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GENETIC DIVERSITY AND POPULATION STRUCTURE OF THE MOUNTAIN SPECIES *TELEKIA SPECIOSA* (ASTERACEAE) IN THE SE CARPATHIANS

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Abstract: *Telekia speciosa* (Schreb.) Baumg. was selected to investigate the phylogeography of tall-herb species, an ecological group in which the Quaternary history has been rarely studied. This species is a characteristic component of mountain forest communities in the Romanian Carpathian Mountains.

The analysis employing Amplified Fragment Length Polymorphism (AFLP) fingerprinting has revealed a notable absence of a well-defined phylogeographical structure among the populations assessed. This finding implies that the various regions of the current distribution range of *Telekia speciosa* in the SE Carpathians have not undergone extended periods of isolation. Such a pattern suggests that this mountain tall-herb species might have experienced the possibility of long-term persistence along a wide altitudinal gradient in isolated mountain ranges, also encompassing the lowlands between them in glacial periods.

Beside the unique vegetation history experienced during the most recent glaciation in the SE Carpathians, the observed weak phylogeographical structure of *Telekia speciosa* can be reasonably attributed to its inherent biological traits, particularly its proficiency in long-distance dispersal. Additionally, the species' ecological adaptations, which facilitated its survival in riparian zones of relatively low, forested mountain ranges, might contributed further to maintaining genetic connectivity among populations, thereby mitigating substantial genetic differentiation across its distribution.

The study concludes that the genetic variation observed in *T. speciosa* is relatively evenly distributed across the species' distribution area.

Key words: AFLP, Carpathian Mountains, genetic biodiversity, phylogeography, tall-herb, *Telekia speciosa*

Introduction

Among the plant species of Europe, much attention has been focused on high-mountain taxa, which are among the best studied groups in terms of genetic diversity, potential refugia, and ongoing microevolutionary processes [18]. However, within the context of mountain vegetation, few studies have addressed the phylogeography of the species that form subalpine tall-herb communities in Central Europe. These communities, composed of perennial plants requiring moist and fertile habitats, play a crucial role in the ecology and functional diversity of the mountain belt [32]. Moreover, their altitudinal and geographical ranges can be extensive [28].

Telekia is a genus of flowering plants belonging to the family Asteraceae. It comprises robust, branched plants with large leaves, and consists of two species: *Telekia speciosissima* (L.) Less., found in Italy, and *Telekia speciosa* (Schreb.) Baumg., which is widespread in Europe, the Caucasus, and Asia Minor [2].

Telekia speciosa is a summer-flowering species distinguished by its striking yellow flowers arranged in large heads, surrounded at the base by an involucre of overlapping leaflets or bracts. These are leathery at the base, with the tips bent outward. The inflorescence consists of yellow ligulate flowers positioned at the periphery of the disc (female), along with tubular, yellowish-brown flowers found centrally within the disc (bisexual). The capitula are long-pedunculate and further arranged in a sparse corymbose configuration [16]. The flowers are primarily pollinated by insects. The seeds, which are 6 mm achenes, possess a small pappus that facilitates wind dispersal [16]. Besides anemochory, the seeds exhibit anthropochorous traits [37], and they can occasionally be transported downstream by adjacent rivers [G. Coldea, personal observation].

The plant exhibits very large, alternate, ovate-oblong leaves: the lower leaves are petiolate with pointed tips and double-serrate margins, while the upper leaves are sessile, rounded or cordiform at the base, serrate, pubescent on the underside, and glabrous on the upper side. This herbaceous perennial is characterized by a rigid stem that lacks flexibility and is slightly branched towards the top, reaching heights of approximately 2 meters. The vigorous, pubescent stem often displays a reddish-brown coloration [2].

This species is widely distributed along forest edges, among scrub, along river-banks, near springs, and on humid, shady slopes in mountainous regions. Its ecology is closely tied to the *Alnion incanae* alliance [4]. It is especially common in the Carpathian Mountains, occurring in both the South-Eastern Carpathians (SE Carpathians) and the Apuseni Mountains, with a sporadic distribution in Central Europe, Ukraine, the Balkan Mountains, the Caucasus, and Turkey [2].

