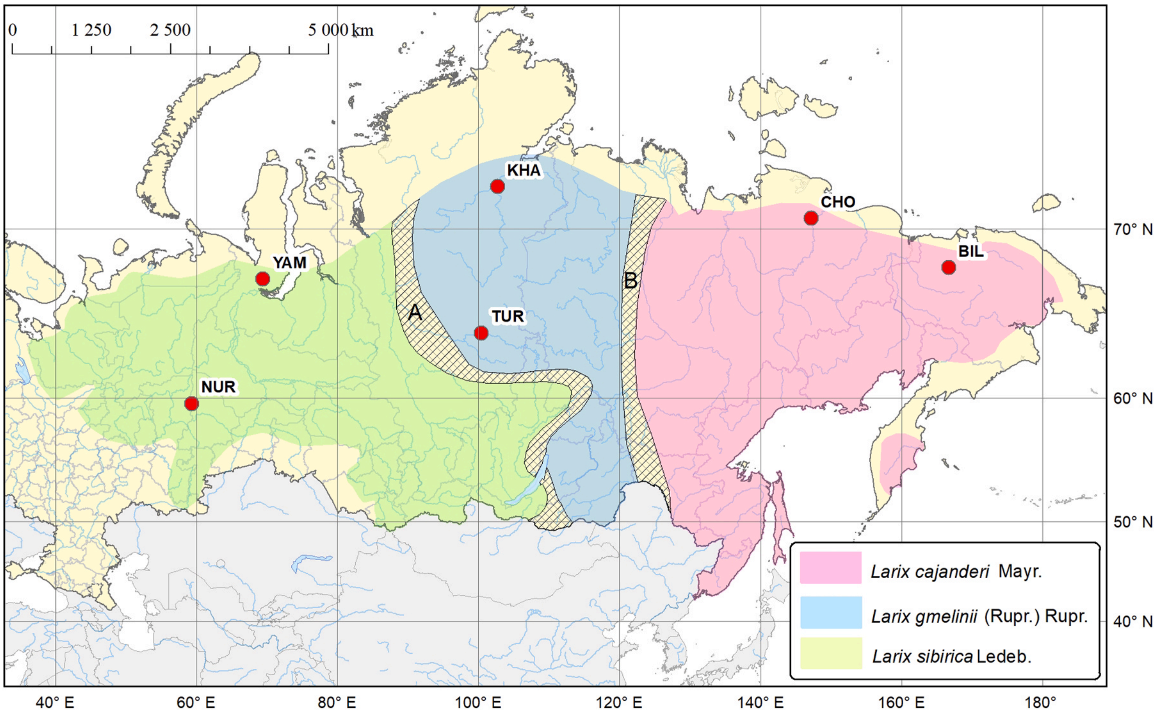

Fig. 1. Geographic ranges of *Larix* species based on Koropachinsky and Milyutin (2011), and the locations of studied populations (red dots). The hatched area “A” shows the zone of introgressive hybridization between *L. sibirica* x *L. gmelinii*, while the “B” between *L. gmelinii* x *L. cajanderi*. Site acronyms include **NUR** for Northern Urals, **YAM** for Yamal Peninsula, **KHA** for Khatanga, **TUR** for Tura, **CHO** for Chokurdakh, and **BIL** for Bilibino.

(Peakall and Smouse, 2006), including: the number of alleles (N_A), number of effective alleles (N_E), observed heterozygosity (H_O), expected heterozygosity (H_E), and the inbreeding coefficient (F_{IS}). Allelic richness (A_R) was calculated using the “hierfstat” package (Goudet, 2005) in R (R Core Team, 2022). Genetic variation partitioning within and among populations was assessed via analysis of molecular variance (AMOVA) in GenAlEx (Peakall and Smouse, 2006), with significance being determined in a permutation test including 999 replications. Population clustering was performed using the unweighted pair-group method with arithmetic mean (UPGMA) based on Nei`s genetic distances (Nei, 1972) implemented the “adegenet” (Jombart, 2008) and “hierfstat” packages (Goudet, 2005) in R. Differences in N_A, N_E, and A_R among species groups (**NUR**/**YAM** vs **TUR**/**KHA** vs **CHO**/**BIL**) were tested using one-way ANOVA or Kruskal-Wallis tests (α=0.05) when assumptions were violated, implemented via ‘car’ (Fox and Weisberg, 2019) package. The ‘dplyr’ package (Wickham et al., 2020) was used to process the data before the tests.

