

Genomic Diversity and Climate-Driven Habitat Shifts of the Endemic Shrub *Sophora moorcroftiana* in Xizang

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Abstract

Background

Sophora moorcroftiana (Benth.) Baker is a leguminous shrub species endemic to Xizang, adapted to arid and alpine environments. Despite its ecological significance, little is known about its genomic diversity and adaptive potential under climate change.

Methods

We performed whole-genome resequencing (WGRS) of 180 individuals across nine provenances, combined with ecological niche modeling (MaxEnt). Genetic diversity indices, population structure, selective sweeps, and climatic drivers were analyzed.

Results

Approximately 28 million high-quality SNPs were identified, revealing structured genetic variation. The Taktse and Lhundup populations exhibited the highest diversity, while Sangzhuzi showed the lowest. Selective sweep analysis identified genes involved in folate biosynthesis and secondary metabolism. MaxEnt models projected northward habitat shifts under climate change, with temperature seasonality and precipitation as key drivers.

Conclusions

This study provides the first genome-wide insight into the genetic diversity and adaptive potential of *S. moorcroftiana*. The results highlight the conservation value of Taktse and Lhundup populations for germplasm preservation and climate-resilient restoration strategies.

Introduction

Sophora moorcroftiana (Fabaceae) is an endemic drought-tolerant shrub predominantly distributed in the Yarlung Zangbo River basin of the Qinghai-Tibet Plateau [1]. Renowned for its extensive root system and extreme stress resistance, this species serves as a critical ecological barrier against desertification, playing an irreplaceable role in stabilizing the fragile alpine ecosystem [2]. As a model organism for studying high-altitude adaptation [3], *S. moorcroftiana* exhibits unique drought and cold tolerance mechanisms, and the abundant secondary metabolites (e.g., alkaloids) of this species confer significant economic value [4]. However, escalating anthropogenic pressures, including overgrazing, land reclamation, and infrastructure development, have led to severe habitat fragmentation, with some populations facing localized extinction risks [5]. Despite the ecological and economic importance of *S. moorcroftiana*, the genomic basis of its adaptive evolution and population genetic dynamics under anthropogenic stressors remains poorly understood, hindering evidence-based conservation and sustainable utilization.

The recent release of a chromosome-level genome assembly (~ 737.35 Mb, contig N50 = 22.5 Mb) has enabled genome-wide studies of *S. moorcroftiana* [6]. However, existing genetic diversity assessments rely predominantly on low resolution markers (e.g., allozymes, simple sequence repeats [SSRs], and genotyping-by-sequencing [GBS]; [7–9]. These markers have, the following three major limitations: (1) sparse genomic coverage (< 50 loci), failing to capture genome-wide variation [10]; (2) insufficient resolution to detect SNPs and indels linked to adaptive traits [11]; and (3) technical biases (e.g., primer specificity or restriction site variation) compromising cross-study comparability [12]. Consequently, the lack of genome wide SNP-based analyses impedes a comprehensive understanding of the evolutionary history and adaptive mechanisms of *S. moorcroftiana*.

Beyond genetic analyses, predicting species' ecological responses to environmental change requires robust modeling approaches. The maximum entropy (MaxEnt) algorithm has become one of the most widely used tools for species distribution modeling, owing to its strong predictive performance with presence-only data and limited sample sizes [13–15]. MaxEnt integrates species occurrence records with environmental variables to estimate the potential distribution of suitable habitats under current and future climatic scenarios [16]. This approach has been extensively applied in biogeography, invasion biology, and conservation planning, particularly under climate change projections [17, 18].

The present study integrated phenotypic, genomic, and ecological niche modeling approaches to address these gaps. First, seed morphological variation and germination rates were quantified across nine natural populations to assess phenotypic diversity. Second, WGRS (Illumina, 15×depth) of 180 shrubs was utilized to characterize population structure, genetic diversity, and signatures of selection. Finally, MaxEnt models with high-resolution environmental layers were leveraged to predict current and future climate-suited habitats under shared socioeconomic pathway (SSP) scenarios, explicitly incorporating soil and topographic variables omitted in prior studies [19].

This study provides the first genome-wide perspective on the genetic diversity and adaptive potential of *S. moorcroftiana*, while delivering actionable insights for conserving this ecologically and economically pivotal species amidst climate change.

Materials and Methods

Study Area and Plant Materials

A total of 180 *Sophora moorcroftiana* shrubs were sampled across three provenances in three major regions in Xizang as follows: Taktse, Lhundup, and Cheshire in Lhasa; Gonggar, Sangri, and Nedong in Shannan; and Sangzhuzi, Panam, and Rinpung in Shigatse (Table 1; Figure S1). For each provenance, 20 healthy shrubs were randomly selected from wild natural populations using a systematic random sampling method, with a minimum spacing of ≥ 10 m between shrubs. Global positioning satellite (GPS) coordinates and elevation were recorded for all sampling points.

The taxonomic identity of all collected individuals was formally confirmed as *S. moorcroftiana* by Dr. Meiduo Zhuoga (Department of Silviculture, Nanjing Forestry University), Dr. Bingzhang Li (President of the Xizang Institute of Forest Trees), and Prof. Fuliang Cao (Academician of the Chinese Academy of Engineering, Nanjing

Forestry University). Although voucher specimens were not deposited in a public herbarium, the seed materials have been preserved in a dedicated seed storage facility at the Tibet Academy of Forestry for long-term conservation and future studies.

All field sampling was conducted in natural habitats with the permission and support of the Tibet Academy of Forestry and the local forestry authorities, and no endangered or legally protected species were harmed during the collection.

Table 1. Geographic information and climatic data of *S. moorcroftiana* samples in Xizang.

location	Lon. (E)	Lat. (N)	Elev. (m)	MAT	MAP	Etmax (°C)	ETMin (°C)	ASH	Sample size
				(°C)	(mm)				
XueTown,Taktse District, Lhasa (Fig.1a)	91.48	29.82	3745	6.22	400	24	-16	3065	20
Nyetang Town, Cheshire County, Lhasa (Fig.1b)	90.92	29.53	3737	7.24	411	29	-31	3000	20
Baingoin Town, Lhundup County, Lhasa (Fig.1c)	91.43	29.82	3682	6.16	405	27	-38	2881	20
Qewa Town, Rinpung County, Shigatse(Fig.1d)	87.74	29.31	3591	4.92	420	28	-33	2300	20
Lhojang Town, Panam County, Shigatse(Fig.1e)	89.14	29.22	3571	5.65	375	28	-33	3200	20
Gyacoxung Town, Sangzhuzi District, Shigatse(Fig.1f)	88.91	29.26	3567	5.53	410	28	-18	3248	20
Sangri Town, Sangri County, Shannan(Fig.1g)	92.07	29.29	3843	6.43	341	30	-31	3095	20
Gyeba Town, Nedong County, Shannan(Fig.1h)	91.85	29.29	3892	6.76	349	29	-22	2936	20
Jagzhulin Town, Gonggar County, Shannan(Fig.1i)	90.92	29.33	3845	8.07	403	29	-16	3194	20

(a) Taktse, Lhasa (3065 m, agro-pastoral ecotone); (b) Cheshire, Lhasa (3000 m, agro-pastoral ecotone); (c) Lhundup, Lhasa (2881 m, agro-pastoral ecotone); (d) Rinpung, Shigatse (2300 m, river valley); (e) Panam, Shigatse (3200 m, sand dune area); (f) Sangzhuzi, Shigatse (3248 m, rocky slope); (g) Sangri, Shannan (3095 m, agro-pastoral ecotone); (h) Nedong, Shannan (2936 m, arid hillside); (i) Gonggar, Shannan (3194 m, agro-pastoral ecotone). The locations correspond to the sampling sites listed in Table 1.

Genomic DNA was extracted from silica-dried seed tissues using a modified cetyltrimethylammonium bromide (CTAB) protocol, following liquid nitrogen grinding. DNA integrity was checked on 0.8% agarose gel

electrophoresis, and purity was evaluated using a NanoDrop spectrophotometer (Thermo Scientific, USA) with an A260/280 ratio of 1.8–2.0. DNA concentration was quantified with a Qubit fluorometer (Invitrogen, USA). Qualified DNA samples (concentration > 1 ng/μL and total DNA > 0.05 μg) were used for library construction with the MGIEasy DNA Library Prep Kit (MGI Tech, Shenzhen, China). Sequencing libraries with an average insert size of ~ 450 bp were sequenced using the DNBSEQ-T7 platform (BGI-Shenzhen, China) to generate 150 bp paired-end reads.