This study aims to unravel the phylogeographical patterns of *T. speciosa* as a representative tall-herb species. It also seeks to test the hypothesis that ecological features (such as a broad altitudinal range) and biological characteristics (such as the ability to disperse over long distances) mitigate strong genetic differentiation in tall-herb species populations within the Carpathians. To achieve this, the present study utilized Amplified Fragment Length Polymorphism (AFLP) as a molecular method. This technique has proven successful in investigating phylogeny and genetic diversity across various plant species, including tall-herb species [29, 30, 32].

Materials and Methods

Sampling Strategy

To investigate the genetic biodiversity of *T. speciosa*, we sampled 14 populations from the Carpathian Mountains in Romania (see Fig. 1 and Table 1). From each population, young, green leaves were collected from five randomly selected individuals and subsequently stored in silica gel for further analysis.

DNA Isolation

Total DNA was extracted from roughly 13 mg of silica gel-dried leaf tissue, using DNeasy 96 Plant Mini Kit (Qiagen) according to the manufacturer’s protocol, except the final elution which took place in 80 µl in order to increase the DNA concentration.

AFLP Fingerprinting

AFLP analysis was conducted following the protocol established by [36], with minor modifications [33]. Due to the absence of gender-specific primers, a relatively high number of primer combinations were tested (as shown in Table 2).

Table 1: Sampled populations of *Telekia speciosa*: numbering, acronym, geographical origin, coordinates, altitude.

Pop. No.	Pop. code	Location	Geographic coordinates	Altitude(m)
1	F61	Rodnei Mountains, Dealul Ştefăniţei	46°35'42.7194"N 24°25'58"E	931
2	F62	Rodnei Mountains, on a left tributary of Anieșului	47°16'18.1554"N 24°27'41.6154"E	610
3	F64	Giumalău-Rarău Mountains, Rarău Massif on the road connecting Chiril and Pietrele Doamnei	47°14' 43.08"N 25°21'1.08"E	796
4	H63	Călimani Mountains, Gura Haitii, on the Neagra Şarului river	47°6'47.16"N 25°9'7.56"E	1040
5	I65	Ceahlău Massif, from the Fântânele cabin to the Duruitoarea waterfall	45°29'44.8008"N 25°33'54.72"E	1230
6	L66	Nemira Mountains, Apa RoșieValley	47°35'38"N 26°15'31"E	787
7	P65	Ciucaş Mountains, on the right side of the Cheiţa stream	45°27'47.56"N 25°55'52.23"E	851
8	P63	Piatra Craiului Mountains, before Zărneşti Gorge	45°31'40"N 25°17'02"E	905
9	O62	Făgăraş Mountains, Valea Sâmbetei, upstream of Floarea Reginei	45°29'44.8008"N 24°47'28.7988"E	807
10	P61	Făgăraș Mountains, Valea Caprei, upstream of Vidraru	45°24'13.7982"N 24°35'0.2004"E	1046
11	P59	Latoriţa Mountains, Valea Mināileasa, upstream of Voineasa	46°42'36"N 23°52'26.3994"E	966
12	Q56	Retezat Mountains, Gura Zlatna-Gura Apei, Zlatuia Valley	46°16'43"N 22°46'31"E	828
13	K57	Muntele Mare, Valea Ierii	45°23'29"N 23° 14' 41"E	1000
14	J56	Vlădeasa Mountains, Valea Seacă, above the Răchițele Waterfall	46°33'00"N 22°49'55"E	1250

