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RESEARCH

The spatial genetic structure and diversity of cedar (*Cedrus* sp.) from Türkiye and Cyprus: evidence from nSSRs

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Abstract

Lebanon cedar (*Cedrus libani*) is a keystone conifer of eastern Mediterranean mountains, and an important species for forest conservation and restoration. However, range-wide patterns of population structure in *C. libani* remain poorly resolved, limiting evidence-based management and conservation efforts. In this study, we investigate the genetic structure and diversity of *C. libani* across its main distribution range of Anatolia and its closely related taxon, *C. brevifolia* (Cyprus cedar). Using 15 nuclear microsatellite markers (nSSRs), we analyzed seed lots from 14 stands across Türkiye and trees from one natural population of *C. brevifolia* in Cyprus. Our results reveal a significant genetic differentiation between *C. brevifolia* and *C. libani* (pairwise FST 0.063 to 0.114), as well as high genetic diversity within both taxa (mean expected heterozygosity $H_E \approx 0.507$; mean allelic richness Ar = 6.97). STRUCTURE analyses identified K = 3 as the primary level of population subdivision, separating *C. brevifolia* from *C. libani* and revealing a clear east–west separation within Anatolian *C. libani*. Subsequent hierarchical analyses resolved five genetically distinct clusters of *C. libani*, corresponding to major geographic regions of the Taurus Mountains (Antalya, Isparta, Konya, Mersin, and Kahramanmaraş). These clusters reflect pronounced spatial structuring and region-specific genetic diversity potentially influenced by macro-scale tectonic and climatic barriers. This study provides a comprehensive assessment of the spatial genetic structure of *C. libani* in Anatolia offering valuable insights for sustainable forest management and gene conservation.

Keywords *Cedrus libani* · *Cedrus brevifolia* · Population genetic structure · Genetic diversity · Nuclear microsatellites · Conservation · Genetic resources

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Introduction

For millennia, the timber of Eastern Mediterranean cedars furnished the great constructions of the ancient Near East — from Egyptian temple reliefs showing cedars felled for pharaohs to biblical accounts of cedars exported for Solomon's palace and temple (Liphschitz and Biger 1992; Alptekin et al. 1997; Hepper 2001; Rich 2013). This long history of human use not only underscores the cultural value of cedar wood, but also highlights the historical decline of cedar forests emphasizing the urgency of understanding the genetic legacy of today's populations.

Cedrus libani A.Rich., the Lebanon cedar, is a long-lived, wind-pollinated conifer of major ecological, cultural, and economic importance across the eastern Mediterranean. Together with *C. atlantica* (Endl.) Manetti ex Carrière, *C. deodara* (Roxb. ex D.Don) G.Don and *C. brevifolia* (Hook. f.) A. Henry, it forms the genus *Cedrus* (Vidaković 1991). Historically widespread across present-day Lebanon, Syria and southern Türkiye, *C. libani* now persists mainly in montane refugia of the Taurus Mountains (OGM, 2024), where rugged terrain has contributed to the preservation of a substantial portion of the species' genetic reservoir (Boydak 2003; Kavgacı and Čarni 2012). These forests face long-standing and ongoing pressures from exploitation dating back to the time of the Pharaohs, land-use change, and habitat fragmentation (Mikesell 1969; Khuri et al. 2000; Jomaa et al. 2008), while climate change increasingly threatens their persistence and functional role in Mediterranean mountain ecosystems (Koc et al. 2022).

Previous genetic studies on *C. libani* and related taxa have documented intraspecific differentiation and adaptive variation (e.g., cold hardiness; Imal et al. 2024) but were often spatially limited or based on low-resolution molecular markers such as isozymes or RAPDs (Panetsos et al. 1992; Bariteau et al. 1999; Piola et al. 1999; Scaltsoyiannes 1999; Bou Dagher Kharrat et al. 2006; Fady et al. 2003, 2008; Kayihan et al. 2006; Kurt et al. 2008; Ayan et al. 2018). Provenance and growth trials in Türkiye (e.g., Gökdemir and Dağdaş 2011) and Europe (Bariteau & Vauthier 2011; Fusaro 2011; Panetsos et al. 2000) further demonstrate the species' high growth performance and drought tolerance, yet also substantial variation among populations. These findings highlight the need for a comprehensive, range-wide assessment of genetic structure and diversity across Anatolia - the core of *C. libani*'s distribution - to inform e.g. seed sourcing, restoration, or assisted migration strategies under changing climatic conditions. This is particularly relevant given the increasing consideration of Lebanon cedar for afforestation and climate-resilient plantings outside its native range in parts of Southern and Central Europe (e.g. Messinger et al. 2015; Kölling 2013).

Nuclear microsatellite (nSSR) markers are well-suited to detect fine-scale population structure and to trace seed sources for restoration and breeding (Hauser et al. 2021). Using a set of 15 microsatellite loci developed for *Cedrus* (Chaib et al. 2006; Eliades et al. 2011; Karam et al. 2015, 2019), we present the first comprehensive, broad-scale Bayesian clustering analysis of the Eastern Mediterranean *Cedrus* complex across Anatolia and Cyprus. Specifically, we aim to:

(i) Assess the genetic differentiation between *C. libani* populations in Türkiye versus *C. brevifolia* in Cyprus,
(ii) Characterize the spatial genetic structure of *C. libani* across its Turkish distribution range, and
(iii) compare genetic diversity within and among the resulting genetic clusters.

This study provides essential insights into the evolutionary history and population structure of eastern Mediterranean cedars, offering a genetic framework to support sustainable forest management, gene conservation, and evidence-based seed sourcing strategies.

Material and methods

Study design and plant material

Our study covers the main distribution range of *C. libani* in Anatolia, including Western Taurus, Central Taurus, and Southeastern Taurus Mountain ranges. Additionally, we include a *C. libani* stand from Afyonkarahisar - Sultandağı (ID EsKar), representing one of the scattered and isolated populations outside of the main range at the transition zone to the Anatolian plateau in the north (Boydak and Çalikoğlu 2008). An overview of the regional distribution of the available and tested seed sources is given in Fig. 1.

Türkiye complies with international seed quality standards, thus, seed imports are regulated and permitted under OECD guidelines on the production of forest reproductive materials. Under this scheme, certified forest reprodutive material (FRM) is marketed in four categories with mandatory documentation (stand name, category, species, region of provenance, altitude, year/lot, and supplier) - whereby *C. libani* propagation material in Türkiye is traded under the categories "selected" and "source identified" (see OECD 2024). This regulatory alignment facilitates the legal transfer and utilization of Turkish *C. libani* reproductive material in European forestry (*Organisation for Economic Co-Operation and Development* 2025). The seed harvest register database of Türkiye lists 21 *Cedrus libani* seed stands of the



Fig. 1 Natural distribution map of Eastern Mediterranean *Cedrus* species (green, EUFORGEN) and sampling units investigated in this study (marked in red) in southern Türkiye (*C. libani*) and Cyprus (*C. brevifolia*) (Caudullo et al. 2017)

category "selected" with a total area of 3,303.5 ha (OGM 2021; Öztürk and Yildiz 2022).

Sampling units were analyzed from seed lots representing 14 Turkish *C. libani* seed stands. These officially designated seed stands represent autochthonous forests within the species' natural distribution range and were sampled through bulked, open-pollinated seed lots. The sampled stands comprised: (i) 10 seed stands classified as "selected" (48% of Turkish cedar seed stands), representing a total stand area of 1,314 ha (40%), and (ii) 4 seed stands classified as "source identified" (OECD 2024). Seed stands classified as "selected" were established between 1971 (MeArs) and 1997 (AnKas), with individual stand areas ranging from 72.2 ha (MeArs) to 298.8 ha (IsBel). Most seed stands in Türkiye consist of pure *C. libani* stands, particularly in the Antalya region, whereas stands in Kahramanmaraş exhibit partial admixture with *Abies cilicica*. Detailed stand information follows the official designations of the Turkish seed stand database (Table 1).

Most seed lots were obtained in the years 2020 and 2024, supplemented by two lots supplied by Kahramanmaraş University (KSU) in 2004, and one lot provided by the Forest Tree and Seeds Improvement Research Directorate (FTSIRD, Ankara) of the Turkish Ministry of Forestry and Environment harvested in 1978 (Table 1). Additionally, three sampling units were supplied as 2-year-old seedlings by "Pelit Tohumculuk Ltd." in 2024. Needles of *C. brevifolia* were collected directly from mature trees in the natural population on Mount Tripylos, Cyprus.