GWRS and SNP Discovery

Raw reads were filtered using fastp v0.20.1 to remove adapter sequences, low-quality bases ($Q < 20$), and reads shorter than 50 bp, generating high-quality clean reads for downstream analyses. Clean reads from each accession were aligned to the *S. moorcroftiana* chromosome-level reference genome (737.35 Mb; contig N50 = 22.5 Mb), which was assembled using a combination of Nanopore long reads and Illumina short reads [20]. The genome contained nine pseudomolecules and 53,640 annotated protein-coding genes, with high completeness (BUSCO score = 98.3%).

Read mapping was performed using BWA v0.7.17 with default parameters [21]. Aligned reads were sorted and converted to BAM format using SAMtools v1.9, and PCR duplicates were removed using Picard v2.23.8. Local realignment around indels was performed using the GATK IndelRealigner tool to minimize false-positive SNP calls.

SNPs were called using GATK v3.8 UnifiedGenotyper [22] with the following parameters: stand_call_conf = 30, stand_emit_conf = 10. SNPs with sequencing depth < 5, quality score < 30, or missing rate > 0.2 were discarded. A total of ~ 28.27 million high-quality SNPs were retained for further analyses.

Functional annotation was performed using ANNOVAR[23], which classified SNPs into exonic, intronic, and intergenic regions. Exonic SNPs were further divided into synonymous and nonsynonymous categories.

Population Genetic Analyses

Genetic Diversity Metrics

Diversity parameters, including observed heterozygosity (H_o), expected heterozygosity (H_e), nucleotide diversity (π), Tajima's D, and inbreeding coefficient (FIS), were calculated using Stacks v1.48. Pairwise genetic differentiation (FST) and within-population π were estimated using VCF tools v0.1.17 [24].

Population Structure and Phylogenetics

A maximum likelihood tree was constructed using Fast Tree v2.1.11 (bootstrap = 1000). ADMIXTURE v1.3.0 was applied to estimate ancestry proportions across $K = 2-10$ clusters, with the optimal K selected via cross-validation (CV) error minimization [25]. Principal component analysis (PCA) was conducted using GCTA, filtering for MAF > 0.05. IBS similarity and G-matrix were calculated using PLINK v1.9 and Gmatrix v2 [26].

Gene Flow and Linkage Disequilibrium (LD)

TreeMix v1.13 (parameters: -m 1–10, -noss) was used to infer inter-population gene flow [27]. LD decay was assessed by Pop LD decay v3.42, using squared correlation coefficient (r^2) with a maximum distance of 1,000 bp.

Selective Sweep and Functional Enrichment

Candidate regions under selection were identified by combining the π -ratio (20 kb windows and 5 kb steps) and the top 5% F_{ST} thresholds. Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway enrichment analyses were performed using cluster Profiler, with the top 10 GO terms and 20 KEGG pathways (lowest false discovery rate [FDR]) retained.

Ecological Niche Modeling

Species Occurrence and Environmental Variables

In total, 169 occurrence records were compiled from field surveys (9 provenances), the Chinese Virtual Herbarium (CVH), and literature. Spatial thinning (minimum 10 km spacing) using the geosphere package in RStudio retained 79 unique locations for analysis (Fig. 2A).

Nineteen bioclimatic variables (BIO01–BIO19) were compiled from WorldClim v2.1[28]. (1970–2000; 5 km resolution). Topographic variables (elevation, slope, and aspect) derived from a digital elevation model (DEM) and 13 soil properties derived from the Food and Agriculture Organization (FAO) World Soil Database (v1.2). were also compiled. Future climate projections were based on the BCC-CSM2-MR model under three shared socioeconomic pathways (SSPs)—SSP1-2.6 (low forcing), SSP3-7.0 (medium–high forcing), and SSP5-8.5 (high forcing)—covering four periods (2021–2040, 2041–2060, 2061–2080, and 2081–2100). Due to the lack of future soil data, current soil conditions were retained for all projections. All environmental variables were spatially processed and standardized in ArcGIS 10.8, resulting in an initial set of 35 variables. To reduce multicollinearity, Pearson correlation filtering ($|r| < 0.8$) was applied, and only variables with MaxEnt contribution scores $> 2\%$ were retained, resulting in seven ultimately selecting 7 key predictors for modeling (Table S1; Fig. 3C).

Model Optimization and Projection

The model parameters were optimized via ENMeval and 96 combinations of feature classes (linear, quadratic, and hinge) and regularization multipliers (RMs = 0.5–6.0; increment of 0.5) were tested. The optimal configuration ((linear, quadratic, and hinge [LQH] features and, RM = 2.0) was selected based on the minimum delta Akaike information criterion coefficient (AICc) [24, 29]. MaxEnt v3.4.4 [13] was utilized with the following settings: 75% training data and 25% testing data; 500 iterations; 10 bootstrap replicates; and logistic format output. Model performance was evaluated using area under the curve (AUC) values, which were interpreted as follows: 0.9–1.0 (excellent), 0.8–0.9 (good), 0.7–0.8 (fair), 0.6–0.7 (poor), and ≤ 0.6 (unreliable). The optimized model was used to project current and future habitat suitability under three SSP scenarios (SSP1-2.6, SSP3-

7.0, and SSP5-8.5) using BCC-CSM2-MR climate projections, and the results were visualized in ArcGIS 10.8. [30, 31].

Results

WGRS and Population Genomic Analysis

Resequencing Summary

In total, 180 samples were resequenced at an average depth of 15×, generating 1,973.44 Gb of high-quality data ($Q20 \geq 99.12\%$ and, $Q30 \geq 97.30\%$). The average mapping rate was 99.62%, with a genome coverage of 92.64% (Table S2). A total of 35,030,273 SNPs and 23,419,967 small indels were identified. Of note, 28,166,121 high-quality SNPs were used for downstream analysis. The transition (Ti)/ transversion (Tv) ratio was 2.18, and it was dominated by transitions (Fig. 4; Table S3). Most SNPs were located in intergenic (65.45%), intronic (16.12%), upstream (6.7%), and downstream (5.98%) regions, with 5.39% SNPs in exons. Nonsynonymous SNPs (964,000) significantly outnumbered synonymous SNPs (496,000) (Table 2). Only 3.09% of indels were located in coding regions (Table S3).

Table 2
Summary of SNP functional annotations in the *S. moorcroftiana* genome.

Type	Number	Percentage
Synonymous SNV	496052	1.76
Nonsynonymous SNV	964186	3.42
Stopgain	52464	0.19
Stoploss	4578	0.02
Unknown	109	0
Splicing	12297	0.04
Intronic	4541742	16.12
Intergenic	18435812	65.45
Upstream	1886623	6.7
Downstream	1684885	5.98
Upstream;Downstream	87373	0.31
Total	28166121	100

Note:(1)Synonymous SNV, synonymous single nucleotide variant (silent mutation); (2)Nonsynonymous SNV, missense variant causing amino acid change; (3)Stopgain, SNP introducing a premature stop codon; (4)Stoploss, SNP eliminating a stop codon; (5)Unknown, SNP with undefined function; (6)Splicing, SNP located within 2 bp of splicing junctions; (7)Intronic, located in introns; (8)Intergenic, located between gene regions;

(9)Upstream, within 1 kb upstream of transcription start site; (10)Downstream, within 1 kb downstream of transcription termination site; (11)Upstream/Downstream: overlapping region between upstream of one gene and downstream of another.

Genetic Diversity

Nine provenances exhibited moderate genetic differentiation (mean $FST = 0.066$) (Table 3). The Lhundup population had the greatest diversity ($Ho = 0.3002$ and $\pi = 0.2789$), while the Sangzhuzi population had the lowest diversity ($Ho = 0.2178$ and $\pi = 0.2435$). *Tajima's D* values were all positive (1.0782–1.2805), indicating possible balancing selection or past bottlenecks. FIS analysis revealed excess heterozygosity in the Taktse and Lhundup populations ($FIS < 0$), while inbreeding was present in the Sangzhuzi and Panam populations ($FIS > 0$) (Table 4).