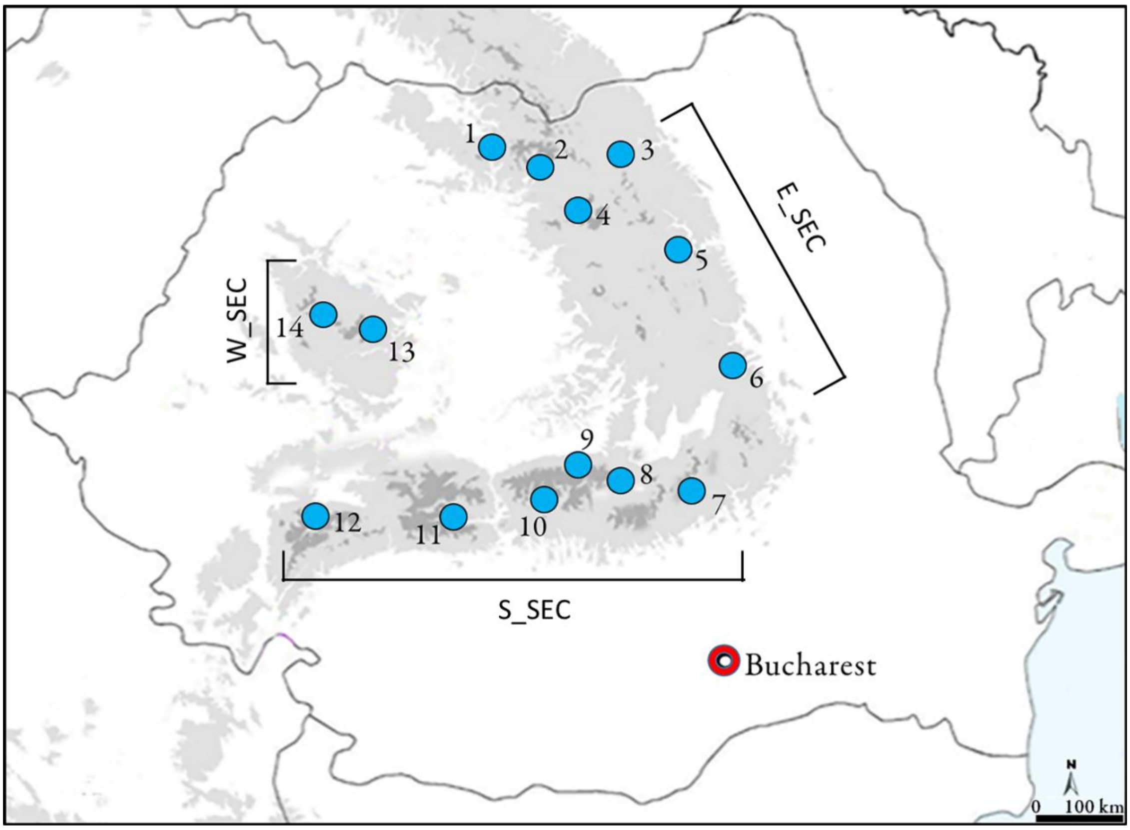

Fig. 1: Location of *Telekia speciosa* populations sampled for molecular analysis. The numbers 1 to 14 correspond to the populations from Table 1. E_SEC: eastern part of the SE Carpathians, S_SEC: southern part of the SE Carpathians, W_SEC: western part of the SE Carpathians.

Table 2: Selective primers evaluated to optimize the AFLP technique for the species *Telekia speciosa*.

No.	Primer combinations tested	No.	Primer combinations tested	No.	Primer combinations tested
1	E-ACA/M-CAA	17	E-ACG/M-CAG	33	E-AGG/M-CAC
2	E-ACA/M-CAC	18	E-ACG/M-CAT	34	E-AGG/M-CTT
3	E-ACA/M-CAG	19	E-ACG/M-CTG	35	E-AAG/M-CTC
4	E-ACA/M-CAT	20	E-ACG/M-CTC	36	E-AAG/M-CAG
5	E-ACA/M-CTT	21	E-ACT/M-CAA	37	E-AAC/M-CAC
6	E-ACA/M-CTA	22	E-ACT/M-CAT	38	E-AAC/M-CTA
7	E-ACA/M-CTG	23	E-ACT/M-CAC	39	E-AGC/M-CAG
8	E-ACC/M-CAA	24	E-ACT/M-CTG	40	E-AGC/M-CAT
9	E-ACC/M-CAC	25	E-ACT/M-CTGA	41	E-AGC/M-CTGA
10	E-ACC/M-CTA	26	E-ACT/M-CAG	42	E-AGC/M-CTT
11	E-ACC/M-CAG	27	E-ACT/M-CTC	43	E-ATC/M-CAG
12	E-ACC/M-CAT	28	E-AGG/M-CAG	44	E-AGA/M-CTG
13	E-ACC/M-CTG	29	E-AGG/M-CTG	45	E-ATG/M-CAG
14	E-ACC/M-CTT	30	E-AGG/M-CAT	46	E-ATG/M-CTC
15	E-ACG/M-CAA	31	E-AGG/M-CTA		
6	E-ACG/M-CAC	32	E-AGG/M-CTC		

Following the tests, out of the 46 primer combinations assessed, the following were identified as providing optimal AFLP profiles: E-ACT/M-CTC [15], E-AAG/M-CAG [12], E-ACA/M-CAA, E-ACA/M-CAC [22], and E-ATG/M-CAG [35].

