

Article

Ecological, Anatomical, and Genomic Insights into the Rare Tree Species *Fraxinus sogdiana*, *Celtis caucasica*, and *Betula jarmolenkoana* from the Northern Tien Shan

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Abstract

This study provides a comprehensive assessment of the population structures, anatomical adaptations, and chloroplast genome organizations of three rare tree species—*Fraxinus sogdiana* Bunge, *Celtis caucasica* Willd., and *Betula jarmolenkoana* Golosk.—from the Northern Tien Shan region of Kazakhstan. Field surveys revealed species-specific demographic patterns, with *F. sogdiana* and *B. jarmolenkoana* populations displaying a complete age spectrum and signs of ongoing regeneration, while *C. caucasica* exhibited a lack of juvenile stages, indicating regeneration failure. Anatomical analysis of leaf and stem tissues highlighted adaptive features aligned with habitat conditions: *F. sogdiana* showed mesophytic traits suited for riparian environments, *C. caucasica* displayed xeromorphic structures reflecting drought tolerance, and *B. jarmolenkoana* demonstrated structural reinforcement adapted to high-altitude stressors. Whole chloroplast genome sequencing revealed conserved quadripartite architecture across species, with minor variations in gene content and inverted repeat boundaries suggesting lineage-specific evolution. The findings underscore the ecological sensitivity and conservation priority of these species and provide foundational data for future ecological monitoring, restoration efforts, and phylogenomic research in Central Asian montane ecosystems.

Keywords: *Fraxinus sogdiana*; *Celtis caucasica*; *Betula jarmolenkoana*; threatened species; chloroplast genome



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1. Introduction

The mountainous regions of the Northern Tien Shan in southeastern Kazakhstan harbor a diverse assemblage of woody plant species, several of which are endemic or relict and play essential ecological roles in maintaining ecosystem structure and function [1,2]. Characterized by sharp altitudinal gradients, heterogeneous topography, and a mix of sub-alpine, montane, and riparian habitats, this region supports complex ecological networks

that are increasingly threatened by climate change and anthropogenic disturbances [3–7]. Among the notable woody taxa in this region are *Fraxinus sogdiana* Bunge, *Celtis caucasica* Willd., and *Betula jarmolenkoana* Golosk., which are of particular interest due to their restricted distributions, ecological importance, and increasing conservation concern. All three species are formally listed in the Red Book of the Republic of Kazakhstan, which designates them as taxa of national conservation concern and provides a legal framework for their protection [8]. *F. sogdiana*, commonly known as the Sogdian ash, is a relict deciduous tree endemic to Central Asia, where it predominantly inhabits riparian zones and floodplains. It thrives on nutrient-rich alluvial soils under moderate precipitation regimes, forming key structural components of riverine ecosystems across the Charyn and Temirlik valleys. Its presence supports critical ecological functions, such as riverbank stabilization, water quality regulation, and habitat provision for aquatic and terrestrial biota [9–12]. Studies in Charyn Canyon report that *F. sogdiana* occupies over 800 ha of the floodplain, exhibits physiological stress, and suffers canopy decline due to grazing and habitat disturbance [12]. *C. caucasica*, the Caucasian hackberry, is more widely distributed across Central Asia and the Caucasus, including the Tien Shan range. Notable for its ecological plasticity, this species contributes to forest regeneration, nutrient cycling via leaf litter, and biodiversity enhancement through its interactions with wildlife. Its fruits serve as a vital food source for birds and small mammals, while the tree itself associates with a variety of co-occurring deciduous species [13–15]. However, populations are often fragmented and located near human-modified landscapes, leading to reduced recruitment and edge-related stress [16]. *B. jarmolenkoana* (considered a synonym of *B. tianschanica* in some recent taxonomic treatments) is a rare and narrowly distributed birch species endemic to the subalpine and alpine zones of Kazakhstan. It is adapted to cool, moist conditions at elevations between 1800 and 2500 m, where it occupies fragile high-mountain ecosystems [17,18]. Due to its restricted range, sensitivity to environmental fluctuations, extremely limited occupancy, observed habitat decline from fire, and increasing disturbance from grazing and tourism, this species is classified as Critically Endangered under IUCN criteria [18–20].

None of these species are currently covered by species-specific conservation programs, and active interventions such as assisted regeneration, seed banking, or ex situ cultivation are largely absent. Their ecological roles, ranging from floodplain stabilization to forest regeneration and biodiversity support, underscore their significance as foundational components of the Northern Tien Shan flora. However, their continued persistence is undermined by direct anthropogenic impacts, policy gaps, and insufficient ecological monitoring. Despite their recognized significance, comprehensive assessments of their current statuses, habitat preferences, and roles in ecosystem functioning remain limited. This study aims to comprehensively assess the bioecological, anatomical, and genomic characteristics of *F. sogdiana*, *C. caucasica*, and *B. jarmolenkoana* in the mountainous regions of the Northern Tien Shan in southeastern Kazakhstan. Through the integration of population structure analysis, morphometric assessments, leaf anatomical investigations, and comparative chloroplast genome profiling, this study seeks to (i) elucidate the ecological adaptations and structural traits of these species, (ii) evaluate their current population dynamics and conservation statuses in natural habitats, and (iii) characterize and compare the chloroplast genome organizations and gene contents across species to assess genome-level conservation and structural variation.

2. Materials and Methods

2.1. Plant Material, Geobotanical Survey, and Population Assessment

Field investigations were conducted in the Northern Tien Shan, specifically along the Ile Alatau and Uzynkara Ridges, using a combination of field-based and stationary

methods. Specimens were collected from natural habitats during the flowering stage to facilitate accurate morphological identification and taxonomic verification. *C. caucasica* individuals were sampled in the Small Almaty Gorge of the Ile Alatau Ridge at an elevation of 1418 m above sea level. *B. jarmolenkoana* specimens were collected on the Uzynkara Ridge near Narynkol village (Raiymbek District, Almaty Region) at an altitude of 2248 m a.s.l. *F. sogdiana* was recorded in the Kirgizsay Gorge, also within the Uzynkara Ridge, with collections carried out at an elevation of 1216 m a.s.l. (Figure 1). Floristic identification was performed using standard regional references, including Flora of Kazakhstan [21], Identifier of Plants of Central Asia [22], and the Illustrated Identifier of Plants of Kazakhstan [23]. Taxonomic classifications of genera followed guidelines from S.A. Abdullina [24], and species nomenclature was adopted from S.K. Cherepanov [25].