For three seed stands - Konya-Beyşehir (ID KoBey), Konya-Kazancı (ID KoKaz), and Mersin-Arslanköy (ID MeArs) - multiple harvest years (offspring generations) were analyzed, enabling the evaluation of possible temporal genetic variation. Altogether, our dataset comprised 18 different seed lots representing 14 *C. libani* seed stands plus the one natural *C. brevifolia* population, totaling 19 sampling units (Table 1).

DNA extraction and genotyping

Seeds were germinated and seedlings raised at the nursery of the research garden "Knoedelhuette", BOKU University, Vienna. Needle tissue was collected from 30 to 35 randomly selected individuals for each of the 19 different *Cedrus* sampling units, resulting in a total of 635 individuals for processing in the laboratory.

Table 1 Sampling units investigated in this study: Information on the two investigated *Cedrus* species, sampling unit name (ID), their country (ISO 3166-2), province or forest region, forest office/stand name, number of individuals (N), coordinates (longitude, latitude), elevation, harvest year and type of shipment, category of the seed stand

Species	ID	Country	Province /forest region	Forest office - stand name	*N*	Long [°*E*]	Lat [°N]	Elevation [m]	Harvest year, shipment type	Category
C. brevifolia	**CBCyp**	CY	Cyprus	Mt. Tripylos - Pafos Forest	33	32° 41’	34° 59’	1200	2023, A	-
C. libani	**AnElm**	TR	Antalya	Elmalı - Çığlıkara	30	29° 48’	36° 33’	1850	1978, B	TM
C. libani	**AnKas**	TR	Antalya	Kaş - Karacay	25	29° 26’	36° 23’	1550	2021, C	TM
C. libani	**EsKar**	TR	Eskişehir	Afyon/ Karahisar- Sultandağı	25	31° 09’	38° 32’	1400	2019, B	TM
C. libani	**IsBel**	TR	Isparta	Eğirdir- Şarkikaraağaç (Belceğiz)	23	30° 45’	37° 44’	1550	2019, B	TM
C. libani	**IsKiz**	TR	Isparta	Şarkikaraağaç (Kızıldağ)	21	31° 17’	37° 52’	1610	2021, C	TM
C. libani	**IsSen**	TR	Isparta	Isparta - Senirkent	21	30° 42’	38° 05’	1600	2019, B	TM
C. libani	**KaAnd**	TR	Kahramanmaraş	Andırın	22	37° 06’	37° 46’	1500	2004, B	TM
C. libani	**KaGok**	TR	Kahramanmaraş	Göksun	21	36° 25’	38° 03’	1650	2004, B	TTS
C. libani	**KaSuc**	TR	Kahramanmaraş	Onikişubat - Suçatı	20	36° 35’	37° 33’	1350	2019, B	TTS
C. libani	**KoBey1**	TR	Konya	Beysehir	23	31° 42’	36° 55’	1475	2023, B	TTS
C. libani	**KoBey2**	TR	Konya	Beysehir	20	31° 42’	36° 55’	1475	2021, C	TTS
C. libani	**KoHad**	TR	Konya	Hadim	25	32° 18’	37° 02’	1436	2023, B	TTS
C. libani	**KoKaz1**	TR	Konya	Ermenek - Kazancı	23	32° 46’	36° 31’	1750	2019, B	TM
C. libani	**KoKaz2**	TR	Konya	Ermenek - Kazancı	23	32° 46’	36° 31’	1750	2023, B	TM
C. libani	**KoKaz3**	TR	Konya	Ermenek - Kazancı	25	32° 46’	36° 31’	1750	2021, C	TM
C. libani	**MeArs1**	TR	Mersin	Mersin - Arslanköy (618 Herzog)	22	34° 14’	37° 00’	1800	2022, B	TM
C. libani	**MeArs2**	TR	Mersin	Mersin - Arslanköy	23	34° 14’	37° 00’	1800	2023, B	TM
C. libani	**MeKoz**	TR	Mersin	Bozyazi - Kozağacı	19	32° 58’	36° 19’	1350	2019, B	TM

Shipment type: A, DNA samples; B, seeds; C, seedlings aged 2 years. Category: TM, selected; TTS, source identified

A total of 19 sampling units were analyzed, including 14 *C. libani* seed stands from Anatolia/Türkiye, with the stands KoBey, KoKaz, and MeArs represented by multiple seed lots collected in different years (KoBey1–2, KoKaz1–3, MeArs1–2), plus one *C. brevifolia* population of from Cyprus

Total genomic DNA was extracted from 12 mg of silica gel dried needles using a commercial kit (DNeasy 96 Plant Kit, Qiagen, Germany), following the manufacturer’s protocol. We amplified 15 nuclear microsatellite markers by means of PCR (polymerase chain reactions) in three multiplex reactions using three reference samples in each run. We modified the marker set established by Karam et al. (2015, 2019), and Chaib et al. (2006), combining 15 microsatellite markers into three multiplex group combinations (for details see Suppl. Table S1):

(i) A (CatITgD4, CatXITcD12, GN-18, GN-24, CaTssr_41),
(ii) B (GN-16, GN-02, DWOTR_A, GN-19, CaTssr_175, CaTssr_171, CaTssr_31), and
(iii) C (EQJYX_A, CatXIITcC6, CatXIIITcA3).

PCRs were performed in the three different multiplex combinations using the Multiplex PCR Kit (QIAGEN, Germany). Therefore, the protocol from Karam et al. (2019) was adapted as follows: a reaction volume of 10 µl, consisting of 5 µl of 2× QIAGEN Multiplex PCR Master Mix, 3 µl of RNase-free water, 1 µl of DNA (1 to 10 ng DNA), and 2 µM of each primer. Forward primers were labeled with fluorescent dyes 6-FAM (blue), HEX (green), or Atto 550/565 (yellow) (biomers.net GmbH, Germany) (for details see Suppl. Table S1).

The PCRs were carried out in a Mastercycler X50s® thermocycler (Eppendorf, Germany). The thermal profile for multiplex A and B included an initial step at 95 °C for 5 min, followed by 35 cycles at 95 °C for 30 s, 57 °C for 90 s, and 72 °C for 30 s, with a final 30-min extension step at 60 °C. For locus EQJYX_A, a single PCR was conducted in separate tubes under identical conditions, except for an adjusted annealing temperature of 58.1 °C instead of 57 °C. The resulting PCR products were subsequently added to multiplex C for capillary electrophoresis. In multiplex C (including locus EQJYX_A), a Touch-Down PCR protocol was employed, with an initial denaturation step of 5 min at 95 °C, followed by 10 cycles consisting of 30 s at 95 °C, 60 s with the annealing temperature decreasing from 60 °C to 51 °C in 1 °C increments per cycle, and 30 s at 72 °C. The process continued with 30 additional cycles of 30 s at

95 °C, 60 s at 51 °C, and 30 s at 72 °C, concluding with a final extension step of 30 min at 60 °C.

The PCR products were analyzed with the SeqStudio™ Genetic Analyzer (Applied Biosystems, USA) via capillary electrophoresis using the GeneScan™ 500 ROX™ (Applied Biosystems, UK) Size Standard. Fragment sizes and allele calls were determined using GeneMapper software (version 6.0, Applied Biosystems, USA). Each plate included three reference individuals to serve as a standard.

Relatedness assessment using COLONY

We started our analysis by evaluating the familial relationships within each of our 19 *Cedrus* sampling units. This step aims to detect and account for potential genetic relatedness, minimizing its impact on subsequent analyses to ensure robust and unbiased results (for discussion see Anderson and Dunham 2008). The software COLONY (version 2.0.7.1, Jones and Wang 2010) was applied to determine the kinship inference which defines possible relationships between genetic samples. For individuals identified as full-sibs or selfed offspring with posterior probability ≥ 0.8 (i.e., same mother tree), we formed sibship groups. In cases where only a pair was detected, one individual was removed at random; when larger sibships were detected, we retained one individual at random and excluded the others from the dataset.