Reproducibility tests for the AFLP analysis [3] included three random samples from the total sample set, extracted twice as within-plate replicates. The AFLP analysis was performed on all individuals collected from each population.

Data Analysis

AFLP fragments were manually scored within the size range of 50–500 bp using Gene Mapper version 4.0 (Applied Biosystems). The reliability of the data was assessed by comparing duplicates. Only those fragments that could be unambiguously separated were included in the analysis. The distribution of these fragments was encoded into a binary presence/absence matrix. The AFLP error rate was calculated as the number of mismatches (0/1 or 1/0) divided by the total number of matches (0/0 and 1/1) in each pair of replicates [3]. Fragments with mismatches across more than one pair of replicates were excluded from further analysis.

For each population, we estimated the proportion of polymorphic loci, Nei's gene diversity [13], and the frequency down-weighted marker values (DW) [27] using the AFLPdat R-script [6]. We constructed a phylogenetic network using the Neighbor-Joining method based on Nei and Li distance [14], implemented in the SplitsTree version 4.10 software [10]. Bootstrap values were calculated from 1000 replicates.

Additionally, relationships among individuals were analyzed using Principal Coordinate Analysis (PCoA) based on Jaccard index [11], computed with PAST software version 4.13 [9]. A hierarchical analysis of molecular variance (AMOVA) was performed using ARLEQUIN version 3.5 [8], partitioning genetic variance at three different levels: within populations, among populations, and among geographical groups. Genetic distances were also computed in ARLEQUIN version 3.5 as pairwise population F_{ST} values.

Furthermore, we applied a Bayesian inference of population structure to detect genetic groups using STRUCTURE version 2.3.4 software [20] with the "Admixture" model. The Markov Chain Monte Carlo (MCMC) algorithm implemented in the program was used to estimate the optimal number of clusters (K). Parameters were set to include 10,000 burn-in periods followed by 20,000 MCMC simulations, with ten independent runs performed for each K value ranging from 1 to 10. The best K was determined based on the highest value according to the ad hoc criterion and ΔK [7]. The identification of the best K value was facilitated using the online program Structure Harvester [5, 38].

Results and Discussions

Genetic Diversity, Within- and Among-Population

A total of 421 fragments were scored, of which 54.51% were polymorphic across the dataset. The repeatability of the AFLP results was exceptionally high, at 99.56% for the overall test. The fragment lengths ranged from 41 to 452 bp.

The analysis of genetic diversity among the *T. speciosa* populations revealed relatively uniform genetic diversity across all evaluated populations. The values varied within a narrow range. The lowest genetic diversity was observed in the population from the Călimani Mountains (H63, mean 0.1), while the highest genetic diversity was recorded in that from the Rodnei Mountains (F62, mean 0.3). The proportion of variable markers across the 14 populations of *T.*

speciosa studied ranged from a mean value of 0.222 in the population from the Călimani Mountains (H63) to a mean value of 0.611 in that from the Rodnei Mountains (F62).

The highest number of private markers was found in the population from the Rodnei Mountains (F62, mean 3.368), while the lowest number of private markers was recorded in the population from the Ceahlău Mountains (I65, mean 1.815) (Table 3).

Table 3: Genetic parameters in *Telekia speciosa* populations: proportion of variable markers; gene diversity; frequency-down-weighted marker values (DW), mean of the genetic parameters, and standard deviation (SD).