Population genetic structure was inferred using a Bayesian clustering in STRUCTURE v.2.3.4 (Pritchard et al., 2000). The analysis was performed with an admixture model and correlated allele frequencies. The analysis was run with K values ranging from 1 to 6, using 100,000 burn-in iterations followed by 500,000 Monte Carlo Markov simulations. Twenty repetitions were set for each run. The optimal number of clusters was determined using the ΔK parameter and mean likelihood value $L(K)$ according to Evanno et al. (2005) implemented in StructureSelector web-based program (Li and Liu, 2018). Results from replicated runs were average using CLUMPP v. 1.1.2. (Jakobsson and Rosenberg, 2007). Individuals were classified as purebreds ($q < 0.1$ or $q > 0.9$) or admixture ($0.1 \leq q \leq 0.9$) based on admixture coefficient (q-value; Huang et al., 2024; Li et al., 2021).

Isolation-by-distance (IBD) was tested via Mantel test (Mantel, 1967) comparing genetic and geographical distances. In addition, to check whether IBD present in continuous clines of genetic differentiation or in distant patches, 2-dimensional kernel density estimation was applied using the “MASS” and “ggplot2” R packages (Venables and Ripley, 2013). Genetic differentiation was further explored via principal component analysis (PCA) using the "hierfstat" (Goudet, 2005) and "FactoMineR" (Lê et al., 2008) R packages.

3. Results

3.1. Tree age and growth patterns

Dendrochronological measurements and cross-dating reveal age variations among sites, with the oldest sampled tree (513 years old) occurring in **CHO** (*L. cajanderi*), and the youngest (49 years old) in **YAM** (*L. sibirica;* Fig. S1; Table S4). Mean tree age varies by species and site: *L. sibirica* populations range from 60 ± 8 (mean ± SD) to 112 ± 34 years, *L. gmelinii* from 191 ± 34–300 ± 55 years, and *L. cajanderi* from 164 ± 22–332 ± 118 years. Tree-ring width measurements show distinct growth patterns, with the lowest mean radial growth in **CHO** (0.20 ± 0.08 mm) contrasting with the highest in **NUR** (*L. sibirica*; 0.98 ± 0.56 mm). Morphometric data indicate **CHO** contains the shortest (6.3 ± 1.3 m) and narrowest trees (DBH: 17.8 ± 4.3 cm), while **TUR** has the tallest trees (12.2 ± 1.44 m) and **KHA** the widest (DBH: 22.3 ± 2.25 cm; *L. gmelinii*; Table S4). The primary value of the dendrochronological data is contextual, not diagnostic, providing ecological context and stand history for the genetic populations.

3.2. Genetic diversity

The nine microsatellite loci show high polymorphism across populations, with N_A ranging from 7.4 (**BIL**) to 11.0 (**KHA**; Table 1). N_E vary from 3.8 (**NUR**) to 6.6 (**TUR**). *L. sibirica* populations exhibit the lowest A_R (8.6) and H_O (0.850), while *L. gmelinii* populations display the highest values ($A_R = 10.5$ and $H_O = 0.883$). H_E ranges from 0.738 in *L. cajanderi* to 0.794 in *L. gmelinii*. All populations exhibit heterozygote excess (mean $F_{IS} = -0.163$), with significant deviations from the Hardy-Weinberg equilibrium (HWE) except for **TUR** (Table S5).

Neither one-way ANOVA ($\boldsymbol{N_A}$ $F(2) = 1.292$, $p = 0.394$; $\boldsymbol{N_E}$ $F(2)$

Table 1
Genetic diversity parameters averaged across nine microsatellite loci for each *Larix* population.