This filtering step prior to population structure analysis is important because close kinship inference within a sampling unit may distort allele frequency estimates and artificially inflate signals in population differentiation. Thus, we followed the recommendations by Wang (2011), who emphasizes that relatedness must be accounted for when working with structured populations. We retained half-sib relationships in the dataset as their influence on allele frequencies and population structure is generally much smaller than that of full-sib sampling. Unlike pairwise comparisons, COLONY employs a full-pedigree likelihood method which considers the likelihood of the entire population structure, thereby enabling the simultaneous inference of parentage and sibship. COLONY predicts the full siblings (full-sibs) without information on parental genotypes (Jones and Wang 2010).

We used COLONY with the full likelihood approach with medium likelihood precision, no prior sibship size, and a medium run length. All individuals were treated as offspring in the analysis as no parentage was assumed. Our analysis assumed both female and male polygamy, included inbreeding, and was applicable to monoecious species.

Population structure

For the population structure analysis, we retained only "unrelated" individuals within each sampling unit. This filtering process produced a dataset including all *C. libani* sampling units along with the *C. brevifolia* population for interspecific analysis. For detection of intraspecific genetic differentiation in *C. libani*, *C. brevifolia* individuals were excluded from the dataset.

We assessed the genetic differentiation by employing the individual-based Bayesian genetic assignment approach implemented in STRUCTURE 2.3.4. (Pritchard et al. 2000, 2010). The approach infers population structure and identifies genetic clusters by optimizing the Hardy-Weinberg and linkage equilibrium within the clusters (Pritchard et al. 2000). For computational efficiency, we performed the analyses in parallel across 40 central processing units (CPUs) using STRAUTO (version 1.0), a Python script developed by Chhatre and Emerson (2017).

We conducted 20 independent runs for each predefined number of assumed genetic populations (K) ranging from 1 to the number of tested populations, applying a burn-in phase of 50,000 iterations followed by 100,000 Markov chain Monte Carlo (MCMC) iterations. The analyses utilize the correlated allele frequencies and the admixture model.

For the interspecific analysis we did not apply any prior. Intraspecific runs were performed by using the "LocPrior" option (population ID as location information), which is recommended when genetic differentiation between populations is low (Hubisz et al. 2009). To aggregate, average and visualize the results for each K, we employed CLUMPAK (Clustering Markov Packager Across K) (Kopelman et al. 2015), which integrates the CLUMPP method (Jakobsson and Rosenberg 2007) to identify different clustering modes and calculate the mean log probability of data along with its standard deviation for each mode within a given K.

The optimal number of K (identified clusters) for each STRUCTURE dataset and model was determined using a combined approach of (a) the method proposed by Puechmaille (2016), implemented in StructureSelector (Li and Liu 2018), and (b) assessment of clustering consistency and biological interpretability, along with corresponding Q-value (estimated membership proportion) distributions using CLUMPAK (for review see Lawson et al. (2018). Notably, we did not employ the Delta K method of Evanno et al. (2005) to determine the optimal K, as studies (e.g., Janes et al. 2017) have shown that this method can underestimate population structure. Furthermore, we followed recommendations to apply hierarchical structuring (Zhang et al. 2022), which allows for a more nuanced exploration of genetic substructure.

Following this, we applied the hierarchical Bayesian clustering approach (Pritchard et al. 2010; Vähä et al. 2007) to further improve the detection of subtle genetic patterns and avoid underestimating population structure. This involved conducting additional STRUCTURE analyses within the clusters identified in the initial analysis, using the same parameter settings to refine cluster resolution (Hintsteiner et al. 2018; Wang 2017). The procedure included three main steps: (i) determining the optimal K-value as described above, (ii) assigning sampling units to K clusters based on a defined Q threshold, and (iii) repeating the analysis within each resulting cluster until no further substructure was detected.

Finally, we refined the graphical representation of STRUCTURE outputs using DISTRUCT (version 1.1) by Rosenberg (2004) for visualization and mapped the results using the open-source software QGIS (version 3.22.5-Białowieża) (QGIS Development Team 2022).

In addition to the Bayesian approach, we used a distance-based method to explore relationships between the two *Cedrus* species and within *C. libani*. Pairwise F_{ST} values were calculated in GenAlEx 6.5 (Peakall and Smouse 2006, 2012) to assess genetic differentiation among sampling units and to generate a principal coordinate analysis (PCoA). Additionally, Nei's (1972) genetic distance matrix was calculated to quantify genetic divergence between sampling units. For graphical representation of the genetic distances, the UPGMA (unweighted pair group method using arithmetic average) clustering algorithm was conducted in R using the *ape* package (Paradis and Schliep 2019).

Genetic diversity

Genetic diversity metrics were assessed for each sampling unit, as well as for clusters identified in the population structure analysis. Metrics calculated in GenAlEx 6.5 (Peakall and Smouse 2006, 2012) include the number of effective alleles (N_e), number of private alleles (N_p), observed heterozygosity (H_O), expected heterozygosity (H_E), and inbreeding coefficient (F_{IS}) using Weir and Cockerham's estimate for Wright's F_{IS} (Weir and Cockerham 1984). Allelic richness with rarefaction (Ar) was evaluated as a measure of diversity, accounting for sample size dependence (Petit et al. 1998) using FSTAT (version 2.9.4) (Goudet 2003).

Analysis and results

Population genetic differences between *C. libani* and *C. brevifolia*

We started our analysis by investigating the population structure of *C. libani* and *C. brevifolia* to assess genetic differentiation between the two species. After checking family structures and excluding full-sibship and selfing, 444 individuals remained from the original dataset of 635 representing 15 Cedar stands in 19 sampling units (see Table 1).

Subsequently, we conducted a large-scale STRUCTURE analysis of the Eastern Mediterranean *Cedrus* species using these 444 individuals until species separation was visible.

STRUCTURE runs were consistent up to K = 4 in terms of the mean estimated ln probability of the data (Fig. S2A). We selected K = 3 as the most robust solution for the primary level of structure (Fig. 2A). This decision is supported by the fact that K = 3 is the lowest K at which *C. libani* and *C. brevifolia* are clearly separated while also capturing the strong east–west differentiation within *C. libani*. In contrast, K = 2 fails to separate the two taxa and likely underestimates the genetic structure due to the weak representation of *C. brevifolia* in the sample (Neophytou 2014; Puechmaille 2016). Furthermore, K = 3 yields biologically meaningful clusters, whereas higher K-values mainly subdivide *C. libani* sampling units, suggesting that fine-scale differentiation should be addressed through subsequent hierarchical analyses (Suppl. Fig. S1- S3). The distinctiveness of the Cyprus population (CBCyp), which differed strongly from all Turkish sampling units (Q-value of 0.90), was further confirmed by the PCoA, where CBCyp also formed a separate group apart from Turkish *C. libani* (Fig. 2 and Suppl. Table S2). Furthermore, a separation between East (containing seed stands KoBey, KoHad, KoKaz, MeArs, MeKoz, KaAnd, KaGok, KaSuc) versus West (containing seed stands AnElm, AnKas, IsBel, IsKiz, IsSen) was evident, following a structural border between the regions Isparta and Konya (Fig. 2). Only cedar stand EsKar showed intermediate membership proportions (Suppl. Table S2) and could not be assigned to either the western Cluster 1 (blue) or the eastern Cluster 2 (red). However, based on its geographical location, we assigned it to western Cluster 1 at this level of analysis (Fig. 2).