Table 3. Statistics of Genetic differentiation results among species populations									
Pop	1.Ts	2.Cs	3.Ld	4.Rp	5.Pn	6.Sz	7.Sr	8.Nd	9.Gg
1.Ts		0.0575	0.0153	0.0725	0.0717	0.0756	0.0673	0.057	0.046
2.Cs			0.0591	0.0616	0.0606	0.0645	0.079	0.070	0.0375
3.Ld				0.0741	0.0732	0.0776	0.0702	0.059	0.0473
4.Rp					0.0515	0.0603	0.0896	0.080	0.052
5.Pn						0.037	0.0871	0.077	0.0514
6.Sz							0.0892	0.078	0.0536
7.Sr								0.040	0.064
8.Nd									0.0533

Note: Lower triangle values represent pairwise FST statistics, which indicate the level of genetic differentiation between populations. Higher values indicate greater differentiation.

Ts: Tsktse; Cs: Chrshire; Ld: Lhundup; Rp: Rinpung; Pn: Panm; Sz: Sangzhuzi; Sr: Sangri; Nd: Nedong; Gg: Gonggar.

Table 4. Statistics of the genetic diversity results of each population						
Pop	N	Ho	He	Pi(π)	Fis	Tajima's D
1.Taktse	19.228	0.2826	0.2709	0.2782	-0.0032	1.2366
2.Cheshire	19.3984	0.2622	0.2524	0.2591	-0.0009	1.1098
3.Lhundup	19.5453	0.3002	0.2717	0.2789	-0.0477	1.2805
4.Rinpung	19.2152	0.2609	0.2424	0.2489	-0.0249	1.1812
5.Panam	19.4965	0.2381	0.2444	0.2508	0.0431	1.0914
6.Sangzhuzi	19.5565	0.2178	0.2373	0.2435	0.0762	1.1317
7.Sangri	19.4655	0.2484	0.2457	0.2522	0.0192	1.1736
8.Nedong	19.3666	0.2526	0.2559	0.2627	0.0367	1.1597
9.Gonggar	18.9512	0.262	0.2671	0.2744	0.04	1.0782
Mean	19.3581	0.2472	0.2542	0.261	0.0165	1.1603

Note: (1)Pop, Population abbreviation; (2)*N*, Average number of individuals per site; (3)Observed Heterozygosity (*Ho*), proportion of heterozygous genotypes observed in the population; (4)Expected Heterozygosity (*He*), expected heterozygosity under Hardy–Weinberg equilibrium; (5)Nucleotide Diversity (π), average number of nucleotide differences per site between two sequences; (6)*Fis*, inbreeding coefficient within populations; (7) *Tajima's D*, statistic to test for neutrality, in which positive values may indicate balancing selection or population contraction.

Genetic Population Structure Analysis

WGRS data revealed that the 180 *S. moorcroftiana* accessions formed the following four distinct genetic clusters corresponding to their geographic origins: Lhundup-Taktse, Gonggar-Cheshire, Rinpung-Panam-Sangzhuzi, and Sangri-Nedong. The phylogenetic tree demonstrated three key patterns. First, the Cheshire population formed a tight clade with the Rinpung population, while the Taktse population showed marked genetic divergence. Second, the Sangzhuzi population exhibited the longest branch length, suggesting a distinct evolutionary trajectory, whereas the Gonggar population displayed the shortest branch, indicating genetic conservation. Third, population structure analysis using ADMIXTURE (optimal *K* = 4 based on the CV error) revealed that the homogeneous ancestry composition of the Cheshire population contrasted that of the distinct genetic background of the Sangri population. Notably, the Taktse and Lhundup population shared primary ancestry components but differed in admixture levels, while the Gonggar population derived ~ 90% ancestry from the Cheshire population, indicating historical connectivity. Further, the Rinpung population showed ~ 70% ancestry shared with the Panam and Sangzhuzi population, indicating historical gene flow. PCA (PC1 = 6.8% and PC2 = 4.8%) revealed the following patterns: the Sangri-Nedong cluster formed a tight genetic cluster; the Rinpung-Panam-Sangzhuzi cluster displayed continuous genetic variation; the Taktse-Lhundup cluster grouped independently; and the Gonggar population partially overlapped with the Cheshire population while maintaining differentiation. The phylogenetic, ADMIXTURE, and PCA congruent results revealed four genetically distinct groups shaped by both geographic isolation (e.g., limited Taktse-Lhundup admixture

despite sympatry) and historical gene flow (e.g., influence of the Cheshire population on the Gonggar and Rinpung populations).

Gene Flow and LD

Gene flow analysis among the nine geographic populations (Fig. 5A) revealed distinct and somewhat unexpected patterns. Notably, no significant gene flow was detected between the geographically adjacent Taktse and Lhundup populations, despite their close proximity of less than 50 km. This conclusion was supported by a low migration rate estimate ($m = 2$), indicating limited genetic exchange. In contrast, unidirectional gene flow was observed from the more distant Cheshire population to both the Taktse and Lhundup populations, suggesting a possible anthropogenic influence, such as seed dispersal along road networks or historical human-mediated movement. LD decay patterns further highlighted differences in genomic structure among the populations (Fig. 5B). The Taktse population exhibited the most rapid LD decay, with r^2 values declining sharply as genomic distance increased. This rapid decay reflected a high recombination rate and suggested that the Taktse population has experienced relatively little genetic drift or founder effects. In contrast, the Gonggar population displayed the slowest LD decay, with r^2 values remaining high across longer genomic distances, suggesting indicative of a more conserved genomic background and potentially reduced recombination activity.

Selection Signals and Functional Enrichment

Genome-wide scans for selective sweeps were conducted between two geographically distant populations of *S. moorcroftiana*, namely Population 6 (Sangzhuzi and Shigatse) and Population 7 (Sangri and Shannan). Selection signatures were identified using nucleotide diversity ratios ($Q\pi$) and fixation index (FST) metrics (Fig. 6). Despite only moderate genetic differentiation between the two populations, several genomic regions exhibited strong signs of selection.

The joint distribution of the $\theta\pi$ ratio (π Sangzhuzi/ π Sangri) and fixation index (FST) was used to detect putative selective sweep signals. The lower-left quadrant highlights regions with reduced nucleotide diversity in the Sangzhuzi population (green; $\theta\pi$ ratio ≤ -0.793), while the lower-right quadrant highlights regions with reduced diversity in the Sangri population (blue; $\theta\pi$ ratio ≥ 0.622). A threshold of $FST > 0.196$ (top 5%) was used to define highly differentiated regions. The gray dots represent genome-wide background, while the blue and green points represent candidate selective sweep regions specific to each population.

Selective sweep regions were defined as those with extreme $Q\pi$ values (top 5% thresholds: $Q\pi \geq 0.622$ or $Q\pi \leq -0.793$) in combination with significantly elevated FST . These criteria identified genomic loci potentially shaped by divergent selection. Comparative analysis revealed reduced polymorphism ($Q\pi \leq -0.793$) in the Sangzhuzi population, while the Sangri population showed increased diversity ($Q\pi \geq 0.622$), which was consistent with contrasting evolutionary pressures. In total, 99 and 81 candidate genes under selection were identified in the Sangzhuzi and Sangri populations, respectively. Notably, many of the candidate genes were associated with plant stress responses and environmental adaptation. To explore the biological functions of these candidate genes, (GO) and (KEGG) enrichment analyses were performed (Fig. 7). GO enrichment revealed that the candidate genes were significantly involved in molecular functions such as small molecule binding, nucleotide binding, and oxidoreductase activity. The associated biological processes included one-carbon metabolic

process, hormone metabolic process, and cell recognition (Fig. 6A), which may contribute to metabolic plasticity and stress signaling pathways. KEGG pathway enrichment indicated that these genes participate in the following plant secondary metabolic pathways: flavonoid degradation; flavone and flavonol biosynthesis; cyanoamino acid metabolism; monoterpene biosynthesis; and sesquiterpene and triterpene biosynthesis (Fig. 6B). These pathways are well known for their roles in chemical defense, environmental response, and local adaptation in plants. Collectively, these results suggested that natural selection acted on population-specific genomic regions, in response to differing environmental pressures in the Yarlung Tsangpo River valley. These adaptive changes were reflected in both the functional profiles of selected genes and the observed divergence in metabolic pathways between the two populations.