Population	Sample size	N_A	N_E	A_R	H_O	H_E	F_{IS}
L. sibirica							
NUR	20	7.9 (±0.4)	3.8 (±0.4)	7.8 (±0.4)	0.817 (±0.066)	0.717 (±0.026)	−0.140 (±0.088)
YAM	20	9.6 (±1.6)	6.0 (±1.3)	9.4 (±1.7)	0.883 (±0.041)	0.764 (±0.041)	−0.202 (±0.110)
Mean		8.8 (±1.0)	4.9 (±0.9)	8.6 (±1.1)	0.850 (±0.053)	0.741 (±0.034)	−0.171 (±0.099)
L. gmelinii							
TUR	20	10.4 (±1.8)	6.6 (±1.6)	10.2 (±1.9)	0.922 (±0.844)	0.781 (±0.807)	−0.209 (±0.072)
KHA	20	11.0 (±1.3)	6.2 (±1.0)	10.8 (±1.4)	0.844 (±0.056)	0.807 (±0.026)	−0.070 (±0.098)
Mean		10.7 (±1.6)	6.4 (±1.3)	10.5 (±1.7)	0.883 (±0.450)	0.794 (±0.417)	−0.140 (±0.085)
L. cajanderi							
CHO	20	10.3 (±1.2)	5.1 (±0.8)	10.1 (±1.2)	0.872 (±0.830)	0,768 (±0.707)	−0.161 (±0.105)
BIL	19	7.4 (±1.0)	4.1 (±0.6)	7.4 (±1.0)	0.830 (±0.079)	0.707 (±0.042)	−0.198 (±0.131)
Mean		8.9 (±1.1)	4.6 (±0.7)	8.8 (±1.1)	0.851 (±0.455)	0.738 (±0.375)	−0.180 (±0.118)
Overall Mean		9.4 (±1.2)	5.3 (±1.0)	9.3 (±1.3)	0.861 (±0.319)	0.757 (±0.275)	−0.163 (±0.101)

N_A - number of alleles; N_E - number of effective alleles; A_R - allelic richness; H_O - observed heterozygosity; H_E - expected heterozygosity; F_{IS} - inbreeding coefficient; ± standard errors in parentheses. Site acronyms include **NUR** for Northern Urals, **YAM** for Yamal Peninsula, **KHA** for Khatanga, **TUR** for Tura, **CHO** for Chokurdakh, and **BIL** for Bilibino.

$= 2.012$, $p = 0.279$; $\boldsymbol{A_R}$ F $(2) = 1.336$, $p = 0.385$) nor Kruskal-Wallis rank sum test ($\chi^2 = 3.43$, df = 2, $p = 0.18$) reveal significant differences in diversity indices among species groups, with Levene's F test indicating that the assumption of homogeneity of variances among the groups is not met. AMOVA indicates only 8% variance among species (Table 2), with lowest differentiation between *L. sibirica* and *L. gmelinii* populations ($F_{ST} = 0.056$; $p < 0.01$) and highest between *L. sibirica* and *L. cajanderi* populations ($F_{ST} = 0.114$; $p < 0.01$). The variance among *L. gmelinii* and *L. cajanderi* populations is 5% ($F_{ST} = 0.045$; $p < 0.01$). The pairwise F_{ST} matrix (Fig. 2A) shows maximal differentiation between **NUR** and **BIL**, the two most geographically distant populations, and minimal between **TUR** and **KHA** populations. UPGMA clustering identifies two groups: one comprising the two *L. sibirica* populations (**NUR** and **YAM**), and the second group consisting of *L. gmelinii* (**TUR** and **KHA**) and *L. cajanderi* (**CHO** and **BIL**) populations (Fig. 2B).

df, degrees of freedom; SS, sum of squares; MS, mean of the squares; Est. Var., estimated variance of components; %, percentage of total variance contributed by each component; *p,* probability.