To further evaluate the separation between *C. libani* and *C. brevifolia* detected at K = 3, we conducted additional interspecific STRUCTURE analyses with reduced datasets, running STRUCTURE with *C. brevifolia* population exclusively with stands from *C. libani* west and east cluster. Both STRUCTURE analyses revealed a split between the two taxa at K = 2 (Suppl. Fig. S4, S5), confirming that the lack of separation at K = 2 in the full dataset was caused by

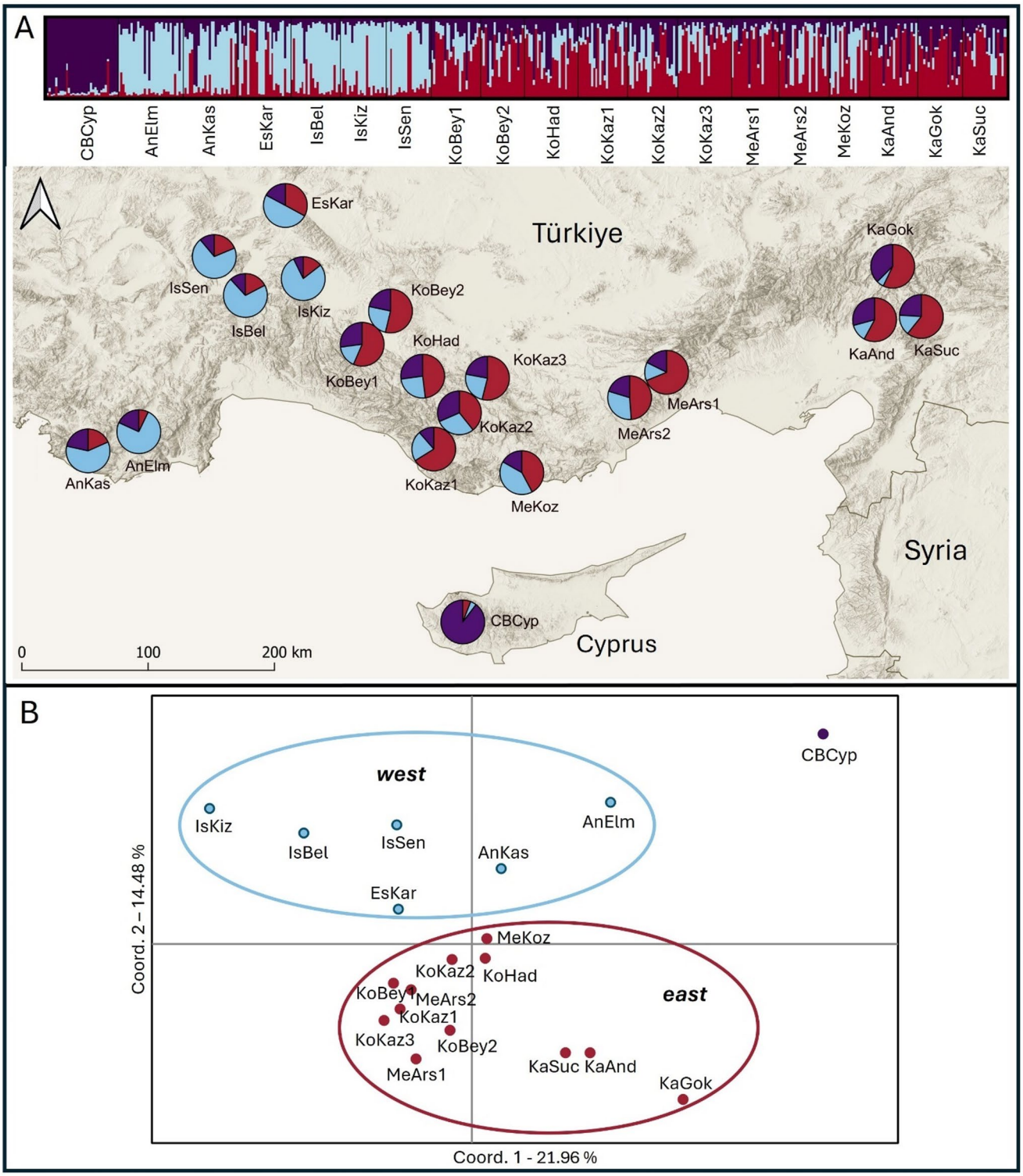


Fig. 2 Graphical display of the large-scale genetic structure of *Cedrus libani* (Türkiye) and *Cedrus brevifolia* (Cyprus) **A** Top: STRUCTURE results at K = 3. Bottom: Results transferred to spatial level according to corresponding coordinates. Each sampling unit is represented by a pie chart, colors indicate membership proportions for each inferred genetic cluster. Significant distinction between Cyprus and Turkish sampling units visible as well as east-west separation within Turkish distribution. **B** Principal Coordinate Analysis (PCoA) showing the genetic distances (F_{ST}, Nei 1972). Circles indicate east (red) and west (blue) separation, with Cyprus distant to both (purple). Groups formed in accordance with STRUCTURE results

underrepresentation of the *C. brevifolia* population rather than an absence of genetic differentiation (Puechmaille 2016). These findings were fully consistent with the PCoA results, which showed the same grouping of sampling units along the first and second coordinates (Fig. 2B). Together, these analyses demonstrate that a genetic distance is evident between *C. libani* and *C. brevifolia*, as well as between the eastern and western clusters of *C. libani*.

Spatial genetic structure of *C. libani* across Anatolia

Building on the primary STRUCTURE analysis (Fig. 2), which identified three main genetic groups (*C. brevifolia*, eastern *C. libani*, and western *C. libani*), we followed the hierarchical clustering approach focusing exclusively on the Turkish *C. libani* sampling units. For this intraspecific analysis, *C. brevifolia* was excluded, resulting in a dataset of 411 individuals from 18 sampling units. The major mode for K = 5 was selected, as it captured the maximum amount of regional structure without conflicting results and was supported by Puechmaille´s (2016) metrics and Q-values > 0,4 (see Fig. 3A, Suppl. Table S5, Fig. S5-S7).

As shown in Fig. 3, five genetic clusters are detectable according to the following geographic regions: (i) Antalya (with seed stands AnElm, AnKas), (ii) Isparta (IsSen, IsBel, IsKiz), (iii) Konya (KoBey, KoHad, KoKaz), (iv) Mersin (MeArs, MeKoz), and (v) Kahramanmaraş (KaSuc, KaAnd, KaGok). For seed stand EsKar in Afyonkarahisar, again, no assignment was possible (Fig. 3A). To further investigate the finer-scale structure, we additionally ran STRUCTURE on two subsets: a western subset containing 6 sampling units (145 individuals) and an eastern subset containing 12 sampling units (266 individuals).

Within the western cluster, Antalya and Isparta split at K = 2 with Q-values exceeding 0.6 (Fig. 3B, Suppl. Fig. S9-S11, Suppl. Table S4A). At this level, EsKar was assigned to the Antalya cluster. Due to the ambiguous assignment of EsKar in the previous STRUCTURE analyses (Figs. 2 and 3A and D), we conducted an additional sublevel analysis excluding EsKar from the western cluster. Without EsKar (AnElm, AnKas, IsBel, IsSen, IsKiz), STRUCTURE revealed an even stronger separation between Antalya and Isparta, with Q-values exceeding 0.75 (Suppl. Table S4B), confirmed by StructureSelector.

Within the eastern cluster, we identified K = 3 as the optimal number of clusters, representing the Konya, Mersin, and Kahramanmaraş regions. This solution maximized regional resolution and produced Q-values above 0.55 for each sampling unit (Fig. 3C, Suppl. Fig. S12-S14, Suppl. Table S5).

For verification, we performed targeted hierarchical analyses on geographically neighboring regions, creating two additional subsets: Konya with Mersin and Mersin with Kahramanmaraş (Suppl. Table S6). In both cases, STRUCTURE again showed strong population assignments, confirming the stability of the five-cluster model.

Fig. 3 Graphical display of the fine-scale genetic structure of cedar sampling units **A-C** Top: Population genetic structure of *Cedrus libani* (Türkiye) based on STRUCTURE results. Bottom: Results transferred to spatial level according to corresponding coordinates. Each sample is represented by a pie chart; colors indicate membership proportions for each inferred genetic cluster. The order of the samples remains the same. **A** K = 5 for Turkish *C. libani* sampling units (EsKar not assigned to a cluster); **B** K = 2 for western *C. libani* sampling units; **C** K = 3 for eastern *C. libani* sampling units. **D** UPGMA dendrogram of *C. libani* (Türkiye) and *C. brevifolia* (Cyprus) sampling units based on genetic distances (Nei 1972)

This genetic structure is further supported by analyses of genetic distance at population level (Fig. 3D). The UPGMA dendrogram identified five distinct clusters within the Turkish population, which is consistent with our previous findings (Figs. 2 and 3). Solely EsKar showed ambiguous results clustering with Mersin sampling units. Note, that the regionally isolated Cyprus cedar population (see Fig. 2A) forms a genetically distinct group vs. the Turkish cedar sampling units from seed stands represented by a single long branch in the dendrogram (Fig. 3D).