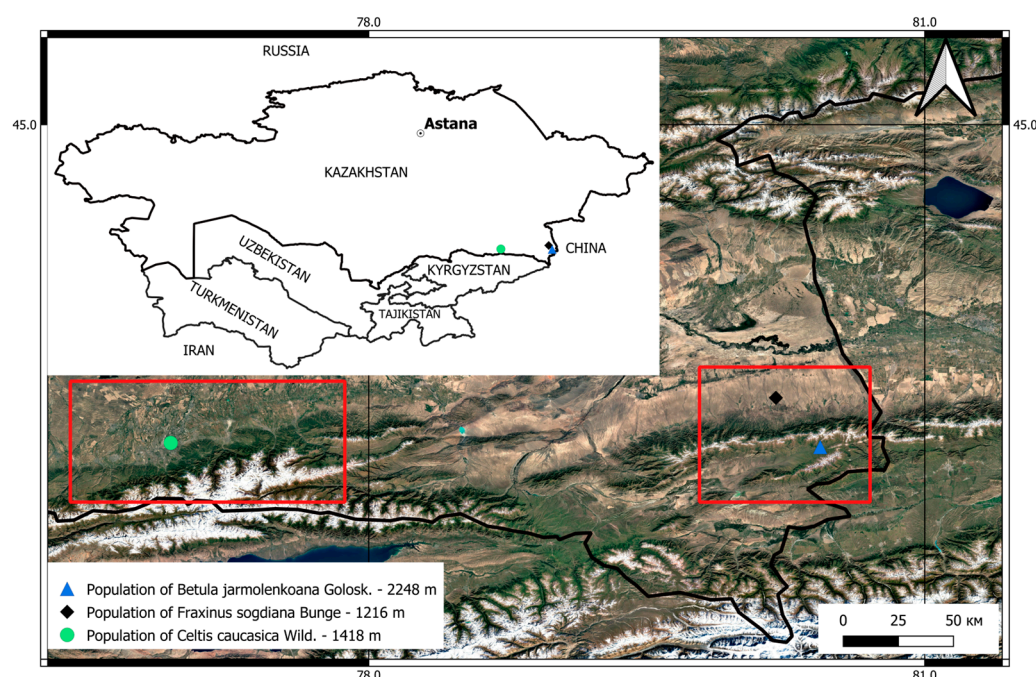


Figure 1. Study area and sampling sites of rare and threatened plant species in the Northern Tien Shan. The map shows the distribution of three target species: *Celtis caucasica* Willd. (Small Almaty Gorge, 1418 m a.s.l.), *Betula jarmolenkoana* Golosk (Narynkol village, Uzynkara Ridge, 2248 m a.s.l.), and *Fraxinus sogdiana* Bunge (Kirgizsay Gorge, Uzynkara Ridge, 1216 m a.s.l.).

The ecological statuses and regeneration capacities of *F. sogdiana*, *B. jarmolenkoana*, and *C. caucasica* were assessed through route-reconnaissance surveys in the Ile Alatau and Uzynkara Ridges. Sample plots of 100 m × 100 m, 50 m × 50 m, and 25 m × 100 m were established within populations. In each plot, 2 m × 2 m quadrats placed at 10 m intervals were used to assess undergrowth abundance and seedling viability.

Species abundance was estimated using the Drude scale. Age classes were determined based on morphological and developmental traits, following established criteria in forest population ecology [26,27]. Individuals were classified as juvenile (young plants with underdeveloped root systems and no reproductive structures), immature (non-reproductive individuals with larger vegetative growth), virginile (mature individuals that have reached the potential for reproduction but were not observed flowering or fruiting during the study period), and generative (individuals actively producing flowers or fruits). Morphological comparisons among age groups were also conducted. Vegetation cover was characterized using 100 m² plots, and GPS coordinates, elevation, topography, and plant composition were recorded. Life forms were classified according to Raunkier and Serebryakov [28,29]. Data were analyzed using SPSS (v.20) with independent sample *t*-tests ($p < 0.05$).

2.2. Morphological and Anatomical Analysis

Microscopic analysis was conducted on plant material from the target species. Samples were fixed in a 1:1:1 solution of alcohol, glycerin, and water. Anatomical sections were prepared using standard protocols [30,31]. Stems were softened in 5% NaOH, rinsed, and examined under low and high magnification after epidermis removal. Sections were prepared using an OL-ZSO freezing microtome (Inmedprom, Yaroslavl, Russia). Morphometric measurements were taken with an MOV-1-15 eyepiece micrometer (LOMO, St. Petersburg, Russia) ($\times 10$ objective, $\times 40.10.7$ magnification). Microphotographs were obtained using an MC 300 microscope (Micros, Veit an der Glan, Austria) equipped with a CAM V400/1.3M digital camera (jProbe, Yokohama, Japan).

2.3. DNA Extraction and Chloroplast Genome Assembly

Genomic DNA was extracted from 100 mg of leaf tissue from *B. jarmolenkoana*, *C. caucasica*, and *F. sogdiana* using a modified CTAB protocol. DNA quality and concentration were assessed using a NanoDrop One spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and a Qubit 4 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). Whole-genome sequencing was performed on the SurfSeq 5000 platform (Genemind, Shenzhen, China). Chloroplast genomes of the same three species were assembled from whole-genome sequencing reads using GetOrganelle v1.7.7 with default parameters [32]. Complete circular assemblies were annotated using the GeSeq web service v1.93 with BLASTX for protein-coding genes, BLASTN for rRNA genes, and tRNAscan-SE v2.0.7 tRNA identification [33,34]. Genome structural organization and inverted repeat boundaries were identified using OGDRAW v1.4 [35]. Annotations were exported in GFF3 format for comparative analysis.

Genomic features were extracted from GFF3 files and analyzed using R v4.3.0 with the tidyverse package v2.0.0 [36,37]. Descriptive statistics for gene lengths, feature counts, and genomic organization were calculated using dplyr v1.1.0. Comparative visualizations including feature distributions, gene length histograms, strand orientation, and genome structure were generated using ggplot2 v3.4.2 with viridis color palettes [38,39].