3.3. *Clustering and hybridization*

Bayesian clustering analysis reveals the highest ΔK value at $K = 2$, with sub-clustering occurring at $K = 3$ (Fig. 3A). The highest rate of change of the likelihood distribution together with lowest variance occur at $K= 3$ (Fig. 3B). At $K = 2$ (Fig. 3C, E), *L. sibirica* populations (**NUR** and **YAM**; green) are separated from *L. gmelinii* and *L. cajanderi* populations (**TUR**, **KHA**, **CHO** and **BIL**; pink), with individuals from **TUR** and **KHA** showing slight admixture (Fig. S2). At $K = 3$ (Fig. 3D, F), the populations separate into three groups corresponding to the three putative species, with **CHO** individuals showing high admixture. PCA results are consistent with the $K = 2$ STRUCTURE analysis, with the first two components explaining 71.27% of the variation. The two *L. sibirica* populations (**NUR** and **YAM**) form one group, while the remaining populations cluster together (Fig. S3A). PCA plot displaying all *Larix* individuals also show that two *L. sibirica* (**NUR** and **YAM**) populations constitute one cluster and individuals of *L. gmelinii* and *L. cajanderi* populations (**TUR**, **KHA**, **CHO** and **BIL)** constitute the other cluster (Fig. S3B).

The Mantel test demonstrates significant isolation-by-distance across

Table 2
Analysis of molecular variance (AMOVA).

Source	df	SS	MS	Est. Var.	%	Fixation index (F_{ST})	*p*
L. sibirica, L. gmelinii and L. cajanderi							
Among populations	5	74.648	14.930	0.288	8%	0.076	0.001
Within populations	232	811.470	3.498	3.498	92%		
Total	237	886.118		3.786	100%		
L. sibirica and *L. gmelinii*							
Among populations	1	20.706	20.706	0.214	6%	0.056	0.001
Within populations	158	568.125	3.596	3.596	94%		
Total	159	588.831		3.810	100%		
L. sibirica and *L.cajanderi*							
Among populations	1	39.035	39.035	0.450	11%	0.114	0.001
Within populations	156	542.072	3.475	3.475	89%		
Total	157	581.108		3.925	100%		
L. gmelinii and *L.cajanderi*							
Among populations	1	16.982	16.982	0.170	5%	0.045	0.001
Within populations	156	559.822	3.589	3.589	95%		
Total	157	576.804		3.758	100%		