The genetic differentiation among the Turkish seed stands within the geographic clusters, assessed using the fixation index F_{ST}, ranged from 0.012 to 0.024 and reached an overall value of 0.043 (Suppl. Table S7). Pairwise F_{ST} values revealed high differentiation between Cyprus and all Turkish seed stands (0.063 to 0.114), with the greatest divergence evident for the Cyprus and the inland seed stands of Isparta (especially IsKiz: 0.114) and Konya (KoKaz: 0.078 to 0.109, KoBey: 0.075 to 0.086), as well as Mersin (0.074 to 0.095; Suppl. Table S8).

Within *C. libani*, the highest differentiation occurred between IsKiz and KaGok (0.101), and generally between IsBel, IsKiz, and the Kahramanmaraş cluster. In Antalya, pairwise F_{ST} values were high between AnElm versus IsBel, IsKiz (0.054 and 0.062, respectively), whereas IsSen showed lower separation from all other sampling units (Suppl. Table S8).

Genetic diversity across and within populations

Genetic diversity metrics provide insights into the distribution and extent of genetic variation within and across populations throughout the species' range. Based on STRUCTURE results, we assessed genetic diversity both at cluster and population levels (Tables 2 and 3).

At large-scale level (411 individuals of *C. libani*, excluding *C. brevifolia*) (Table 2), the western region exhibited higher observed heterozygosity (H_O = 0.503) and less

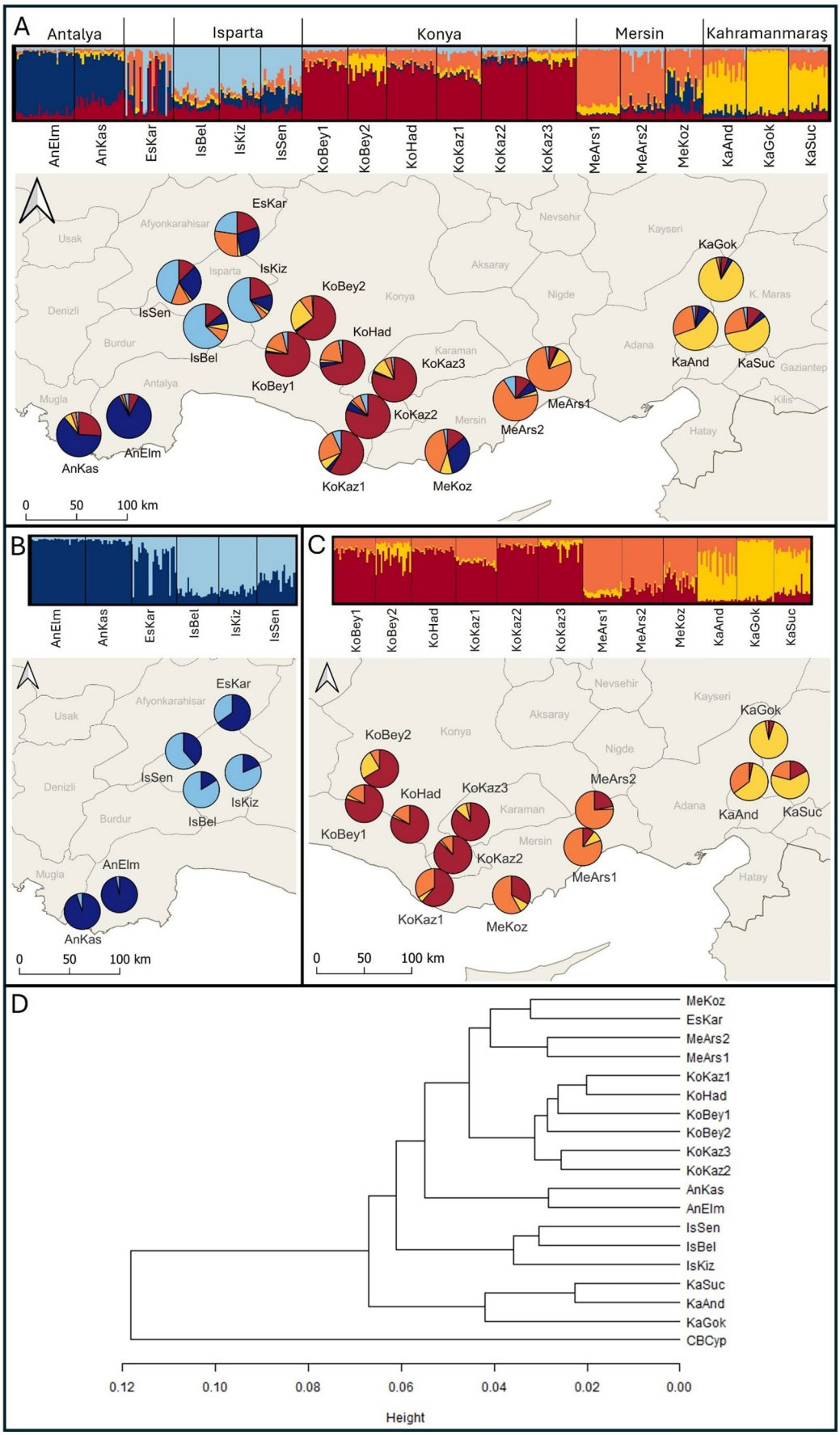

A
Antalya
Isparta
Konya
Mersin
Kahramanmaraş
AnElm
AnKas
EsKar
IsBel
IsKiz
IsSen
KoBey1
KoBey2
KoHad
KoKaz1
KoKaz2
KoKaz3
MeArs1
MeArs2
MeKoz
KaAnd
KaGok
KaSuc
Afyonkarahisar
Usak
Nevsehir
Kayseri
Aksaray
Denizli
Burdur
Karaman
Adana
K. Maras
Gaziantep
Mugla
Kilis
Hatay
0 50 100 km
B
C
D
CBCyp
0.12 0.10 0.08 0.06 0.04 0.02 0.00
Height

Table 2 Genetic diversity metrics of *Cedrus libani* in its Turkish distribution area at 15 microsatellite loci for the western and the eastern range, respectively

Cluster	*N*	N_e	N_p	H_O	H_E	F_{IS}	Ar
West	80	4.050 (0.912)	7	0.503 (0.086)	0.524 (0.091)	0.021 (0.024)	8.70
East	331	4.358 (1.224)	19	0.464 (0.085)	0.514 (0.094)	0.071 (0.025)	9.30

N, number of individuals; N_e, number of effective alleles; N_p, number of private alleles; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient = (He - Ho)/He; Ar, mean allelic richness computed with a rarefaction to sample size of 78 individuals. Values are means, standard errors given in parentheses

Table 3 Genetic diversity metrics at 15 microsatellite loci for each *C. libani* sampling unit and *C. brevifolia* population by sampling unit and cluster range resulting from STRUCTURE