3. Results

3.1. Bioecological Characteristics of the Studied Species

3.1.1. Population of *F. sogdiana*

F. sogdiana forms small thickets in floodplain habitats of the Uzynkara Ridge (Figure 2). Mature trees reach heights of 25–35 m and possess a straight, fully lignified trunk with finely fissured, light gray bark. Branches are reddish or gray, with young shoots exhibiting pubescence. Leaflets are ovate-lanceolate, glabrous on the abaxial surface, and sparsely pubescent adaxially, reaching up to 20 cm in length. The inflorescence is a raceme, typically up to 5 cm long.

The species occurs in isolated stands along the lower Temirlik River, with additional fragmented populations recorded along the Charyn River and the Sarytogay tract, where it forms mixed ash and ash–poplar forests extending over 25 km. It is also sporadically distributed in the Charyn River delta and was historically present near the Ili River in the Ayak-Kalkan tract, now submerged by the Kapchagay Reservoir. The total area of the studied population is estimated at 0.3 ha, with individuals occurring in isolated, discontinuous patches.

In the studied population of *F. sogdiana* in the Temirlik River floodplain, age structure analysis revealed the presence of 15 juvenile, 20 immature, 34 virginile, and 70 generative individuals (Table 1). Mean plant height increased with ontogenetic stage, ranging from 30.0 ± 5.0 cm in juvenile individuals to 533.3 ± 76.4 cm in generative trees. Correspond-

ing leaf lengths ranged from 4.00 ± 1.00 cm to 17.33 ± 2.52 cm. The population also included 10 subsenile and senile individuals, indicating limited representation of older age classes. This skewed age distribution is likely the result of anthropogenic disturbance, particularly intensive grazing, which may impede successful recruitment and long-term population stability.



Figure 2. Natural habitats of *F. sogdiana*. (a) Riparian habitat along the Temirlik River within the Uzynkara Ridge; (b) compound leaves of *F. sogdiana* displaying lanceolate leaflets with entire margins and a drooping arrangement, typical of mesophytic adaptation.

Table 1. Comparative morphological characteristics of *Fraxinus sogdiana* Bunge at different developmental stages.

Age Group	Number of Individuals	Leaf Length (cm) $\pm$ SD	Plant Height (cm) $\pm$ SD
Juvenile (j)	15	4.00 ± 1.00	30.0 ± 5.0
Immature (i)	20	7.67 ± 0.58	66.67 ± 15.28
Virginile (v)	34	16.00 ± 3.61	316.67 ± 47.26
Generative (g)	70	17.33 ± 2.52	533.33 ± 76.38

Differences at specific developmental stages were statistically significant ($p < 0.05$).

3.1.2. Population of *C. caucasica*

C. caucasica occurs in isolated populations within the Ile Alatau Ridge, notably in the Small Almaty Gorge (Figure 3). It is typically found on rocky slopes, screes, and in river valleys, growing either as individual trees or in small groves within mixed shrub communities. It is a small tree, 4–8 m in height, with smooth gray bark and a dense crown. Flowers are solitary and axillary, and the fruit is a spherical drupe. Reproduction occurs both generatively and vegetatively, with flowering in April–May and fruiting from September to early October.

The population does not form monospecific stands and is embedded in a two-tiered plant community comprising associated tree species such as *Malus sieversii*, *Armeniaca vulgaris*, *Crataegus songarica*, *Acer semenovii*, and *Populus tremula*, as well as shrubs including *Rosa platyacantha*, *Euonymus semenovii*, *Cotoneaster oliganthus*, and *Spiraea lasiocarpa*.

Field assessments indicate that individuals of *C. caucasica* in this location are in the middle-aged generative stage, with an average height of 6–7 m and age of approximately 35–40 years. Seedlings, juvenile, and senile individuals were not observed. Virginile individuals exhibited only growth-specialized shoots, a developmental stage typically reached by five years of age. The total number of individuals recorded in the population was limited (Table 2).

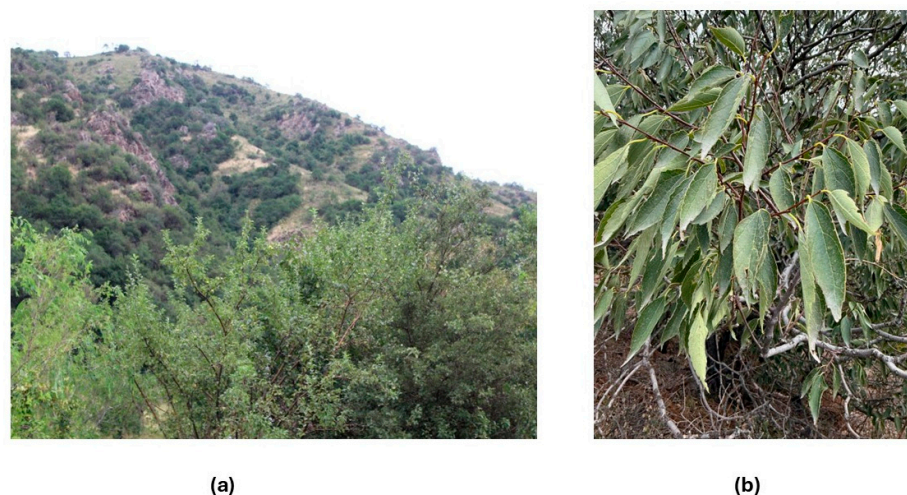


Figure 3. Morphological features and habitat of *C. caucasica*. (a) Natural population of *C. caucasica* in the Small Almaty Gorge, Ile Alatau Ridge; (b) simple leaves with serrated margins and rough surface texture, indicative of xeromorphic adaptation.

Table 2. Comparative morphological characteristics of *Celtis caucasica* Willd. at different developmental stages.