MaxEnt Modeling of Current and Future Suitable Habitats

Model Optimization

For model optimization, 79 spatially thinned occurrence records and seven selected bioclimatic variables were utilized. With regard to parameter tuning, the ENMeval package was used to evaluate 96 combinations of feature classes and RMs. The best performing model (Feature combination [FC] = LQHPT and RM = 6) demonstrated the lowest delta AICc value while balancing model fit and generality (Fig. 8A). The optimized model achieved an average AUC of 0.981, which surpassed the default model performance (AUC = 0.973), confirming high predictive accuracy (Fig. 8B).

Present and Future Suitable Ranges

Under the current climate conditions, the model identified highly suitable habitats concentrated primarily in the Lhasa, Shannan, and Shigatse regions, covering approximately 139,600 km² (Table S5; Fig. 1B). These optimal habitats represented a relatively restricted portion of the study area, while low-suitability zones predominated. Notably, the Ali and Nagqu regions were consistently classified as unsuitable.

Future projections under the Coupled Model Intercomparison Project Phase 6 (CMIP6) scenarios revealed distinct patterns across emission trajectories. The low-emission scenario (SSP1-2.6) projected expansion of both total and high-suitability areas. Medium emissions (SSP3-7.0) showed moderate fluctuations but maintained an overall increasing trend. Moreover, the high-emission scenario (SSP5-8.5) predicted substantial northward range shifts coupled with pronounced contraction of high-suitability zones by the end-century period (2081–2100) (Table S5; Fig. 9).

The columns represent SSP1–2.6 **(A)**, SSP3–7.0 **(B)**, and SSP5–8.5 **(C)**. The rows represent future time periods of 2021–2040 (1), 2041–2060 (2), 2061–2080 (3), and 2081–2100 (4).

Key Environmental Drivers

Temperature seasonality (BIO4) emerged as the most influential environmental driver, contributing 30.6% to the model, followed by precipitation of the coldest quarter (BIO19, 20.4%) and precipitation of the warmest quarter (BIO18, 19.3%), collectively accounting for over 70% of the predictive power of the model (Table S6). Response curve analysis revealed the following key ecological thresholds: suitability increased when mean temperature of the coldest quarter (BIO11) exceeded – 5°C; precipitation during the warmest quarter (BIO18)

showed optimal suitability between 200–300 mm; and temperature seasonality (BIO4) demonstrated peak suitability at 600–650 (Figure S2).

Synthesis and Ecological Interpretation

As a drought- and cold-tolerant species, *S. moorcroftiana* has potential to expand under low-to-medium climate scenarios. However, under high-emission scenarios, ecological space may contract, suggesting a “short-term gain and long-term threat” pattern. The MaxEnt projections supported the population structure and adaptation signals findings, thereby providing a spatial framework for conservation planning, introduction strategies, and ecological restoration.

Discussion

Genetic Diversity Despite Low Germination

From an evolutionary perspective, dormancy is a key mechanism for surviving environmental uncertainty [32]. Traits, such as small seed size and low germination are often selected in seasonal climates, while large, non-dormant seeds are predominant in aseasonal regions. The observed low germination but moderate genetic diversity in seeds from Taktse and Lhundup may reflect an evolutionary capacity to respond to environmental change, consistent with the view that standing genetic variation underpins adaptive responses to climate change[33].

WGRS (15×depth) identified ~ 28 million SNPs, providing a high-resolution view of population structure. Diversity indices ($H_o = H_e = 0.25$) indicated moderate genetic variation, with the Sangzhuizi population showing the lowest diversity ($H_e = 0.2373$). This pattern corresponds with the elevation–diversity decline hypothesis, as Sangzhuizi (3650 m) lies at the lowest altitude and may be more isolated, reducing gene flow and enhancing drift [34].

Compared with SSR-based studies ($H_e = 0.32–0.78$) [7, 9], the present SNP-based estimates were lower due to the biallelic nature of SNPs, which are less polymorphic but more suitable for identifying adaptive loci [35]. Selective sweep analysis highlighted candidate genes involved in folate-mediated one-carbon metabolism, which may be relevant to high-altitude ultraviolet (UV) adaptation.

Population Structure and Gene Flow Asymmetry

Genetic clustering (neighbor-joining [NJ] tree and PCA) grouped 180 shrubs into four genetic clusters generally consistent with geographic origin. The highest differentiation ($F_{st} = 0.0896$) existed between the Rinpung and Sangri populations, which was driven by large geographic (≥ 80 km) and climatic separation (~ 150 mm precipitation difference). Gene flow appeared to occur from the Cheshire population to Taktse and Lhundup, but not directly between the latter two. One possible explanation is that agricultural land-use and infrastructure may influence dispersal routes, although additional data would be needed to confirm this.

Positive Tajima's D values (1.08–1.28) across populations suggested balancing selection. The Lhundup and Taktse populations had the highest values (1.28), which may indicate polygenic adaptation[36–38]. For example, flavonoid degradation genes were enriched in the Sangzhuizi population under hot-humid conditions

(FDR < 0.01), whereas the Sangri population retained polymorphisms in terpene biosynthesis genes, possibly contributing to cold resistance (-31°C). These results may be consistent with the hypothesis that extreme environments can maintain genetic variation [39].

Climate-Driven Habitat Shifts and Conservation Implications

MaxEnt modeling achieved high predictive accuracy (AUC = 0.981), with temperature seasonality and precipitation during the warmest and coldest quarters identified as the dominant climatic drivers of *S. moorcroftiana* distribution. Moderate temperature and moisture appear to be essential for germination and seedling establishment [40], whereas excessive precipitation or high temperatures may lead to soil waterlogging, root hypoxia, and disease outbreaks. Model results suggested that the optimal precipitation range for this species during the warmest quarter is 200–300 mm; increases beyond this range could constrain its distribution. While near-term warming may facilitate range expansion, long-term climate change may impose new abiotic and biotic stresses, creating a dual effect of “short-term expansion and long-term constraint.” Given the ecological importance of *S. moorcroftiana* in soil stabilization and desertification control, conservation efforts such as ex situ collection, germplasm banking, and adaptive cultivation are recommended to help safeguard the genetic integrity and sustain its ecological functions. Strategies including assisted gene flow, prioritization of rear-edge populations, and integration of adaptive genetic variation into vulnerability assessments could potentially enhance the resilience of *S. moorcroftiana* under future climate scenarios[41–43].

Limitations of the study

Although this study provides novel insights into the genetic diversity and climate-driven distribution dynamics of *Sophora moorcroftiana*, several limitations should be acknowledged. First, the sampling was restricted to nine natural populations across three regions of Xizang, which may not fully capture the entire genetic variation of the species across its broader range. Expanding the geographic coverage to include peripheral or isolated populations could provide a more comprehensive understanding of population history and local adaptation. Second, although whole-genome resequencing allowed the identification of millions of SNPs, the moderate sequencing depth (~ 15×) may have limited the detection of rare alleles and structural variants. Third, ecological niche modeling relied on a selected set of climatic and environmental variables; while these were ecologically meaningful, the exclusion of certain factors (e.g., soil microbiota, anthropogenic disturbance) might have influenced model accuracy. Fourth, the projections of future suitable habitats were based on CMIP6 models under specific SSP scenarios, which inevitably involve uncertainties related to climate model assumptions and emission trajectories. Finally, the adaptive candidate genes identified through selective sweep analyses (e.g., folate metabolism and flavonoid biosynthesis genes) were inferred based on statistical associations and lack experimental functional validation. Further physiological, transcriptomic, or transgenic studies are required to confirm their roles in stress adaptation. Addressing these limitations in future work would help refine the conservation and management strategies for this ecologically important shrub.