Cluster	Population	*N*	N_e	N_p	H_O	H_E	F_{IS}	Ar
Cyprus	CBCyp	33	3.402 (0.655)	11	0.477 (0.084)	0.511 (0.086)	0.079 (0.062)	5.60
	Overall*	**33**	**3.402 (0.655)**	**11**	**0.477 (0.084)**	**0.511 (0.086)**	**0.079 (0.062)**	**6.08**
Antalya	AnElm	30	3.507 (0.670)	3	0.480 (0.083)	0.511 (0.089)	0.030 (0.030)	5.45
	AnKas	25	3.782 (0.972)	1	0.508 (0.092)	0.497 (0.092)	-0.044 (0.038)	5.92
	Overall	**55**	**3.774 (0.833)**	**4**	**0.493 (0.086)**	**0.512 (0.091)**	**0.009 (0.025)**	**6.21**
Isparta	IsBel	23	3.206 (0.617)	1	0.451 (0.088)	0.466 (0.092)	0.003 (0.030)	5.06
	IsKiz	21	3.147 (0.613)	0	0.432 (0.082)	0.469 (0.090)	0.038 (0.039)	4.79
	IsSen	21	3.362 (0.636)	2	0.453 (0.088)	0.488 (0.092)	0.036 (0.040)	5.23
	Overall	**65**	**3.510 (0.701)**	**3**	**0.445 (0.085)**	**0.486 (0.093)**	**0.040 (0.033)**	**5.56**
Eskisehir	EsKar	25	3.908 (0.825)	0	0.525 (0.088)	0.526 (0.088)	-0.006 (0.030)	5.79
	Overall*	**25**	**3.908 (0.825)**	**0**	**0.525 (0.088)**	**0.526 (0.088)**	**-0.006 (0.030)**	**6.22**
Konya	KoBey1	23	3.586 (0.818)	2	0.515 (0.087)	0.509 (0.085)	-0.034 (0.042)	5.91
	KoBey2	20	3.887 (1.005)	1	0.490 (0.095)	0.488 (0.094)	-0.017 (0.022)	6.12
	KoHad	25	3.599 (0.822)	3	0.469 (0.095)	0.496 (0.091)	0.068 (0.069)	5.70
	KoKaz1	23	3.666 (1.012)	1	0.478 (0.092)	0.482 (0.092)	-0.008 (0.031)	5.64
	KoKaz2	23	3.623 (0.950)	0	0.483 (0.089)	0.495 (0.085)	0.059 (0.052)	6.12
	KoKaz3	25	3.062 (0.599)	0	0.443 (0.085)	0.467 (0.087)	0.045 (0.046)	5.13
	Overall	**139**	**3.972 (1.089)**	**13**	**0.479 (0.088)**	**0.502 (0.090)**	**0.041 (0.029)**	**6.56**
Mersin	MeArs1	22	3.593 (0.735)	1	0.485 (0.083)	0.510 (0.089)	0.013 (0.035)	6.11
	MeArs2	23	3.606 (0.706)	2	0.484 (0.089)	0.500 (0.093)	0.010 (0.024)	6.13
	MeKoz	19	3.535 (0.753)	1	0.491 (0.084)	0.511 (0.088)	-0.001 (0.047)	6.11
	Overall	**64**	**3.856 (0.810)**	**5**	**0.486 (0.084)**	**0.518 (0.092)**	**0.021 (0.029)**	**6.75**
K.Maraş	KaAnd	22	3.872 (0.876)	1	0.402 (0.080)	0.499 (0.094)	0.196 (0.037)	5.78
	KaGok	21	3.122 (0.668)	0	0.420 (0.086)	0.465 (0.090)	0.086 (0.040)	5.14
	KaSuc	20	3.680 (0.871)	0	0.463 (0.094)	0.490 (0.094)	0.058 (0.034)	5.63
	Overall	**63**	**4.001 (1.047)**	**1**	**0.428 (0.085)**	**0.497 (0.095)**	**0.132 (0.030)**	**6.13**
Total		***444***	***3.775 (0.318)***	***37***	***0.476 (0.032)***	***0.507 (0.033)***	***0.044 (0.014)***	***6.97***

N, number of individuals; N_e, number of effective alleles; N_p, number of private alleles; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient = (H_E - H_O)/He; Ar, mean allelic richness computed with a rarefaction to sample size (for sampling units to sample size 18, for clusters to sample size 24). Values are means, standard errors in parentheses. Overall: based on genetic clusters. *Overall values of one sampling unit represent a cluster. Total: mean numbers and standard errors of all sampling units except Ar: weighted Ar over genetic cluster

inbreeding (F_{IS} = 0.021) compared to the eastern region ((H_O = 0.464, F_{IS} = 0.071) while allelic richness is higher in the East (Ar = 9.3 compared to 8.7).

On a smaller scale, we analyzed all 444 individuals from 19 *Cedrus* different sampling units of the Eastern Mediterranean region using 15 SSR markers. In total, we detected 200 different alleles, 189 of them within *C. libani*. Across clusters, the effective number of alleles (N_e) ranged from 3.402 in Cyprus to 4.001 in Kahramanmaraş (Table 3). Observed (H_O) and expected heterozygosity (H_E) were similar across all sampling units, with H_O ranging from 0.428 in Kahramanmaraş to 0.525 in EsKar, and H_E from 0.486 in Isparta to 0.526 in EsKar.

Private alleles (N_p) were most frequent in the Konya cluster (13), likely reflecting its large sample size, followed by the population of *C. brevifolia* in Cyprus (11). EsKar exhibited no private alleles but showed the highest observed and expected heterozygosity (0.525 and 0.526, respectively) as well as the lowest inbreeding (-0.006).

Allelic richness (Ar) was highest in the central regions Mersin (6.75) and Konya (6.56). Conversely, the cluster far east in Kahramanmaraş displayed the lowest heterozygosity

(0.428), highest inbreeding (0.132), and only one private allele. The Isparta cluster showed the lowest overall allelic richness (5.56), associated with a low heterozygosity (0.486), reflected by the metrics of the three single Isparta stands (Table 3).

Overall, genetic diversity patterns at cluster level were mirrored at population level. Sampling unit KaAnd exhibited the lowest H_O (0.402) and highest F_{IS} (0.196) among all sampling units, while all three Kahramanmaraş sampling unit showed relatively low H_O and H_E, along with the strongest loss of heterozygosity (Table 3). The Mersin sampling units (MeArs1, MeArs2, MeKoz) displayed the highest allelic richness (6.11–6.13), reflecting regional richness. The most diverse cluster was Konya, where sampling unit KoKaz2 and KoBey2 showed the highest Ar (both 6.12), while KoKaz3 displayed a low Ar (5.13) and the lowest heterozygosity ($H_O = 0.443$; and $H_E = 0.467$, Table 3).

Comparisons of seed lots (offspring years of identical source) revealed limited variation. The offspring sampling units from Mersin-Aslanköy seed stand (MeArs1 and MeArs2) showed nearly identical diversity metrics. Small differences were evident between KoBey1 (Ar = 5.91) and KoBey2 (Ar = 6.12). The most pronounced variation was found within the different seed lots of KoKaz seed stand, where allelic richness ranged from 5.13 (KoKaz3) to 6.12 (KoKaz2).

The genetic diversity of *C. brevifolia* in Cyprus was within the range of Turkish cedar, with intermediate values of heterozygosity ($H_O = 0.477$; $H_E = 0.511$), moderate allelic richness (Ar = 5.60), and a small heterozygosity deficiency ($F_{IS} = 0.079$) (Table 3).

Discussion

Genetic differentiation within and between *C. libani* versus *C. brevifolia*

Using nuclear microsatellite (nSSR) markers, we detected a clear genetic distinction between *C. libani* seed stands from Türkiye versus the population of *C. brevifolia* from Cyprus (Fig. 2A). Pairwise F_{ST} estimates, STRUCTURE clustering, and PCoA consistently indicated spatial isolation and limited gene flow between the two taxa (Fig. 2, Suppl. Table S8). The sea barrier of 70–100 km between southern Türkiye and Cyprus likely restricts pollen-mediated gene exchange, given that pollen dispersal in cedars is rather limited (e.g. mostly less than 1 km in *Cedrus deodara*, Khanduri and Sharma 2002).

The strong molecular divergence between the two taxa may reflect an "island effect," where long-term geographic isolation, reduced population size, and genetic drift elevate pairwise F_{ST} values. The comparatively high F_{ST} estimates between Cyprus and most Turkish sampling units - often exceeding those among Turkish sampling units themselves - support this interpretation. This is further corroborated by the relatively high number of private alleles in *C. brevifolia*, consistent with expectations for a long-isolated, relict island population.

Previous phylogeographic work of *C. libani* populations has been geographically limited, focusing mainly on subsets of populations in Lebanon and Türkiye (Panetsos et al. 1992; Scaltsoyiannes 1999; Bou Dagher Kharrat et al. 2001; Fady et al. 2008). Our results are broadly consistent with earlier molecular and morphological studies that reported divergence between *C. libani* and *C. brevifolia* (Qiao et al. 2007; Jasinska et al. 2012). However, Karam et al. (2019) found that *C. brevifolia* is genetically closer to Anatolian *C. libani* than to Lebanese and Syrian *C. libani.* Since these studies differ in sampling scope, and our dataset includes no Lebanese or Syrian populations, conclusions regarding interspecific differentiation should be drawn cautiously. The genetic distinction we observe between the *C. brevifolia* population and multiple *C. libani* sampling units (Fig. 1) is likely reinforced by the long-term geographic isolation of Cyprus and associated island effects, including restricted gene flow and genetic drift. Nonetheless, our data do not allow a conclusive distinction between species- versus subspecies-level divergence, nor do they capture the full extent of variation across the entire eastern Mediterranean cedar complex.