Age Group	Number of Individuals	Leaf Length (cm) $\pm$ SD	Plant Height (cm) $\pm$ SD
Juvenile (j)	3	2.33 $\pm$ 0.58	25.00 $\pm$ 5.00
Immature (i)	5	3.50 $\pm$ 0.71	70.00 $\pm$ 10.00
Virginile (v)	4	6.00 $\pm$ 1.41	270.00 $\pm$ 20.00
Generative (g)	5	8.00 $\pm$ 1.00	346.67 $\pm$ 25.17

Differences at specific developmental stages were statistically significant ($p < 0.05$).

3.1.3. *B. jarmolenkoana* Population

B. jarmolenkoana is a small tree reaching 2–5 m in height, characterized by yellowish-gray bark, a broad spreading crown, and small rhombic-ovate leaves with wedge-shaped bases and finely serrated margins (Figure 4). It occurs as scattered individuals or in small groups within the mid-elevation zones (1900–2100 m) of the Uzynkara Ridge, particularly near the villages of Narynkol and Sarydzhaz. The species inhabits tugai forests and hummocky, marshy meadows along mountain rivers in the Kegen Valley, where the projective vegetation cover is estimated at 60%–65%.



Figure 4. Habitat and morphological features of *B. jarmolenkoana*. (a) Natural stand of *B. jarmolenkoana* in the tugai forest of the Bayankol River valley, near Narynkol village (Uzynkara Ridge); (b) fruiting branch of *B. jarmolenkoana* showing characteristic leaf shape and infructescence.

B. jarmolenkoana is found within mixed riparian and montane forest communities along the Bayankol River. In these habitats, it coexists with dominant tree species such as *Picea schrenkiana* and *Hippophae rhamnoides*, as well as with various shrubs including *Salix caesia*, *S. tenuijulis*, *S. wilhelmsiana*, *S. niedzwieckii*, *Lonicera albertii*, *L. tatarica*, *L. stenantha*, *L. hispida*, *Berberis sphaerocarpa*, *Caragana aurantiaca*, *Myricaria squamosa*, and *Juniperus sabina*.

Age structure analysis revealed the presence of all ontogenetic stages, with a predominance of generative individuals (80%). Specifically, the population included 50 juvenile, 39 immature, 73 virginile, and 113 generative trees (Table 3). Morphometric measurements showed that generative individuals had an average height of 356.67 ± 60.28 cm and a leaf length of 3.00 ± 0.00 cm. However, field observations recorded a few exceptionally tall individuals reaching up to 8–13 m in height and up to 53 cm in trunk diameter. Most trunks were curved and multi-branched, with a general diameter range of 12–38 cm. Additionally, a 15%–20% crown dieback was observed in some mature trees, indicating signs of physiological stress.

Table 3. Comparative morphological characteristics of *Betula jarmolenkoana* Golosk.at different developmental stages.

Age Group	Number of Individuals	Leaf Length (cm) $\pm$ SD	Plant Height (cm) $\pm$ SD
Juvenile (j)	50	1.00 ± 0.27	66.67 ± 15.28
Immature (i)	39	2.00 ± 0.35	113.33 ± 35.12
Virginile (v)	73	1.92 ± 0.53	256.67 ± 90.18
Generative (g)	113	3.00 ± 0.46	356.67 ± 60.28

Differences at specific developmental stages were statistically significant ($p < 0.05$).

3.2. Anatomical Structure

3.2.1. Leaf Anatomy of *F. sogdiana*

The leaf of *F. sogdiana* displays a dorsoventral structure with differentiated upper and lower epidermal layers composed of oval, compressed cells with thickened walls. The cuticle is thin, and stomata of the dicotyledonous type are clearly developed. The upper epidermal cells measure 7.11 ± 0.8 μ m in thickness, while the lower ones are 5.94 ± 0.31 μ m. The mesophyll consists of a well-defined columnar region adjacent to the upper epidermis and a loose parenchyma layer containing prominent intercellular cavities. Chloroplast-rich parenchyma cells were observed, with the loose mesophyll showing a cell thickness of 7.14 ± 0.3 μ m. Vascular bundles are well developed and encased in sclerenchyma cells, with idioblasts present in both the primary sheath and vascular parenchyma, indicating sites of secondary metabolite accumulation (Figure 5).

3.2.2. Leaf Anatomy of *C. caucasica*

The leaf of *C. caucasica* exhibits xeromorphic adaptations, including a thickened cuticle and the presence of glandular trichomes on both epidermal surfaces. The upper epidermal cell thickness is 8.34 ± 0.6 μ m, while the lower measures 6.17 ± 1.1 μ m. The mesophyll is dorsiventral, with a two-layered columnar zone and a loosely arranged parenchyma containing air cavities and idioblasts. The parenchyma cells in the columnar mesophyll are elongated, with an average thickness of 6.98 ± 0.61 μ m. The vascular bundles are enveloped by parenchymatous sheath cells, and well-developed chloroplasts were observed throughout the mesophyll. Xylem elements form a chain-like pattern with narrowing lumens toward the upper epidermis, and the phloem tubes are distinctly separated (Figure 6).

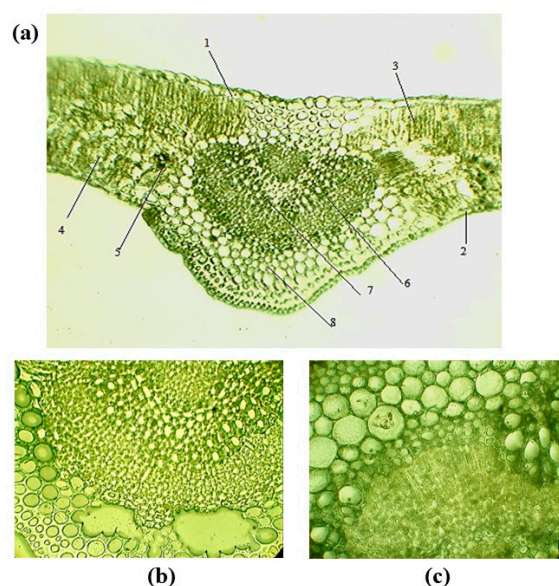


Figure 5. Anatomical structure of the leaf of *F. sogdiana*. (a) Transverse section of the leaf showing tissue organization, including the epidermis, mesophyll, and vascular bundle ($\times 10$); (b) detailed view of a vascular bundle with surrounding xylem and parenchyma cells ($\times 40$); (c) loose mesophyll with idioblast cells and intercellular spaces ($\times 40$). Labelled structures: 1—upper epidermis, 2—lower epidermis, 3—columnar mesophyll, 4—loose mesophyll, 5—idioblast, 6—vascular bundle, 7—xylem, 8—parenchyma.