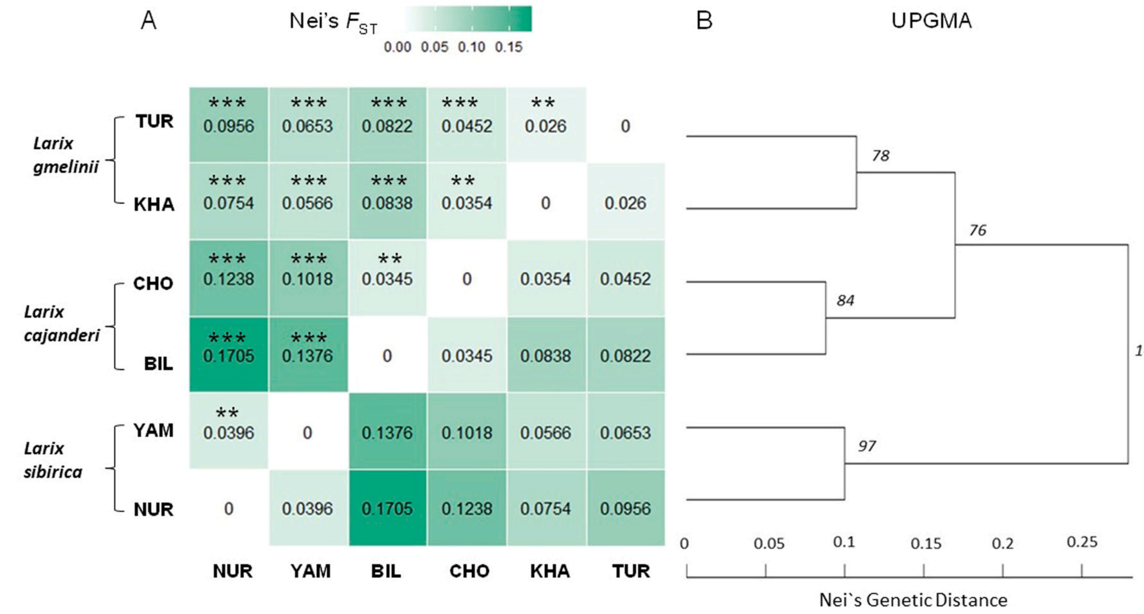

Fig. 2. Heatmap of pairwise *F*st values (Nei, 1987) among six larch populations (A) and UPGMA dendrogram (B). Numbers on branches are bootstrap values based on 1000 replicates. Significance values: ** $P < 0.01$, *** $P < 0.001$. **NUR** refers to Northern Urals, **YAM** to Yamal Peninsula, **KHA** to Khatanga, **TUR** to Tura, **CHO** to Chokurdakh, and **BIL**, Bilibino.

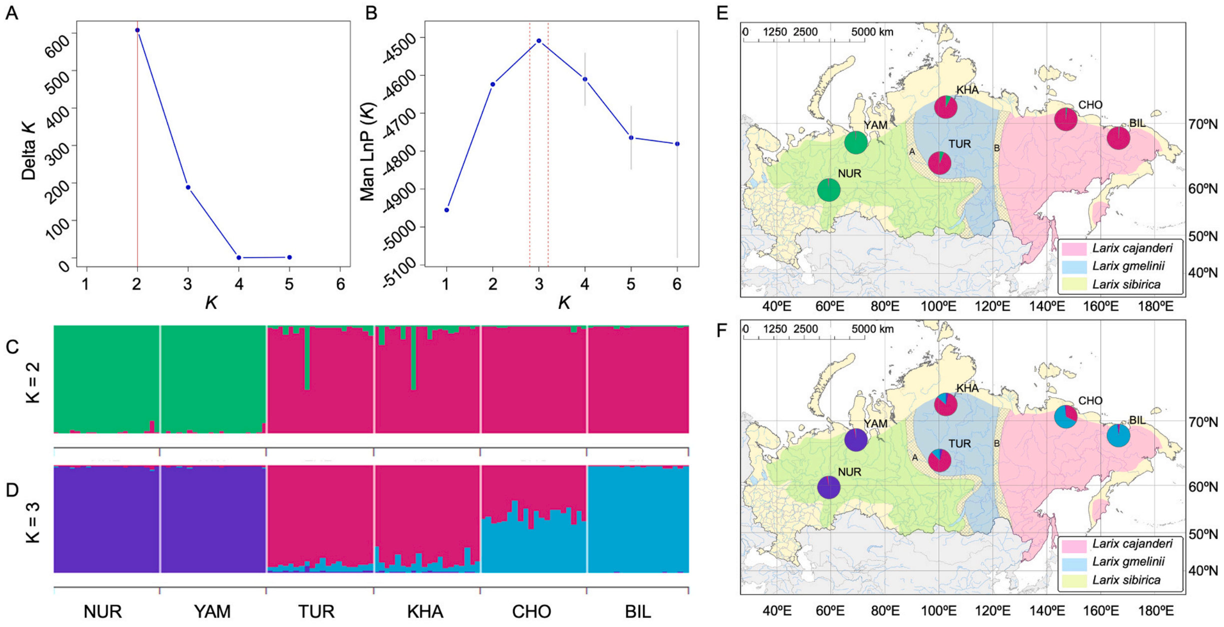

Fig. 3. Estimated population structure based on ΔK (A) and Mean LnP(K) ±SD (B) values. Barplots of population genetic structure for $K = 2$ (C) and $K = 3$ (D). Green, pink, violet, light blue colors correspond to different clusters. Geographic distribution of $K = 2$ (E), $K = 3$ (F). **NUR** refers to Northern Urals, **YAM** to Yamal Peninsula, **KHA** to Khatanga, **TUR** to Tura, **CHO** to Chokurdakh, and **BIL** to Bilibino.

all ($R^2 = 0.88$, $p = 0.006$), confirming that genetic differentiation among the studied larch populations increases with geographic distance (Fig. 4). However, this pattern weakens when considering only *L. gmelinii* and *L. cajanderi* populations ($R^2 = 0.79$, $p = 0.06$), with no significant correlation between genetic distance and geographic distance between these populations.