Conclusions

This study provides a genome-wide assessment of the genetic diversity, adaptive potential, and future distribution of *S. moorcroftiana* through whole-genome resequencing and ecological niche modeling. Genome-wide SNP analysis revealed moderate species-level genetic diversity ($H_e = 0.2542$ and $\pi = 0.2610$), with the Lhundup and Taktse populations exhibiting the highest values and the Sangzhuizi population showing the lowest, likely due to elevation-related isolation. Positive Tajima's D values and asymmetric gene flow patterns suggest signals of balancing selection and possible human-mediated dispersal. Selective sweep analysis identified candidate genes potentially involved in stress adaptation, particularly within folate and flavonoid biosynthesis pathways.

MaxEnt projections indicated potential habitat expansion under low-emission scenarios but contraction under high-emission trajectories. Populations from Taktse and Lhundup, which combined relatively high diversity and signals of adaptability, may serve as important sources for conservation and restoration initiatives. These findings provide a basis for future studies and can inform conservation planning for *S. moorcroftiana*, an endemic species of Xizang with ecological significance for alpine ecosystem stability.

Declarations

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Author contributions

Contributions were structured as follows: Computational Tool Development, Methodological Validation, Data Management and Annotation, Original Manuscript Drafting:Duo Zhuoga Mei; Field Investigation, Resource Acquisition:Bingzhang Li; Conceptual Framework Design, Experimental Methodology:Fangfang Fu; Data Curation, Statistical Analysis, Data Interpretation: Guibin Wang and Shuangyuan Yu; Manuscript Revision and Refinement, Visualization Design, Grant Acquisition Support: Tingting Dai; Project Oversight and Administrative Coordination: Fuliang Cao and Yuhua Liu. All contributing authors have reviewed and approved the final version of the manuscript for publication.

Data availability

The data underlying this article are available in the article and online supplementary material. The reference genome of *Sophora moorcroftiana* used in this study has been archived in the Genome Sequence Archive (GSA), BIG Data Center, National Genomics Data Center (NGDC), Beijing Institute of Genomics, Chinese

Academy of Sciences, under the accession number CRX306560 (<https://ngdc.cncb.ac.cn/gsa/>). The raw resequencing data generated in this study have been submitted to the GSA (<https://ngdc.cncb.ac.cn/gsa/>) and are under review. Accession numbers will be provided once available.

Conflict of interest

The authors declare none.

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Funding

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Authors' contributions

DM designed the study and performed analyses. BL conducted fieldwork. FF and GW contributed to methodology and data analysis. SY assisted with statistical interpretation. FC and YL provided project supervision. TD revised the manuscript and secured funding. All authors read and approved the final manuscript.

Availability of data and materials

The datasets supporting the conclusions of this article are included in this published article and its supplementary information files.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Figures

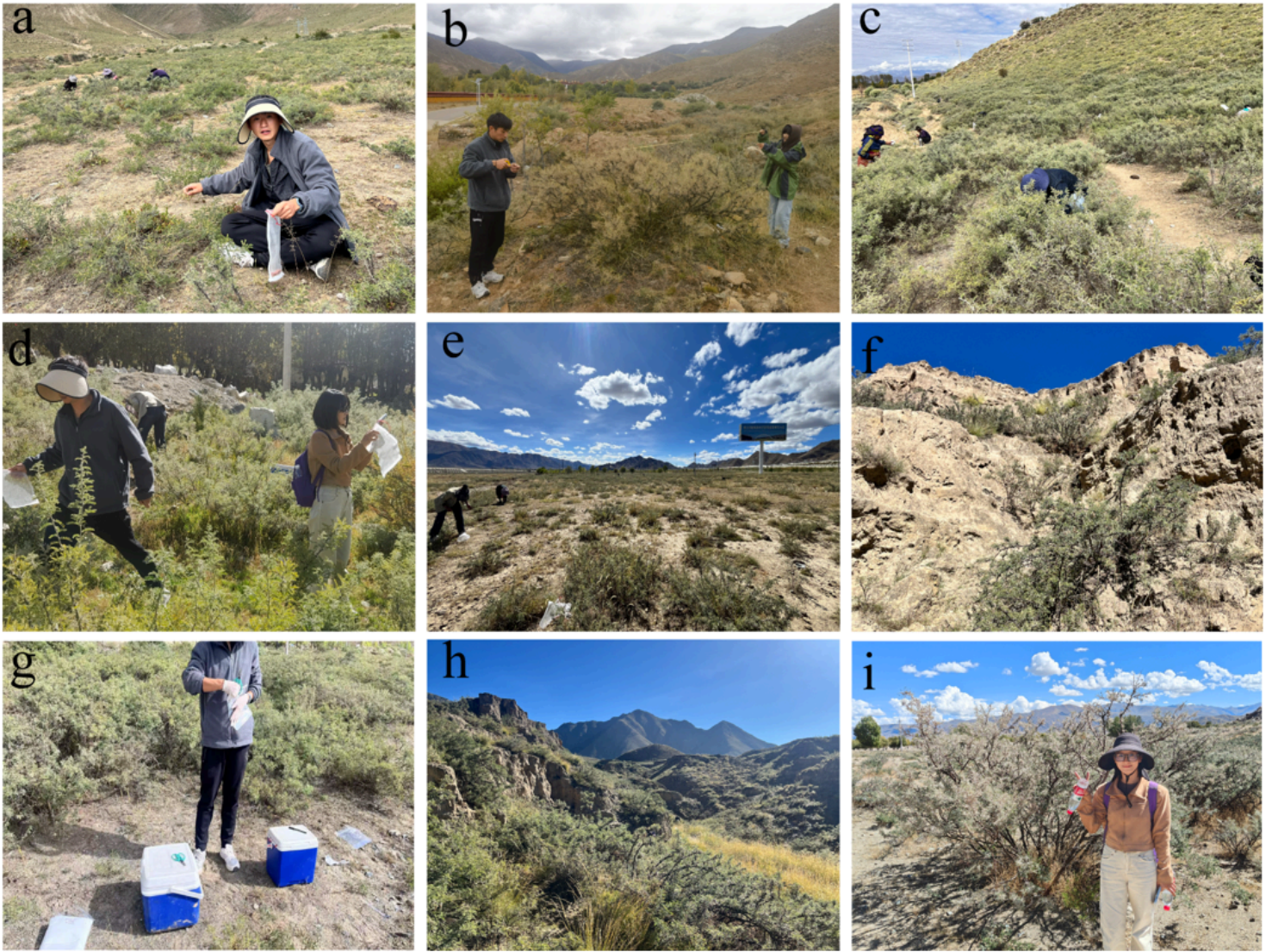


Figure 1

Geographic distribution and typical habitats of *Sophora moorcroftiana* in Xizang.

(a) Taktse, Lhasa (3065 m, agro-pastoral ecotone); (b) Cheshire, Lhasa (3000 m, agro-pastoral ecotone); (c) Lhundup, Lhasa (2881 m, agro-pastoral ecotone); (d) Rinpung, Shigatse (2300 m, river valley); (e) Panam, Shigatse (3200 m, sand dune area); (f) Sangzhuzi, Shigatse (3248 m, rocky slope); (g) Sangri, Shannan (3095 m, agro-pastoral ecotone); (h) Nedong, Shannan (2936 m, arid hillside); (i) Gonggar, Shannan (3194 m, agro-pastoral ecotone). The locations correspond to the sampling sites listed in Table 1.