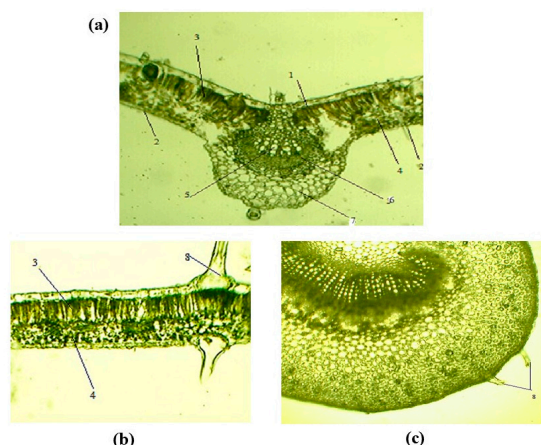


Figure 6. Leaf anatomy of *C. caucasica*. (a) Transverse section showing the upper and lower epidermis, mesophyll, and vascular bundle ($\times 10$); (b) differentiation of columnar and loose mesophyll layers ($\times 40$); (c) central vascular bundle in the midrib region ($\times 40$). Labels: 1—upper epidermis, 2—lower epidermis, 3—columnar mesophyll, 4—loose mesophyll, 5—xylem, 6—vascular bundle, 7—parenchyma, 8—trichome.

3.2.3. Leaf Anatomy of *B. jarmolenkoana*

Leaves of *B. jarmolenkoana* exhibit an isolateral structure with symmetrical development of the upper and lower epidermis. The upper epidermal cells measure $6.17 \mu\text{m}$, and the lower cells are $5.11 \pm 1.41 \mu\text{m}$, both exhibiting thickened, cutinized walls. Stomata are present on both surfaces. The mesophyll consists of columnar and spongy layers, with the latter containing well-defined intercellular spaces. The boundary between the mesophyll zones is distinct, and the spongy mesophyll cells have a thickness of $6.18 \pm 1.61 \mu\text{m}$. Schizogenous cavities and large collateral vascular bundles are prominent, especially in the midrib, where the vascular tissues are encased in three to four rows of sclerenchyma, accompanied by well-developed lamellar collenchyma (Figure 7).

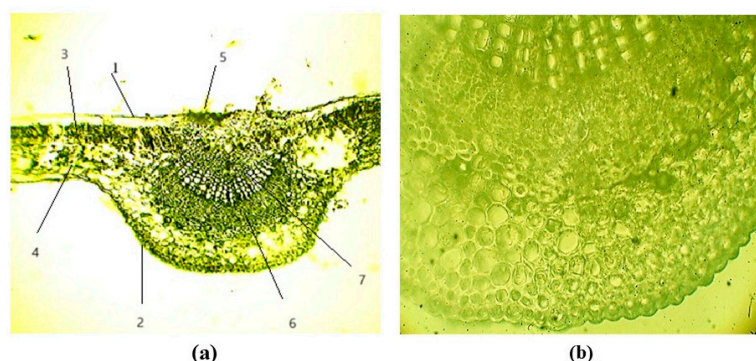


Figure 7. Anatomical structure of the leaf of *B. jarmolenkoana*. (a) Transverse section showing the upper and lower epidermis, columnar mesophyll, sclerenchyma, and a large collateral vascular bundle ($\times 10$); (b) enlarged view of the vascular bundle in the midrib region ($\times 40$). Labels: 1—upper epidermis, 2—lower epidermis, 3—columnar mesophyll, 4—spongy mesophyll, 5—trichome, 6—sclerenchyma, 7—vascular bundle.

3.3. Chloroplast Genome Structure and Comparative Analysis

The three chloroplast genomes showed typical angiosperm organization with comparable sizes ranging from 155.6 kb (*F. sogdiana*) to 160.4 kb (*B. jarmolenkoana*). *C. caucasica* had an intermediate genome size of 158.6 kb. All three genomes exhibited the characteristic quadripartite structure with large single-copy (LSC), small single-copy (SSC), and two inverted repeat (IR) regions.

Comprehensive feature analysis revealed highly conserved gene content across all three species (Figure 8, Supplementary Table S1). The total number of annotated features was remarkably similar, with *C. caucasica* containing 136 genes, *F. sogdiana* containing 133 genes, and *B. jarmolenkoana* containing 130 genes. Protein-coding genes comprised the largest category, with 111, 106, and 106 genes in *C. caucasica*, *F. sogdiana*, and *B. jarmolenkoana*, respectively.