4. Discussion

Our genetic analysis of six larch populations across Siberia's boreal forest reveals a complex pattern of diversity and structure that bears directly on the long-standing taxonomic uncertainty surrounding Siberian larch species. We find high levels of genetic diversity overall and clear evidence of admixture in historical contact zones, indicating that hybridization has played a significant role in shaping the genetic architecture of these forests. Multiple lines of evidence, including population differentiation statistics, cluster analyses, and principal components, converge on a model of two primary genetic lineages: a western lineage corresponding to *L. sibirica* and an eastern lineage that encompasses both *L. gmelinii* and *L. cajanderi.* The following sections interpret these patterns in the context of genetic diversity, hybridization, population structure, and taxonomic implications, while also

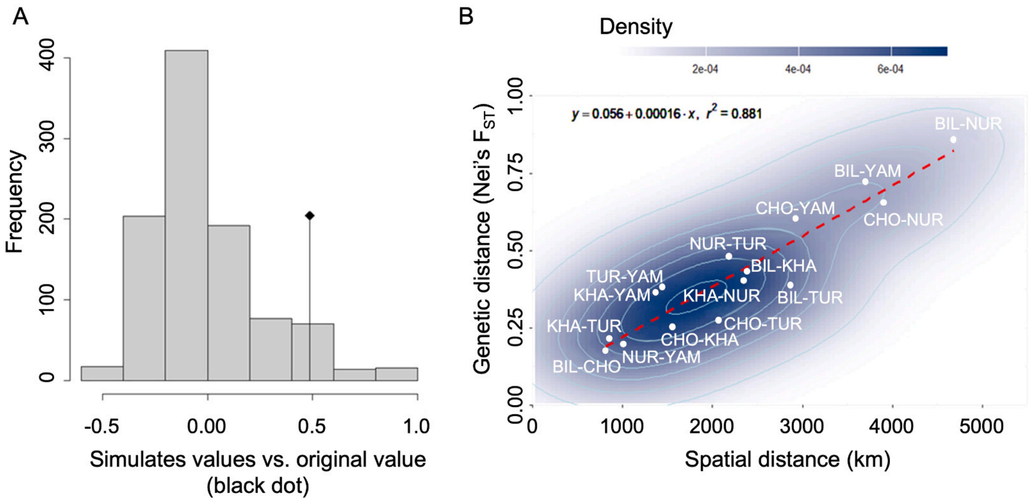

Fig. 4. Isolation-by-distance analyses (IBD). (A) Monte Carlo simulations of permuted values under the absence of spatial structure (histogram). Black diamond represents the original correlation between the distance matrices derived from the reference distribution. (B) The correlation between genetic distance and geographic distance for the studied populations using a Mantel test. **NUR** refers to Northern Urals, **YAM** to Yamal Peninsula, **KHA** to Khatanga, **TUR** to Tura, **CHO** to Chokurdakh, and **BIL** to Bilibino.

acknowledging the limitations inherent in our study.