Pop. code	No. of individuals	Proportion of variable markers	Gene diversity	Rarity (DW)
F61	5	0.44	0.209	2.112
F62	5	0.611	0.305	3.368
F64	5	0.4	0.2	2.087
H63	5	0.222	0.100	2.731
I65	5	0.371	0.178	1.815
J56	5	0.331	0.165	2.036
K57	4	0.337	0.187	2.058
L66	5	0.36	0.170	2.034
P59	5	0.491	0.245	3.173
P61	5	0.434	0.211	3.271
P63	5	0.451	0.212	1.965
P65	5	0.577	0.28	3.013
Q56	5	0.52	0.252	2.953
Q62	5	0.52	0.258	2.788
Mean	**-**	***0.433***	***0.2122***	***2.528***
SD	**-**	***0.0565***	***0.0346***	***0.478***

Inference of Genetic Groups and Relationships Among Populations

The Neighbor-net diagram (Fig. 2) of the 14 populations of *T. speciosa* revealed limited structure within the dataset, with bootstrap support for larger groupings falling below 50%. However, individuals formed several clusters, the most distinct of which comprised individuals from the following populations: P61 (Făgăraş Mountains), H53 (Călimani Mountains), J56 (Vlădeasa Mountains), and L66 (Nemira Mountains). Nevertheless, these groupings were not supported by significant bootstrap values. These findings align with the rarity and genetic diversity data presented in the above paragraph, further confirming the lack of strong phylogeographic structuring in the species.

Table 4: Analysis of molecular variance (AMOVA) of *Telekia speciosa* including different hierarchical levels.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	F_{ST}
Among populations	13	551.973	4.83229 Va	20.58	0.20580
Within populations	55	1025.650	18.64818 Vb	79.42	
Total	**68**	**1577.623**	**23.48047**	**100**	

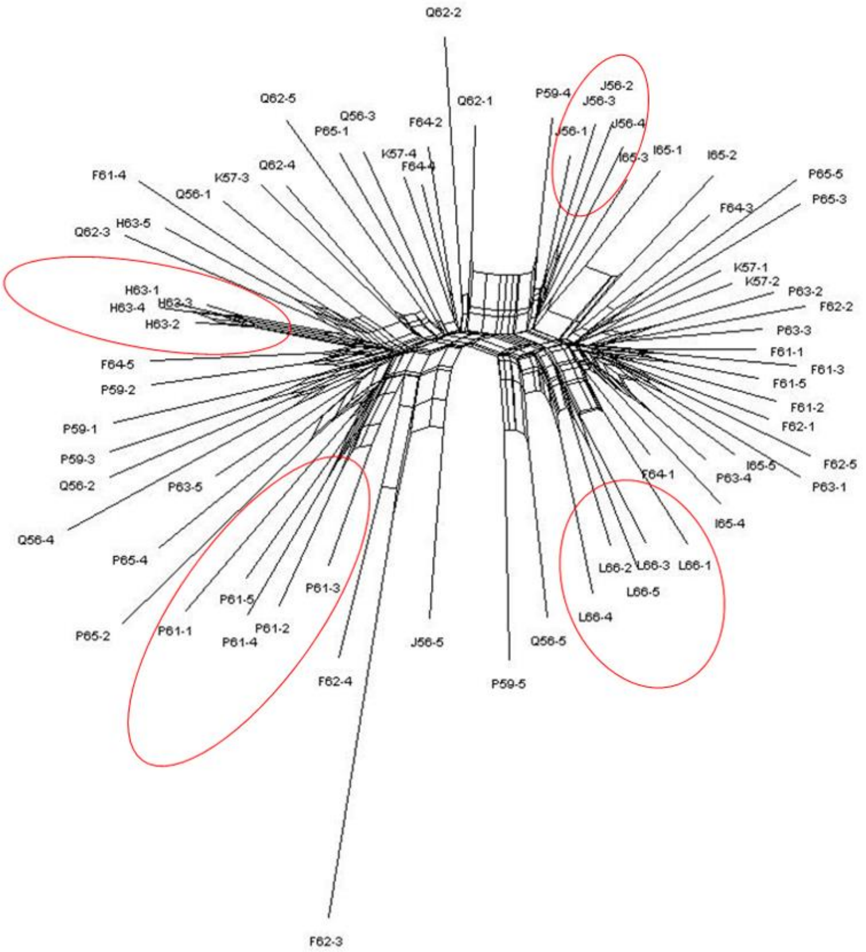

Fig. 2: Neighbor-net diagram of the *Telekia speciosa* populations. Acronym of populations as in Table 1. Bootstrap values for major branches below 50% were not presented.