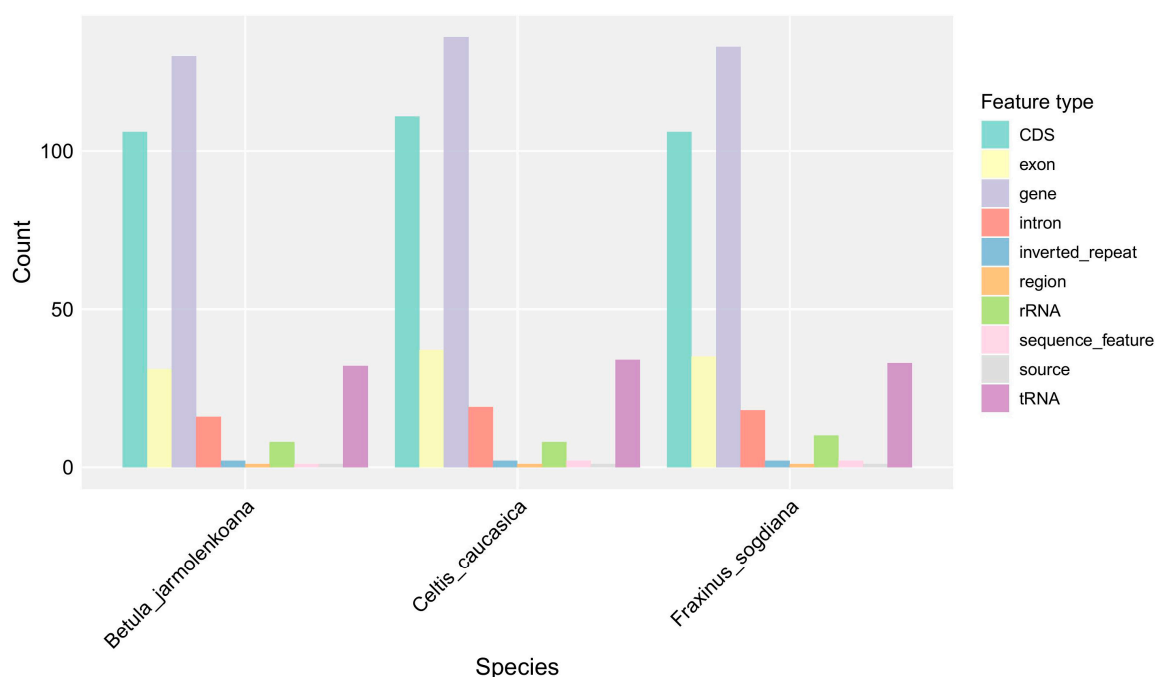


Figure 8. Comparative analysis of genomic feature types across three chloroplast genomes. Bar chart showing the distribution of different feature types (CDS, exon, gene, intron, inverted_repeat, region, rRNA, sequence_feature, source, tRNA) in *B. jarmolenkoana*, *C. caucasica*, and *F. sogdiana*.

Ribosomal RNA genes showed perfect conservation across species, with each genome containing exactly eight rRNA genes. Transfer RNA gene numbers were also highly conserved, ranging from 32 (*B. jarmolenkoana*) to 34 (*C. caucasica*) genes (Figure 9). The presence of exons and introns reflected the complex gene structure typical of chloroplast genomes, with intron-containing genes maintaining consistent patterns across species.

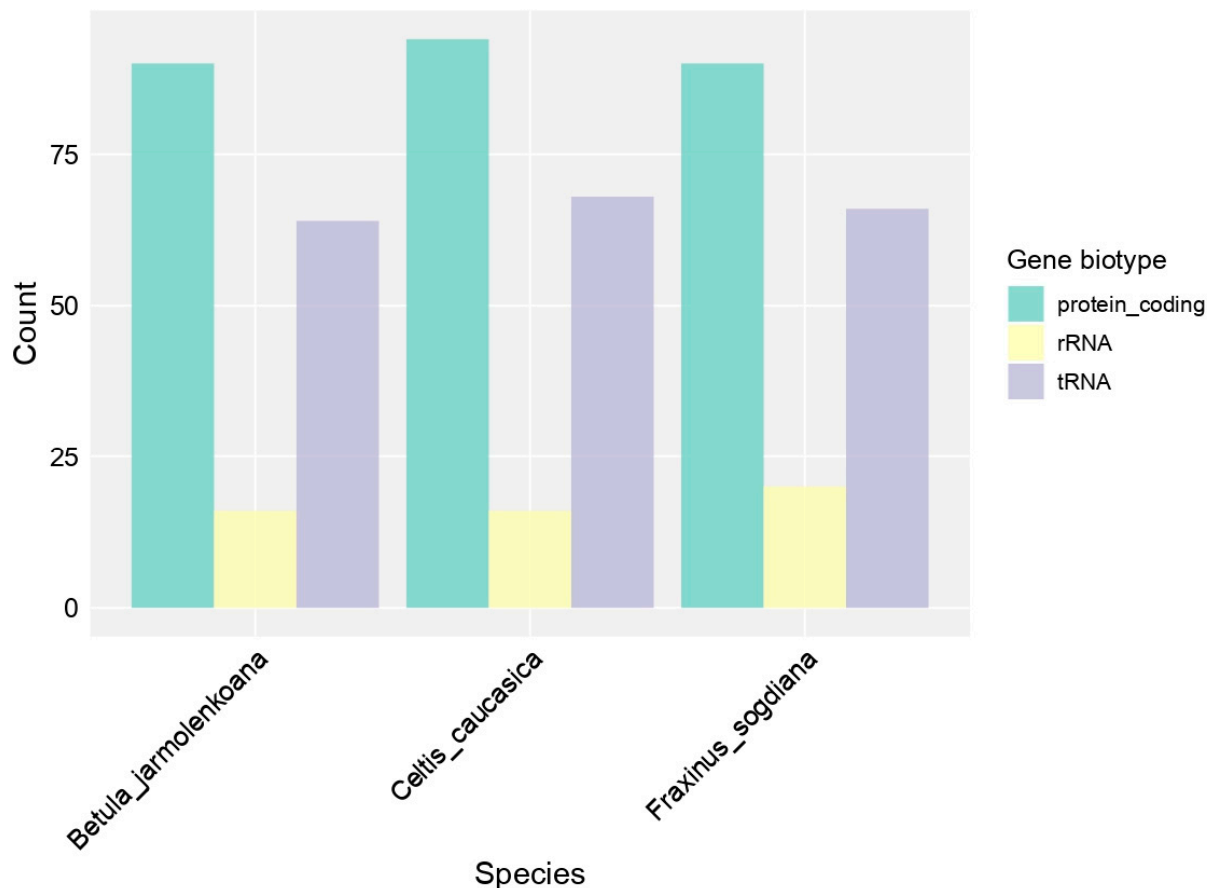


Figure 9. Gene biotype distribution comparison. Bar chart displaying the relative abundance of protein-coding genes, rRNA genes, and tRNA genes across the three species, highlighting the conserved nature of chloroplast gene content.

Strand distribution analysis demonstrated balanced gene orientation across the three chloroplast genomes (Figure 10). All species showed approximately equal numbers of genes encoded on the positive and negative strands, consistent with the typical bidirectional gene arrangement in chloroplast genomes. *B. jarmolenkoana* showed 82 genes on the positive strand and 80 on the negative strand, while *C. caucasica* had 84 and 83 genes, respectively. *F. sogdiana* displayed the most balanced distribution with 81 genes on each strand.