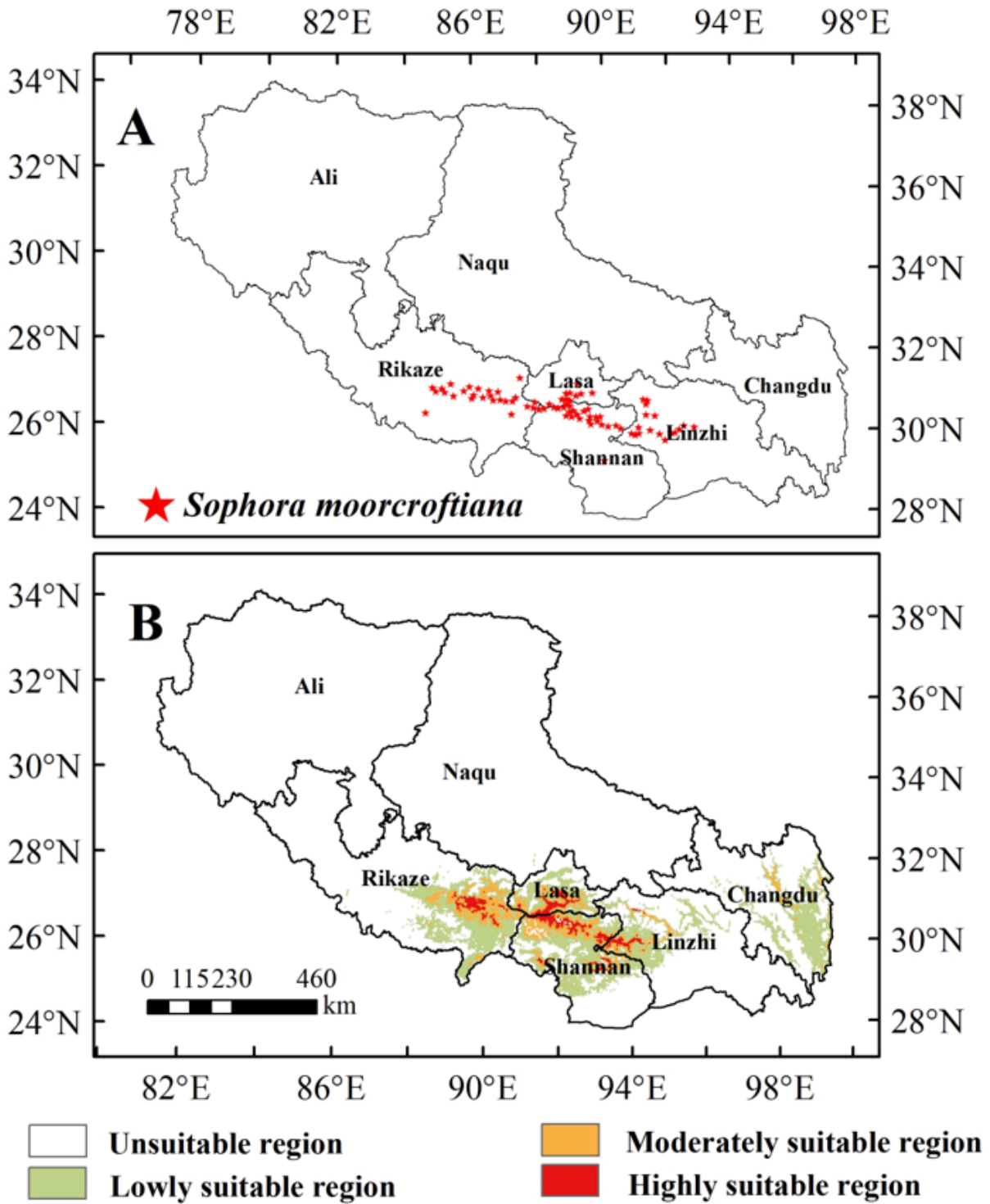


Figure 2

Occurrence records and current potential distribution of *S. moorcroftiana* predicted by MaxEnt. **(A)**Geographic locations of the 79 occurrence records used in the MaxEnt model, selected by spatial filtering (>10 km apart) to reduce sampling bias. **(B)**Current potential distribution under baseline climatic conditions (1970–2000), predicted by MaxEnt. Habitat suitability was classified into the following four categories: unsuitable (0.00–0.06), low suitability (0.06–0.25), moderate suitability (0.25–0.53), and high suitability (0.53–0.86). The

prediction was based on 19 bioclimatic variables, and suitability values ranged from 0 (unsuitable) to 1 (highly suitable).

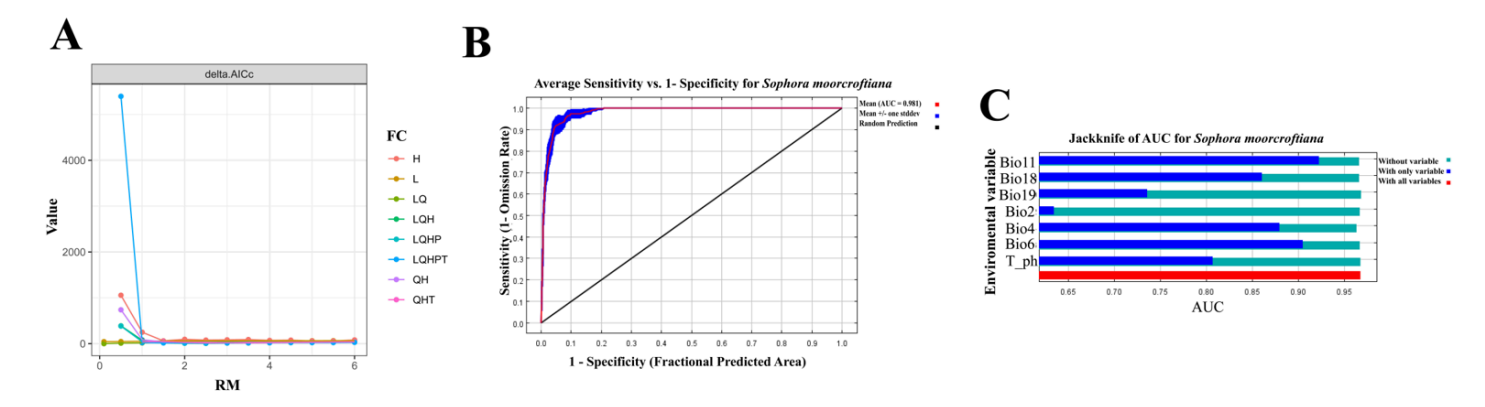


Figure 3

Model optimization and evaluation of the MaxEnt ecological niche model for *S. moorcroftiana*. **(A)** Optimization of FCs and RMs using the ENMeval R package. The delta AICc values were plotted to select the optimal model with the lowest complexity and best fit. **(B)** Receiver operating characteristic (ROC) curve for the tuned model. The (AUC = 0.981) indicates high predictive performance. **(C)** Jackknife test of variable importance based on the AUC value. The model was trained with and without each environmental variable to assess its relative contribution.

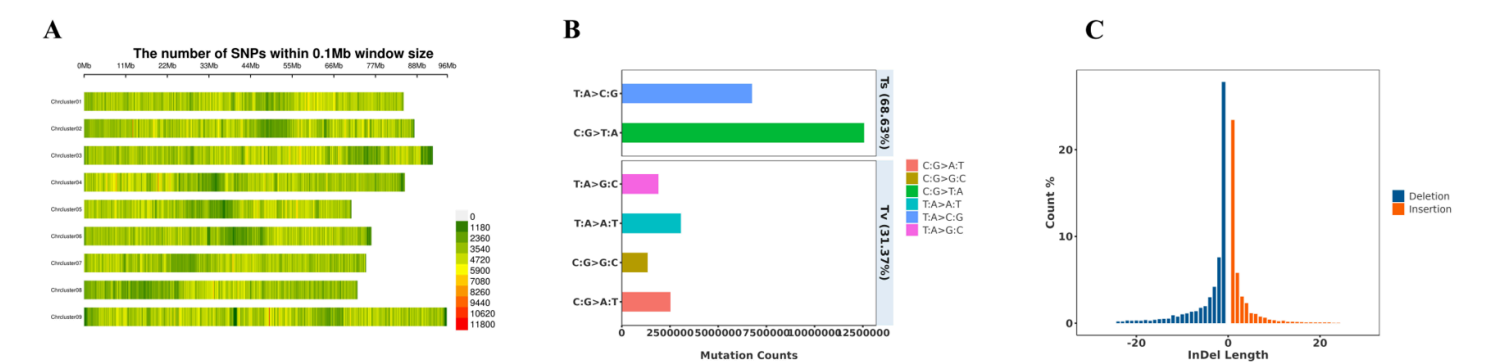


Figure 4

Summary statistics of SNP and inDel variations detected from WGRs data of *S. moorcroftiana*. **(A)** SNP density distribution across the nine chromosomes (Cmochr01–Cmochr09) in 0.1 Mb non-overlapping windows. The color gradient from green to red indicates increasing SNP density. **(B)** Classification and frequency of SNP types. Transition (Tis) mutations (68.63%) were more frequent than transversion (Tv) mutations (31.37%). **(C)** Length distribution of insertions and deletions (indel). The deletions and insertions are shown in blue and orange, respectively, and the majority of variants were shorter than 5 bp.