4.1. Genetic diversity and hybridization patterns

Our analyses of nine nuclear SSRs reveal high genetic diversity across larch populations in Siberia ($H_E = 0.757$), consistent with previous studies of *Larix* species ($H_E = 0.632$–0.879; Gramazio et al., 2018; Isoda and Watanabe, 2006; Kruse et al., 2018; Oreshkova et al., 2013), though cross-study comparisons require caution due to differing marker sets. The clearest genetic differentiation separates western (*L. sibirica*) from eastern populations (*L. gmelinii* and *L. cajanderi*), with peak diversity occurring in contact zones (Abaimov, 2010; Bobrov, 1972) between *L. sibirica* and *L. gmelinii* (**KHA**: $H_E = 0.807$; and **TUR**: $H_E = 0.781$). Here, we identified hybridization (5–20% of sampled trees), supporting historical introgression by cross-pollination in these contact zones. Dendrochronological dating of sampled trees (mean ages: 300 years in **KHA**, 191 years in **TUR**; oldest individuals dating to 1630 and 1779, respectively) suggest prolonged contact facilitating introgressive hybridization, which may increase genetic variation in both groups over the past few centuries. These patterns align with historical reports of *L.* ˣ *czekanowskii* in these regions (Szafer, 1913) and demonstrate hybridization's role in maintaining genetic variation (Suarez-Gonzalez et al., 2018; Szczepański et al., 2024). In contrast, the easternmost population (**BIL**) shows reduced diversity ($H_E = 0.707$), likely reflecting reproductive constraints under northeastern Siberia's harsh climate (Kashin and Kozobrodov, 1994).

4.2. Population structure and taxonomic implications

All populations show heterozygosity excess (mean $F_{IS} = -0.163$) with substantial deviations from the Hardy-Weinberg equilibrium (except for **TUR)**, suggesting selective advantages for heterozygous individuals, a pattern documented in long-lived woody species (Krutovsky et al., 1989; Schaberg et al., 2008; Starova et al., 1990). Consequently, natural selection may favor these individuals (Halliburton, 2004; Hedrick, 2005; Stoeckel et al., 2006). AMOVA reveals that 92% of genetic variance occurs within populations, while only 8% among them. The lowest differentiation (5%) occurs between *L. gmelinii* and *L. cajanderi* populations and the highest differentiation (11%) between *L. sibirica* and *L. cajanderi* populations, lower than the 15% reported by Oreshkova et al. (2013), for populations from Central and northeastern Siberia and Mongolia. This discrepancy likely reflects differences in marker selection between studies, with only five out of seven SSR loci overlapping with those used by Oreshkova et al. (2013), potentially affecting diversity estimates.

UPGMA and STRUCTURE analysis based on ΔK strongly supports two primary clusters ($K = 2$) separating *L. sibirica* from eastern populations, though weaker substructure emerges at $K = 3$. These results challenge the traditional three-species classification (Abaimov et al., 2010), as SSRs nuclear markers show *L. cajanderi* lacks diagnostic differentiation from *L. gmelinii* (Oreshkova, 2012; Potenko and Razumov, 1996; Zimmermann et al., 2019). While organelle markers report subtle divergence (Khatab et al., 2008; Polezhaeva et al., 2010), these patterns may reflect phenotypic plasticity (Abaimov et al., 2010), epigenetic variability (Hrivnák et al., 2017; Yakovlev et al., 2010), incomplete lineage sorting following recent divergence, or differential introgression rather than true species boundaries. On the other hand, Bayesian clustering analysis based on the mean likelihood value L(K) and subclustering emerging at $K = 3$ distinguishes *L. cajanderi* populations. This result is consistent with recent findings by Haupt et al. (2024) that supports its species status based on 8000 single nucleotide polymorphism (SNPs), revealing distinct clusters for *L. gmelinii* and *L. cajanderi.*

Based on the highest ΔK value ($K = 2$), UPGMA clustering and PCA analysis, which support two well defined geographical clusters, our data suggest that *L. gmelinii* and *L. cajanderi* may not be genetically distinct species, at least among the studied populations. Therefore, in the absence of strong, consistent evidence for their separation within our dataset, the most parsimonious interpretation is that *L. gmelinii* and *L. cajanderi* represent a single, genetically cohesive lineage (*L. gmelinii* sensu lato) with internal population structure, rather than two deeply divergent species. These findings contribute to the persistent debate surrounding taxonomic boundaries between the two species. The marker-dependent discordance (e.g., nSSR vs SNP) highlights the complexity of delineating closely related boreal conifers and emphasizes the need for genomic-scale studies that incorporate both neutral and adaptive loci. Such an approach would better capture the full extent of genetic variation and regional differentiation, helping to resolve these taxonomic uncertainties.