From an evolutionary perspective, divergence within the genus *Cedrus* began in the early Eocene, when *C. deodara* separated from the Mediterranean clade, followed by the split of *C. atlantica* from the eastern Mediterranean lineage in the early Miocene (Qiao et al. 2007). The subsequent divergence of *C. libani* and *C. brevifolia* likely coincided with the geological isolation of Cyprus during the Miocene–Pliocene, approximately 6.5–7.8 million years ago (McPhee and van Hinsbergen 2019; Saner 2025), probably driven by long-term geographic isolation and ecological differentiation.

Today, *C. brevifolia* remains restricted to the Troodos Mountains of Cyprus, where it forms small, fragmented stands primarily between 900 and 1,400 m elevation. The species occupies a narrow native range centered around the Tripylos–Cedar Valley area and persists in only a few isolated remnants, resulting in a limited census population size and placing it among the forest taxa of conservation concern on the island (Eliades et al. 2011; Milios et al. 2021). This restricted and fragmented distribution likely amplifies the effects of genetic drift and contributes to the genetic singularity detected in our study. Distinct morphological traits, including shorter, thinner needles and a more

compact growth form may also indicate local adaptation to the dry, rocky environment of the Troodos massif (Ducrey et al. 2008; Jasińska et al. 2012). These characteristics provide essential context for interpreting our findings, which reflect the genetic composition of a key remnant population but may not encompass the full range of variation within the taxon.

Overall, the genetic differentiation observed here indicates that *C. brevifolia* constitutes a distinct evolutionary lineage within the eastern Mediterranean *Cedrus* complex, possibly reflecting island-related demographic processes. From a conservation perspective, this supports its treatment as a separate management and conservation unit, emphasizing the need to preserve its restricted gene pool and ensure species-specific strategies in restoration or breeding programs.

Spatial genetic structure within *C. libani* across its Turkish distribution

Our study covers 14 seed stands distributed across Western Taurus, Central Taurus, and Southeastern Taurus Mountain ranges (Fig. 1). This dataset allows us to assess regional population connectivity patterns and historical divergence with refined resolution.

Our results reveal a pronounced genetic division between western and eastern *C. libani* seed stands, roughly following a geographic line from Antalya to Bucak and Konya (Fig. 3). This pattern coincides with a biogeographic boundary within the Taurus Mountains (Boydak and Çalikoğlu 2008), that separates two major plant community types:

(i) The more humid Abieti–Cedrion forests in the central and eastern Taurus, and
(ii) The drier Lonicero–Cedrion forests in the western Taurus (Boydak 2003; Mayer and Aksoy 1986).

The congruence of genetic and ecological discontinuities indicates that long-term environmental heterogeneity and geological barriers have shaped the spatial genetic structure of *C. libani*. Based on the neutral character of SSR markers, we interpret these correlations with historical demographic processes. The Isparta Angle in the Western Taurus, characterized by Miocene uplift and subsidence (Koçyiğit et al. 2012), likely served as a historical barrier to gene flow, promoting differentiation between western and eastern populations. During the Last Glacial Maximum (LGM) (~22 ka), when cooler and drier conditions limited *C. libani* to glacial refugia within the Taurus Mountains, this divergence may have been further amplified (Atalay 1996; Eastwood et al. 1999; Hajar et al. 2010; Koç et al. 2022). Paleodistribution models and fossil pollen records support this interpretation, indicating long-term persistence within Anatolia and isolation from Levantine populations (Fady et al. 2008; Semaan and Dodd 2008). Such west–east genetic breaks are consistent with phylogeographic patterns observed in other Anatolian taxa, attributed to two corresponding glacial refugia (Bilgin 2011).

Within this broader context, our study revealed a nested hierarchical population structure for 13 of the 14 investigated *C. libani* seed stands. These seed stands grouped into five genetically distinct regional clusters: (i) Antalya, (ii) Isparta, (iii) Konya, (iv) Mersin, and (v) Kahramanmaraş (Fig. 3). Each cluster reflects a unique combination of climatic conditions, topographic isolation, and ecological specificity that has shaped restricted gene flow and may foster local adaptation:

In Antalya, *C. libani* populations are limited to the montane Mediterranean environment such as the Beydağları Massif with rugged, karstic terrain and elevations up to 3,000 m (e.g., Kızlar Sivrisi). These features limit both seed dispersal and pollen flow (Mayer and Sevim 1959; Senitza 1989), possibly contributing to long-term isolation and the unique genetic signature observed in the western cluster (Fig. 3B).

Isparta is located within the geologically complex Isparta Angle and represents a transitional zone between Mediterranean and continental climates (Ayan et al. 2017). Cedar populations here occupy high-altitude, topographically sheltered habitats that are further isolated by surrounding mountain ranges such as the Karakuş Mountains and the Barla Dağı (Atalay et al. 2014).

In Konya, *C. libani* populations cover the southern Central Anatolian Plateau, where the Taurus foothills provide favorable microclimates on calcareous substrates (Boydak and Çalikoğlu 2008; Ayan et al. 2017). This region's continental climate, with low precipitation and significant fluctuations in temperature, combined with natural barriers like Geyik Dağları and Göksu Valley, limits population connectivity and gives rise to a distinct Konya cluster (see Fig. 3C).

The Mersin cedar populations occur at mid to high elevations within the Bolkar and Aladağlar Mountains, experiencing humid Mediterranean conditions. The rugged topography not only isolates Mersin from neighboring regions but also facilitates differentiation within this eastern cluster (Mayer and Sevim 1959). Genetic structuring in this area may reflect both the ancient separation from the western populations, and the more recent fragmentation within the eastern cluster, possibly due to habitat loss and environmental changes.

In Kahramanmaraş, populations are distributed across the Orta Toros Dağları (Middle Taurus) (Kavgacı and Čarni 2012), where Mediterranean and continental climate zones overlap, creating unique humid mountainous climate

conditions. This region features both siliceous and calcareous geological substrates (Atalay et al. 2008), which may drive local ecological adaptations not fully captured by neutral genetic markers.

Overall, these results reveal a nested, hierarchical genetic structure shaped by long-term geological and climatic history and reinforced by contemporary topographic isolation. The identification of five genetically distinct regional clusters provides a reference framework for managing *C. libani* genetic resources. First indications from Turkish provenance trials suggest provenance grouping based on morphology and phenotype (Gökdemir and Dağdaş 2011). Integrating molecular evidence with provenance performance data can strengthen seed zoning and promote the use of locally adapted material in afforestation and conservation programs.

Human influence on the genetic structure of *C. libani*

Although the overall spatial genetic structure of *C. libani* primarily reflects natural historical and environmental processes, localized deviations indicate human-mediated gene flow (Ayan et al. 2017). A notable example is the Eskişehir seed stand (EsKar), which could not be clearly assigned to any of the five regional clusters. Instead, EsKar exhibited genetic admixture from the Antalya, Isparta, Mersin and Konya clusters (Fig. 3A, Suppl. Table S3). Moreover, we note that the UPGMA dendrogram also groups EsKar with sampling units from Mersin region (especially MeKoz, Fig. 3D), which is consistent with the observed admixture. Two complementary mechanisms likely explain this admixed pattern:

i) Historical seed transfer along major trade and transport routes may have facilitated long-distance gene flow. The EsKar region lies at the intersection of ancient communication corridors such as the Phrygian Way and, later, the Ottoman Anatolian Railways (Fidan et al. 2015). Since the Early Bronze Age, these routes facilitated seed and timber exchange across diverse ecological zones, potentially introducing genetic material from geographically distant regions into the EsKar stand (Fig. 3A).
ii) Recent afforestation and anthropogenic admixture associated with 20th-century afforestation programs probably reinforced this genetic mixing. The EsKar stand, located in Afyon-Sultandağı (Table 1), represents a scattered relict population at the edge of the species' natural distribution (Boydak and Çalikoğlu 2008). The surrounding region underwent extensive afforestation programs during the 1960s and 1980s (Ayan et al. 2017; Anonymus 2019), before regional seed transfer zones were established (Atalay 1987; Boydak and Çalikoğlu 2008). Because seed sources were likely drawn from multiple regions, the surrounding plantations may contain mixed genetic backgrounds. Cross-pollination between the relict EsKar population and the surrounding plantations probably generated the admixed genetic structures we observed in the present-day offspring generation (Fig. 3, Suppl. Table S3).