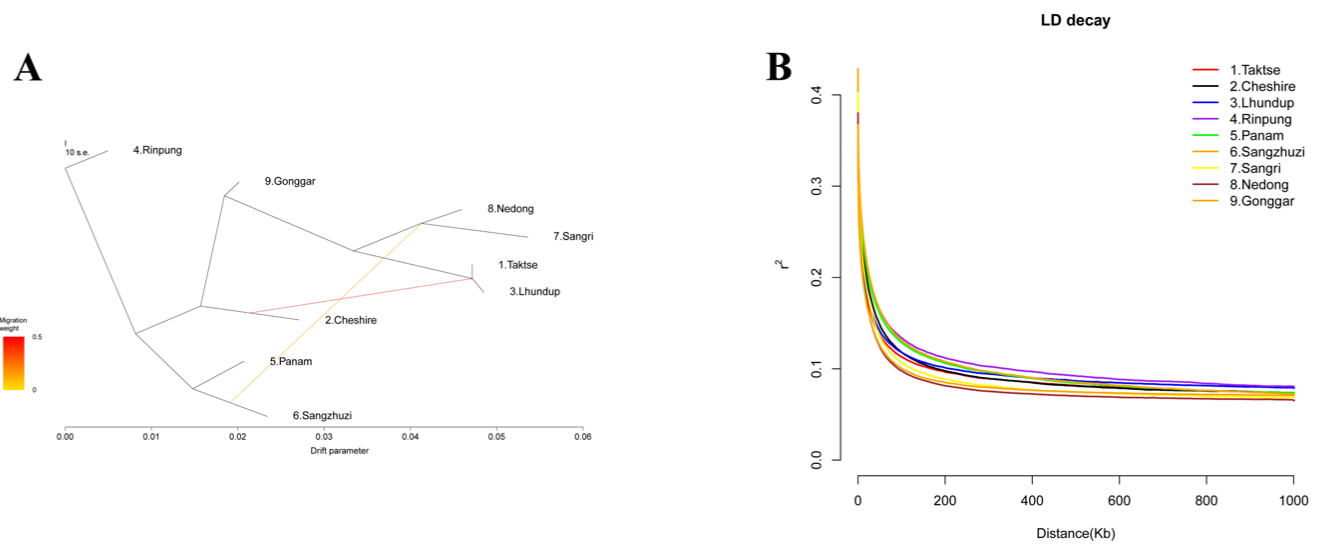


Figure 5

Gene flow and LD decay among nine *S. moorcroftiana* populations. (A) TreeMix analysis showing patterns of historical gene flow and population drift. The arrows represent gene flow events, and the arrow color intensity indicates migration weight (yellow to red). The x-axis denotes the amount of genetic drift, and the y-axis represents population relationships. (B) LD decay curves across populations. LD was measured as r^2 and plotted against physical distance (kb).

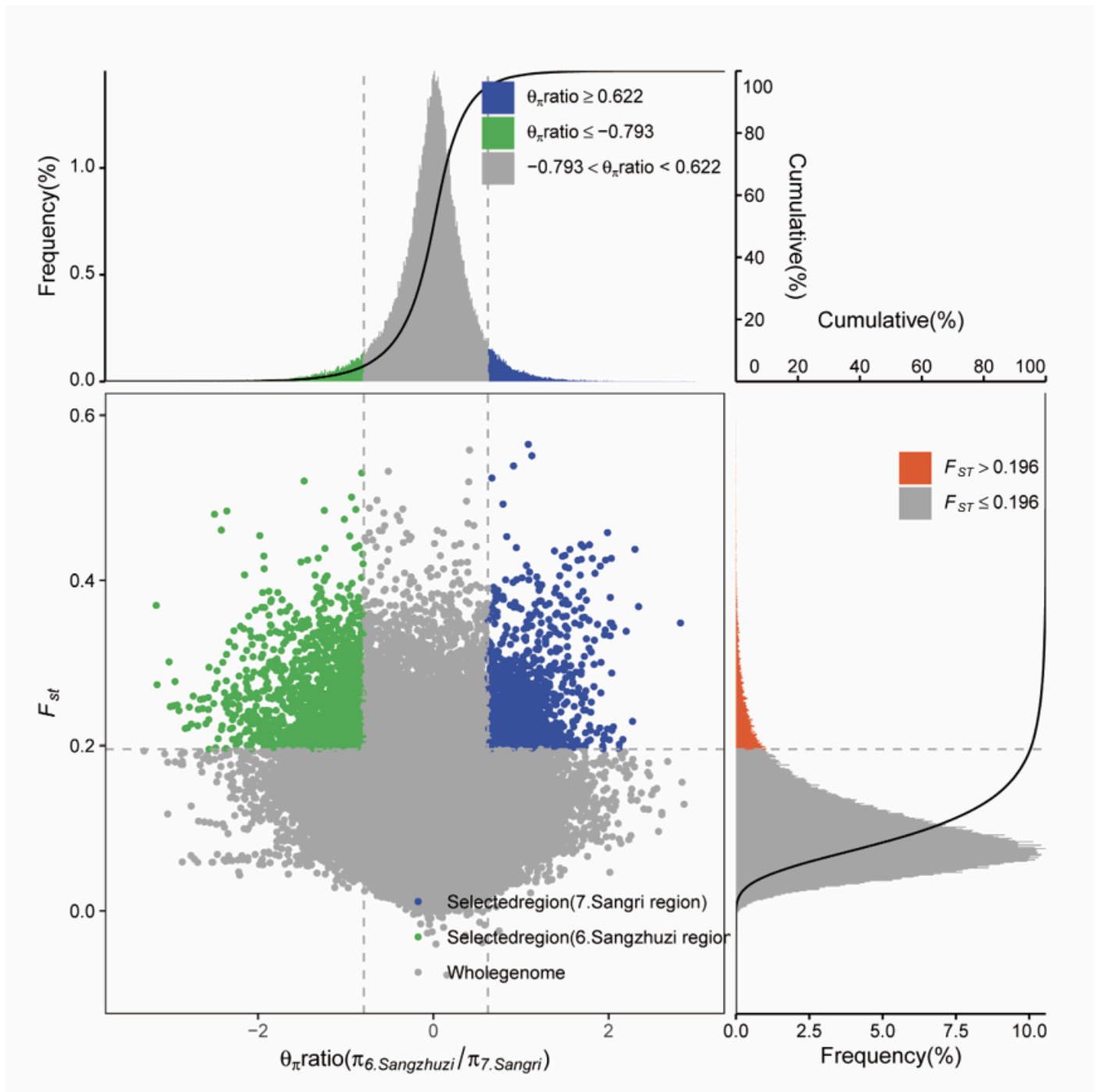


Figure 6

Identification of candidate selective sweep regions between the Sangzhuizi and Sangri populations of *S. moorcroftiana*.