Despite overall conservation, several species-specific variations were observed. Detailed comparative statistics of gene counts and structural categories are provided in Supplementary Table S2. *C. caucasica* showed the highest total gene count and slightly larger inverted repeats, while *F. sogdiana* had the most compact genome. *B. jarmolenkoana* exhibited intermediate characteristics but showed unique patterns in gene length distribution. The presence of fragment genes varied among species, with *C. caucasica* and *F. sogdiana* showing similar fragment patterns, while *B. jarmolenkoana* displayed a different complement of fragmented genes, suggesting lineage-specific evolutionary events.

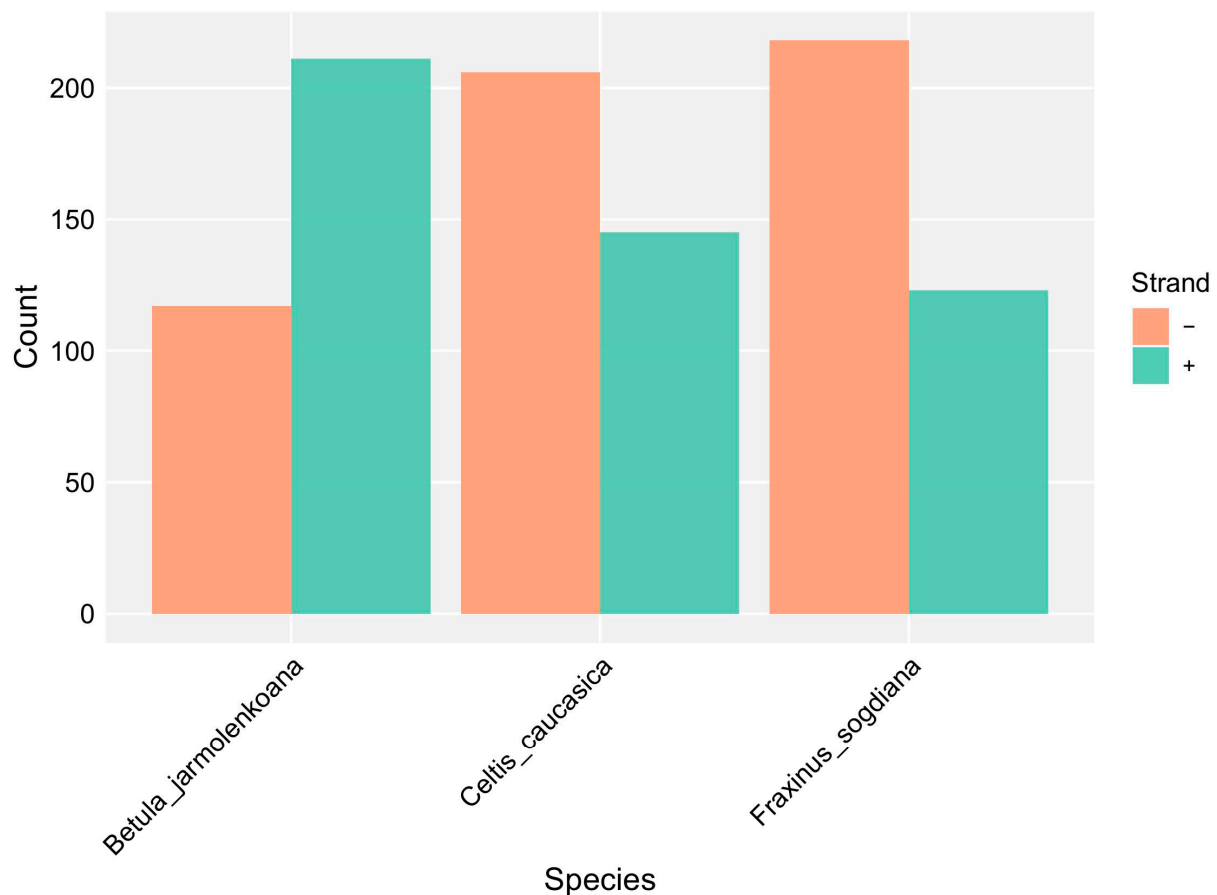


Figure 10. Strand distribution analysis. Bar chart showing the number of genes encoded on positive (+) and negative (−) strands for each species, illustrating the balanced bidirectional gene arrangement typical of chloroplast genomes.

4. Discussion

Assessing the ecological statuses, anatomical traits, and genetic characteristics of rare and threatened plant species provides important insights for developing targeted conservation strategies, particularly in ecologically sensitive regions such as the Northern Tien Shan, which harbors a high concentration of relict and endemic taxa [40]. These integrated assessments help identify critical functional traits, evaluate population stability, and detect adaptive potential, all of which are vital for prioritizing conservation actions and restoring threatened populations [41–44]. Equally, modern genomic approaches such as chloroplast genome profiling enable fine-scale resolution of genetic diversity, demographic history, and evolutionary resilience, forming key guidance for in situ and ex situ interventions [45–47]. Given the region’s high levels of endemism and ecological sensitivity, integrating ecological, anatomical, and genetic information improves our ability to predict and manage habitat shifts, prevent genetic erosion, and sustain ecosystem services in the face of environmental change.

The population analysis of *F. sogdiana*, *C. caucasica*, and *B. jarmolenkoana* revealed distinct levels of demographic stability and ecological resilience. *F. sogdiana* demonstrated a balanced age distribution, including a moderate number of juvenile and immature individuals. This indicates ongoing regeneration and ecological viability under the relatively favorable conditions of riparian habitats. These findings align with demographic patterns observed in riparian *Fraxinus* populations in the Kashgar River basin of China, where sustained regeneration occurs despite moderate mortality among middle-aged trees [48]. In contrast, *C. caucasica* exhibited a clear absence of juvenile and seedling stages, with its

population dominated by middle-aged generative individuals. This demographic skew suggests a failure of natural regeneration, likely driven by anthropogenic pressures such as grazing and habitat fragmentation, along with environmental limitations like poor seed viability and frost sensitivity. This pattern is consistent with previous genetic studies reporting low genetic diversity and fragmented populations of *C. caucasica* in Kazakhstan and the Ili-Alatau region [13]. *B. jarmolenkoana* displayed all age classes, indicating a sustained regeneration dynamic. The predominance of generative individuals, along with observed crown dieback in mature trees and the proximity to disturbed habitats, may suggest ongoing ecological stress and reduced regeneration potential. Although species-specific studies on *B. jarmolenkoana* are currently lacking, similar patterns of physiological decline and regeneration disruption have been documented in other *Betula* species of the northern Tien Shan, with drought and temperature extremes limiting seedling establishment and triggering stress-response pathways under cold stress [49,50]. These observations suggest that *B. jarmolenkoana* may face similar threats from anthropogenic encroachment and climatic stressors.