Beyond EsKar, other populations may also have experienced anthropogenic influences. Large parts of the Taurus Mountains have been subject to afforestation programs (Ayan et al. 2017), and in some cases these may have involved the use of mixed or non-local seed sources. Consequently, several authors demand the consistent application of seed zones in ongoing and future reforestation projects (Boydak and Çalikoğlu 2008; Ayan et al. 2017). Old-growth relict cedar stands in Türkiye are currently under strict protection as nature or gene reserves, and some of these also function as designated seed stands. Despite historical exploitation of many old-growth stands until the first half of the 20th century (Senitza 1989; Boydak and Çalikoğlu 2008), we found no evidence of genetic erosion.

Genetic diversity and structure across the Anatolian range

This spatial genetic structure of *C. libani*, shaped by both long-term evolutionary processes and more recent anthropogenic factors, provides an essential framework for understanding patterns of genetic diversity. Maintaining genetic diversity is critical for the species' adaptive capacity and long-term persistence, especially under increasing pressures from climate change and habitat fragmentation (Booy et al. 2000; Reed and Frankham 2003; Ayan et al. 2018). Consistent with earlier studies showing that *C. brevifolia* retains relatively high diversity despite its narrow island range (Eliades et al. 2011), our analyses likewise reveal levels of genetic diversity comparable to those of *C. libani*, suggesting that long-term population stability and effective population size have buffered *C. brevifolia* from severe genetic erosion to date. Our results demonstrate that *C. libani* exhibits high levels of within-population genetic diversity across its Turkish range (Table 3), aligning with previous findings (Bou Dagher Kharrat et al. 2006; Fady et al. 2008; Kurt et al. 2008). Lower diversity estimates reported from RAPD-based studies (Kayihan et al. 2006) likely reflect methodological differences between marker types, as RAPDs capture a more limited and dominant subset of genomic variation. The high genetic diversity observed here emphasizes the ecological importance of *C. libani* both as a keystone species within its natural distribution range (Fig. 1),

and supports its relevance for long-term forest management, restoration and potential assisted migration strategies in Europe.

While overall genetic differentiation among the five clusters Antalya, Isparta, Konya, Mersin, and Kahramanmaraş was moderate (Suppl. Table S7), the spatial distribution of genetic diversity showed geographic patterns. Mersin and Konya seed stands, located near the center of the species' natural range, exhibited the highest allelic richness. In contrast, Kahramanmaraş and Isparta seed stands displayed lower diversity and allelic richness (Table 3), potentially reflecting historical bottlenecks or edge-of-range dynamics (Chhatre and Rajora 2014; Eckert et al. 2008).

Across sampling units, inbreeding levels (F_{IS}) are low (Table 3), consistent with previous observations of extensive outcrossing and long-distance gene flow in wind-pollinated conifers (Slatkin 1987; Hamrick et al. 1992). Strong alpine winds likely enhance pollen-mediated connectivity among nearby populations (Gerber et al. 2003; Kurt et al. 2008), despite existing topographic barriers. However, specific seed stands such as KaAnd showed elevated inbreeding, a significant heterozygosity deficit, and moderate allelic richness (Table 3). This pattern may reflect local isolation, past bottlenecks, or stand structural constraints reducing effective pollen exchange (e.g., reduced canopy accessibility or topographic barriers).

The EsKar seed stand in Afyonkarahisar remains exceptional within our dataset. We could not assign it to any of our five genetic clusters and it shows a high degree of admixture (Fig. 3A). Notably, EsKar exhibited the highest levels of heterozygosity among all sampling units (Table 3) but lacked private alleles, supporting the hypothesis of cross-pollination from adjacent afforestation stands. These plantations were likely established using mixed seed sources - a common practice in large-scale *C. libani* plantations in Türkiye (Ayan et al. 2017). While this suggests that human-mediated seed transfer contributed to EsKar's genetic makeup, further sampling of nearby plantations will be needed to confirm this hypothesis.

Historical seed transfer along major trade routes may have also facilitated admixture in Central Anatolia. Long-standing human connections between Afyonkarahisar and coastal areas such as Antalya and Mersin likely increased gene flow between otherwise distinct ecological regions. While this may enhance the adaptive potential of Lebanon Cedar, it also raises concerns about preserving local genetic integrity. This highlights the importance of careful seed selection for restoration and afforestation initiatives.

Finally, we observed significant interannual variations in genetic diversity in KoKaz offspring sampling units collected across three different years, with heterozygosity and allelic richness fluctuating markedly (Table 3). This pattern likely reflects the species' irregular mast seeding dynamics (Boydak 2003) but may also be influenced by differences in harvest practices, such as the number of parent trees sampled in each collection year. These findings emphasize the need to account for temporal variation of seed lots when evaluating genetic material for seed banks, reforestation or conservation strategies. At the same time, STRUCTURE consistently assigned all offspring sampling units from different years in KoBey, KoKaz, and MeArs to the same genetic clusters, indicating that despite quantitative fluctuations in diversity, the underlying genetic structure of populations remains stable across years. This demonstrates that the applied SSR markers reliably capture the spatial genetic structure and that seed lots from different years can be regarded as replicates.

Overall, we show that *C. libani* maintains high within-population genetic diversity across Anatolia, while the detected spatial structure highlights the importance of region-specific management and conservation strategies. The observed genetic clusters indicate potential gene flow barriers, shaped by different environmental influences. However, our data do not allow us to determine whether the genetic discontinuities among these regions are driven primarily by ecological, historical, or anthropogenic factors.

Our study provides the most extensive coverage of *C. libani* in Türkiye and complements other studies in the Levante that reported lower genetic diversity and additional east–west structuring (Semaan and Dodd 2008), indicating that species-wide patterns extend beyond those seen in Anatolia. In a broader comparative context, studies across the genus suggest that *C. atlantica* tends to exhibit the highest within-population diversity, followed by Turkish *C. libani*, *C. brevifolia*, and *C. deodara* (Bou Dagher Kharrat et al. 2006; Fady et al. 2008; Ginwal et al., 2020; Šeho et al. 2025). However, since these comparisons draw on different marker systems and study designs, they should be considered as indicative. Taken together, our results expand on earlier regional insights and highlight the value of coordinated, cross-regional analyses using harmonized genomic datasets to resolve diversity patterns within the genus.

Conclusions

This study provides the first comprehensive assessment of the genetic structure and diversity of *C. libani* across its Turkish range, complemented by a comparison with the endemic *C. brevifolia* from Cyprus. Nuclear microsatellite data revealed a significant genetic separation between both taxa, contributing additional insight into the unresolved evolutionary relationships within the eastern Mediterranean cedar complex. Because earlier studies used different

marker types, diversity metrics and structure estimates are not directly comparable across the full range of *Cedrus* species. A comprehensive analysis using a common marker set across all taxa (including Lebanese and Syrian populations) would provide the first fully comparable, range-wide assessment of genetic diversity and relationships within the genus *Cedrus*.

Within Anatolia, we identified a pronounced east–west genetic separation and five well-supported regional clusters (Antalya, Isparta, Konya, Mersin, and Kahramanmaraş). These results provide a robust genetic reference framework for defining and revising seed transfer zones, tracing the origin of planted material, and supporting both in situ and ex situ conservation strategies. The observed spatial structure highlights the importance of region-specific seed sourcing to preserve locally adapted gene pools while maintaining natural connectivity. Microsatellite markers proved effective for resolving population structure and verifying the genetic integrity of forest reproductive material across seed lots and years, underscoring their value for genetic monitoring and quality control.

Our findings offer practical guidance for afforestation, restoration, and sustainable forest management of *C. libani*, emphasizing that genetic structure and diversity must be integral to seed sourcing and climate adaptation strategies. Future work combining genetic, ecological, and environmental data will further clarify the processes shaping these spatial patterns and improve predictions of the species' adaptive responses under changing climatic and management conditions.

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Author contributions RK conceived the study and designed it together with CN and SJ. Population sampling was done by RK (C. libani) and CN (C. brevifolia). Supervision of lab works (sample preparation, DNA extraction, sequencing) was done by LG and SJ. LG performed bioinformatic data analyses and results plotting. LG, SJ and RK wrote the first draft of the manuscript, and all authors revised and approved it.

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Data availability The nuclear microsatellite genotyping data supporting the findings of this study are available upon request from the corresponding author.

Declarations

Conflict of interest The authors declare no competing interests.

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