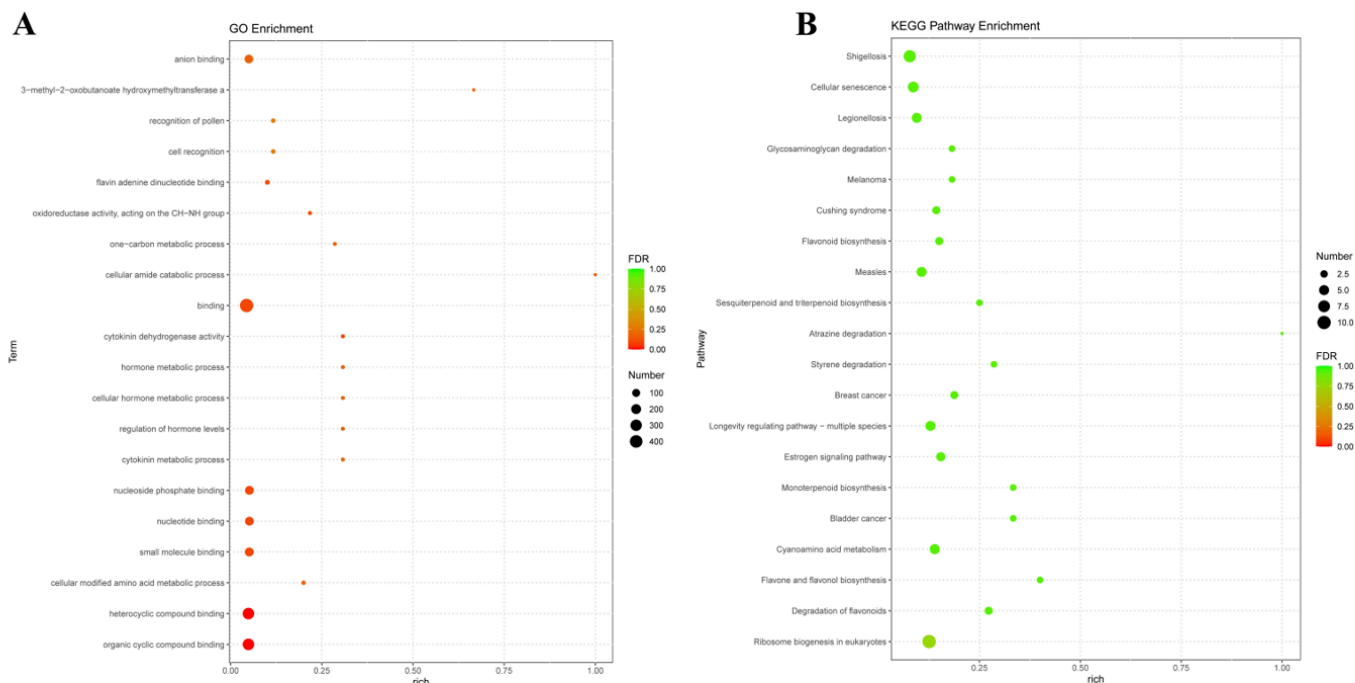


Figure 7

Functional enrichment analysis of genes located in candidate selective sweep regions of *S. moorcroftiana*. The dot size indicates the number of enriched genes, and the color gradient represents the FDR, where lower FDR values (red) indicate higher statistical significance. The x-axis (Rich factor) reflects the ratio of enriched genes to total genes in each pathway.

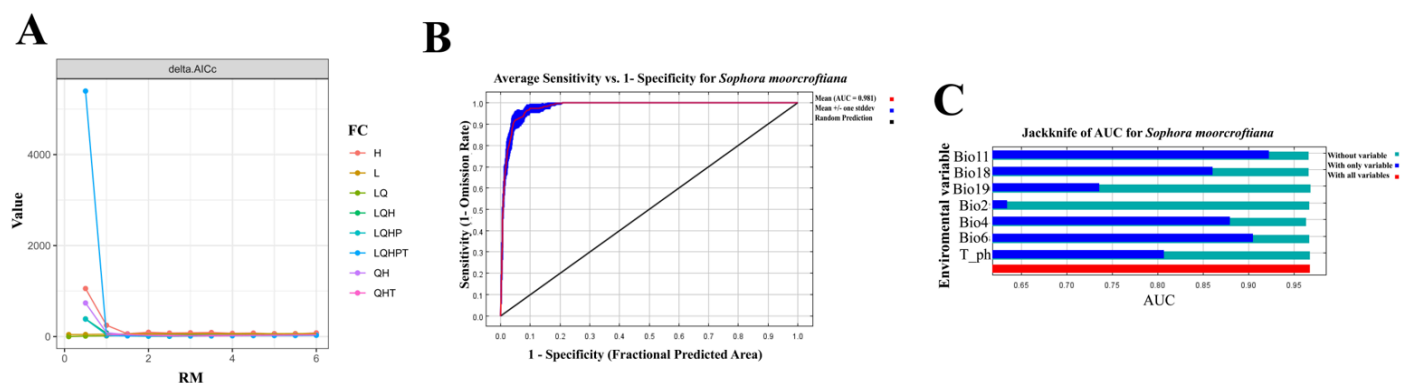


Figure 8

Model optimization and evaluation of the MaxEnt ecological niche model for *S. moorcroftiana*. (A) Optimization of FCs and RMs using the ENMeval R package. The delta AICc values were plotted to select the optimal model with the lowest complexity and best fit. (B) Receiver operating characteristic (ROC) curve for

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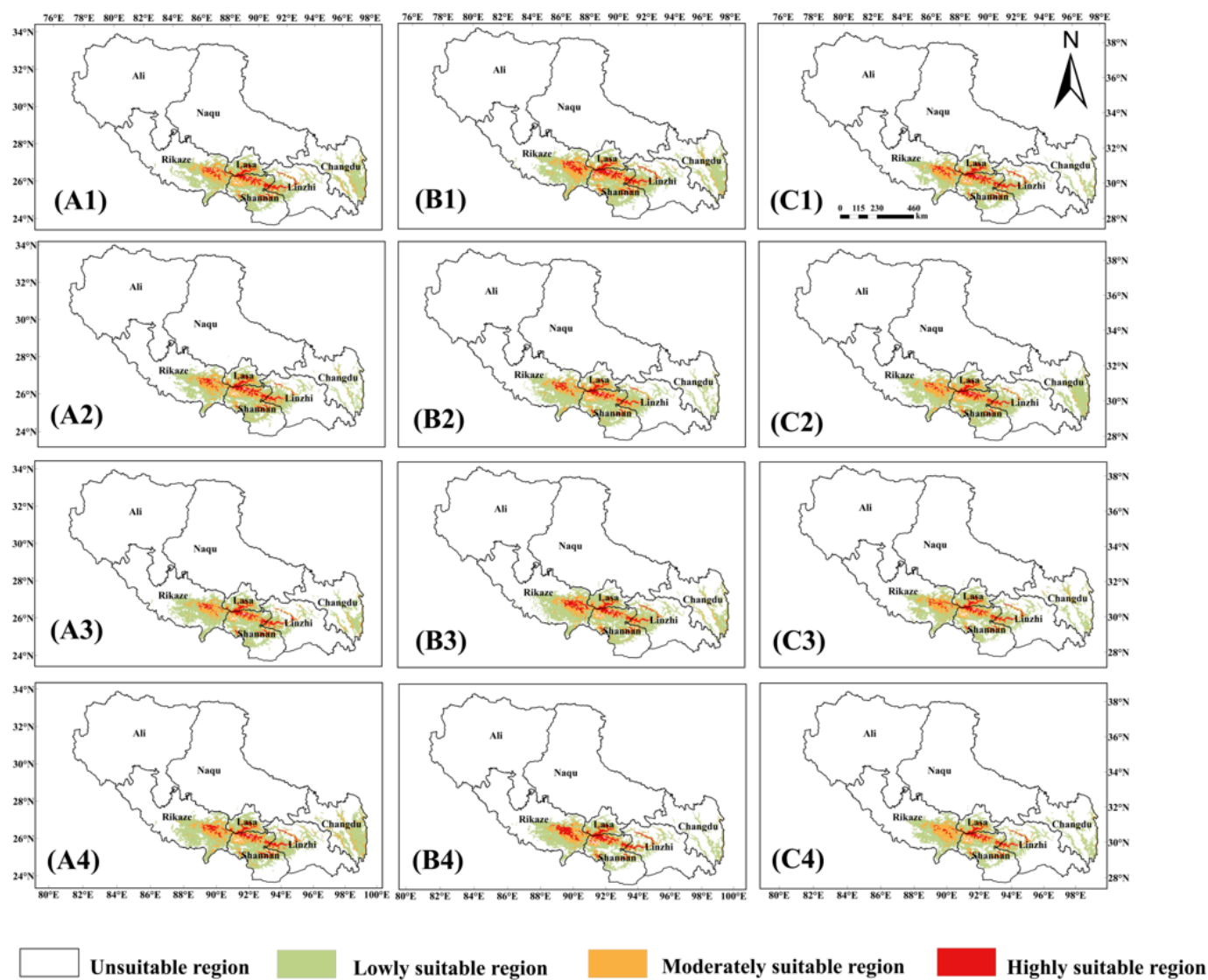


Figure 9
Predicted future habitat suitability of *S. moorcroftiana* under three climate scenarios.

Supplementary Files

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