Anatomical analysis of the leaf tissues supports ecological observations by revealing structural adaptations aligned with habitat conditions. *F. sogdiana*, occupying moist, shaded riparian zones, exhibited a typical dorsiventral leaf structure with developed mesophyll layering and a thin cuticle, consistent with mesophytic adaptation. Idioblast cells and well-defined vascular bundles further indicate active physiological function and potential accumulation of secondary metabolites for protective functions. Similar anatomical features have been documented in other members of the Oleaceae family, where species adapted to mesic environments commonly exhibit dorsiventral leaf organization, reduced cuticle thickness, and idioblasts containing phenolic or calcium oxalate deposits, supporting their roles in defense and metabolic activity [51–53]. In contrast, *C. caucasica* demonstrated several xeromorphic traits, including thickened epidermal layers, a well-developed cuticle, glandular trichomes, and compact columnar mesophyll. These features reflect its adaptation to drier, sun-exposed habitats. Consistent patterns have been documented in xeric-adapted *Celtis* species, notably *C. iguanaea*, which exhibit a single-layered epidermis with secretory and non-secretory trichomes, protruding cystoliths, compact palisade mesophyll, and idioblasts with druse crystals—traits linked to drought resistance and light stress adaptation [54]. *B. jarmolenkoana*, growing in open high-altitude areas, exhibited an isolateral leaf structure with symmetrical mesophyll development and prominent sclerenchyma, indicating adaptations to increased light intensity, cold stress, and potential mechanical reinforcement. Similar trends have been observed in *Betula papyrifera* leaves across different crown positions and in alpine species generally, where increased leaf thickness, palisade mesophyll development, and reinforced epidermal tissues at upper crown positions enhance photoprotection, mechanical stability, and moisture conservation [55].

The chloroplast genomes of *F. sogdiana*, *C. caucasica*, and *B. jarmolenkoana* exhibited the conserved quadripartite structure typical of angiosperms, along with species-specific features reflecting their ecological and evolutionary contexts. The plastome of *F. sogdiana* was relatively compact, measuring approximately 155.6 kbp and comprising 133 genes. This size closely matches that of *F. pennsylvanica* (155 kbp) but is substantially smaller than the 192 kbp plastome reported for *F. excelsior*, indicating notable interspecific variation within the genus *Fraxinus* [56]. *C. caucasica* exhibited a slightly expanded plastome (~158.6 kb) with 136 genes, exceeding the 133 gene annotation typical of *C. sinensis* (~159 kb); its IR expansion and potential duplication of ORFs imply a genomic flexibility consistent with Cannabaceae species adapting to diverse environments [57]. In contrast, *B. jarmolenkoana* featured the largest cpDNA (~160.4 kb) but the fewest genes (130), paralleling findings in *B. platyphylla* (~160.5 kb, 129 genes), where pseudogenization and IR boundary shifts near *rps19* have

been documented [58]. This pattern may be the result of relaxed selective constraints or genome reorganization in response to high altitude ecological pressures. Collectively, the chloroplast genomes of these species highlight a pattern of strong evolutionary conservation in essential gene content, while also exhibiting structural differences such as variations in inverted repeat boundaries and gene fragmentation patterns. These features serve as useful molecular markers for phylogenetic studies and conservation genomics of Central Asian woody lineages.

This integrative study provides novel insights into the anatomical, ecological, and genomic characteristics of three rare tree species in the Northern Tien Shan. The combination of population analysis, anatomical traits, and plastome profiling offers a multidimensional perspective on species vulnerability and adaptation. These findings underscore the importance of protecting biodiversity in Central Asian Mountain ecosystems and support the inclusion of these species in regional conservation strategies. To ensure the long-term viability of these species, we recommend implementing targeted conservation strategies, including habitat restoration, regulation of anthropogenic pressures such as grazing, and reinforcement planting using regionally adapted genotypes. Systematic population monitoring should be established to assess recruitment dynamics, particularly in regeneration-limited taxa like *C. caucasica*. Complementary ex situ measures such as seed banking and propagation under controlled conditions will aid in preserving genetic diversity and supporting future reintroduction efforts. Future studies should aim to investigate the molecular mechanisms, nutrient uptake strategies, and soil-related environmental factors that shape the survival and adaptation of these species, as such insights would further support targeted conservation efforts and practical applications in habitat restoration.

5. Conclusions

The integrative analysis of *F. sogdiana*, *C. caucasica*, and *B. jarmolenkoana* populations in the Northern Tien Shan revealed distinct demographic patterns, anatomical adaptations, and genomic characteristics reflective of their ecological niches and conservation statuses. *F. sogdiana* exhibited a balanced age structure with evidence of active regeneration and anatomical traits consistent with mesophytic adaptation to moist riparian habitats. *C. caucasica*, in contrast, lacked juvenile individuals and exhibited reduced recruitment along with xeromorphic anatomical features, which may reflect adaptation to arid conditions and potential vulnerability to abiotic stressors such as frost and limited seed viability. *B. jarmolenkoana* populations displayed broader age representation, including a high proportion of generative individuals, but signs of physiological stress (e.g., crown dieback) and limited vegetative propagation suggest increasing ecological pressure. Comparative analysis of chloroplast genomes across the three taxa revealed a highly conserved quadripartite architecture, with minor yet consistent lineage-specific structural variations, particularly in inverted repeat boundaries and gene content. These differences may reflect environmentally driven selective pressures and contribute to species-level phylogenetic divergence.

Taken together, the data underscore the urgent need for conservation interventions tailored to the ecological and physiological characteristics of each species. Habitat protection, regeneration monitoring, and ex situ conservation efforts are recommended to mitigate anthropogenic impacts and ensure long-term population viability under changing climatic and land-use conditions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f16081340/s1>, Table S1: Chloroplast genome annotations; Table S2: Comparative genomic feature summary.

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