4.3. Limitations and future directions

While our study confidently demonstrates the presence of two genetic clusters among the sampled populations, several limitations constrain definitive taxonomic conclusions: First, the neutral nuclear SSRs used may overlook adaptive divergence and provide limited resolution for recently diverged lineages. Second, our sampling design (two populations per species with twenty individuals each) may not fully capture intraspecific variation, as recent recommendations prioritize increasing the number of populations over individuals per populations (e.g., more than 20 populations; Aguirre-Liguori et al., 2020). Third, the lack of parallel morphological data limits integrative taxonomic assessment. Fourth, populations of the same genetic cluster were drawn from distinct biomes, potentially confounding genetic patterns with local adaptation. Future studies should employ genome-wide approaches across broader geographic ranges, while incorporating ecological and phenotypic data. Such efforts will clarify whether the observed *L. gmelinii-L. cajanderi* divergence represents population-level variation or justify taxonomic recognition, a distinction with important implications for conserving these ecologically vital forests under climate change.

5. Conclusions

Our analysis of nine nuclear microsatellite markers reveals two fundamental patterns in larch populations across Russia’s boreal forest: high genetic diversity coupled with moderate population differentiation. The genetic evidence challenges the conventional three-species classification, showing that *L. cajanderi* lacks sufficient genomic differentiation from *L. gmelinii* to justify separate taxonomic status. Rather, our results support a revised biogeographic model with two dominant lineages, *L. sibirica* occupying western Siberia and *L. gmelinii* predominating in the east, connected by active hybrid zones. These findings have dual implications for both research and forest management. From a taxonomic perspective, the minimal differentiation between eastern populations combined with heterozygote excess suggests either recent divergence or ongoing gene flow. For conservation, the observed genetic architecture indicates substantial adaptive potential, a critical asset for boreal forests facing unprecedented climate shifts. Moving forward, we recommend prioritizing three research directions: genome-wide analyses to resolve lingering taxonomic questions, landscape genomic studies to map adaptive variation, and monitoring programs to track hybrid zone dynamics.

CRediT authorship contribution statement

Akulinina Kristina V: Writing – review & editing, Data curation. **Jan Esper:** Writing – review & editing, Supervision, Funding acquisition. **Sergeeva Oksana V:** Writing – review & editing, Data curation. **Ulf Büntgen:** Writing – review & editing, Supervision, Funding acquisition. **Agapova Viktoria V:** Writing – review & editing, Data curation. **Kirdyanov Alexander V:** Writing – review & editing, Data curation. **Kukarskih Vladimir V:** Writing – review & editing, Data curation. **Kolmogorov Alexey I:** Writing – review & editing, Data curation. **Alberto Arzac:** Writing – original draft, Funding acquisition, Data curation, Conceptualization. **Tabakova Maria A:** Writing – review & editing, Data curation. **Tóth Endre G:** Writing – review & editing, Formal analysis, Data curation. **Tatiana Bebchuk:** Writing – review & editing, Data curation. **Nadezhda Devi:** Writing – review & editing, Data curation. **Sheller Marina A:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Ibe Aleksey A:** Writing – review & editing, Formal analysis, Data curation. **Sukhikh Tatyana V:** Writing – review & editing, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alberto Arzac reports financial support was provided by Ministry of Science and Higher Education of the Russian Federation. Ulf Buntgen and Jan Esper reports financial support was provided by European Research Council (ERC). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was carried out with the support of the Ministry of Science and Higher Education of the Russian Federation [FSRZ−2020–0014]. UB and JE were supported by the ERC projects MONOSTAR [AdG 882727] and Synergy-Plague [# 101118880].

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2026.125931.

Data availability

Data will be made available on request.

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