The analysis of molecular variance (AMOVA) was conducted in two approaches: first, without assigning population groups based on geographical considerations (Table 4), and second, by dividing the Carpathian chain into three distinct regions to create three population groups: the western part of the SE Carpathians (W_SEC), the southern part of the SE Carpathians (S_SEC), and the eastern part of the SE Carpathians – E_SEC (Table 5).

The AMOVA analysis revealed a rather low percentage of variation (20.58%) among *T. speciosa* populations, indicating the presence of weakly supported phylogeographical groupings, consistent with the conclusions drawn from the Neighbor-net diagram. Conversely, the percentage of variation within populations was high, at 79.42%, suggesting a significant degree of diversity inside the *T. speciosa* populations sampled in this study (F_{ST} = 0.20580). All pairwise F_{ST} values were significant ($P < 0.05$) and the mean value amounted to 0.2095.

When applying the division into *a priori*-defined geographical groups (i.e., W_SEC, S_SEC, and E_SEC), 2.59% of the variability was observed between the groups and 18.73% between populations within the groups (F_{ST} = 0.21320). The majority of the variance was attributed to the within-populations component (78.68%), reaffirming the homogeneity and lack of strong differentiation among these Carpathian populations. Genetic variation based on F_{ST} values indicated a modest increase when applying a division into three *a priori*-defined geographical groups versus non-hierarchical AMOVA for all the individuals. Overall, the results of AMOVA indicated a markedly higher proportion of variation within populations than between populations (mean F_{ST} = 0.2095, Table 4 and 5).

The AMOVA results complemented the Neighbor-net analysis, indicating some phylogeographical separations among *T. speciosa* populations. However, these separations are not supported by significant bootstrap values.

Additionally, a PCoA analysis based on the AFLP data for all individuals confirmed the weak structuring of the dataset, showing limited separation based on phylogeographic criteria (Fig. 3).

Table 5: Analysis of molecular variance (AMOVA) of *Telekia speciosa* including different hierarchical levels and geographical groups.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	F_{ST}
Among groups	2	105.165	0.61427 Va	2.59	0.21320
Among populations within groups	11	446.808	4.43899 Vb	18.73	
Within populations	55	1025.650	18.64818 Vc	78.68	
Total	68	1577.623	23.70145	100	

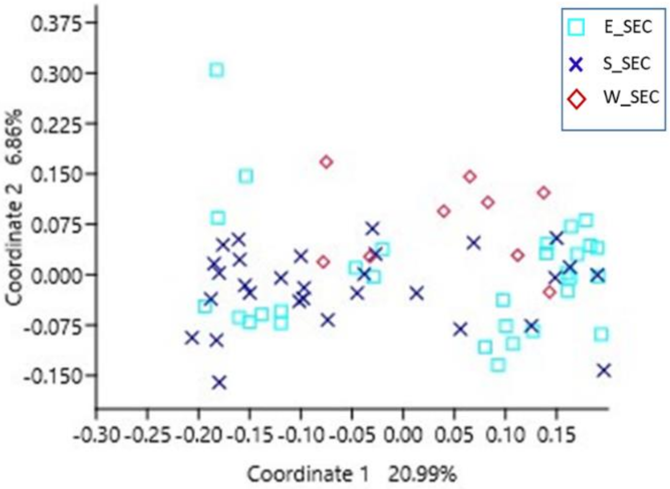

Fig. 3: Principal Coordinate Analysis (PCoA) based on AFLP data of *Telekia speciosa* individuals. E_SEC: eastern part of the SE Carpathians, S_SEC: southern part of the SE Carpathians, W_SEC: western part of the SE Carpathians.

The results of the Bayesian STRUCTURE clustering were consistent with the inferences drawn from clustering and ordination methods (Fig. 4A). The mean L(K) and ΔK values identified K=5 as the most appropriate clustering for the entire dataset (Fig. 4B). This also demonstrated a strong correlation between the clusters and populations computed by

STRUCTURE (Fig. 4A) and the groupings observed in the consensus Neighbor-net diagram (Fig. 2) and the PCoA analysis (Fig. 3).

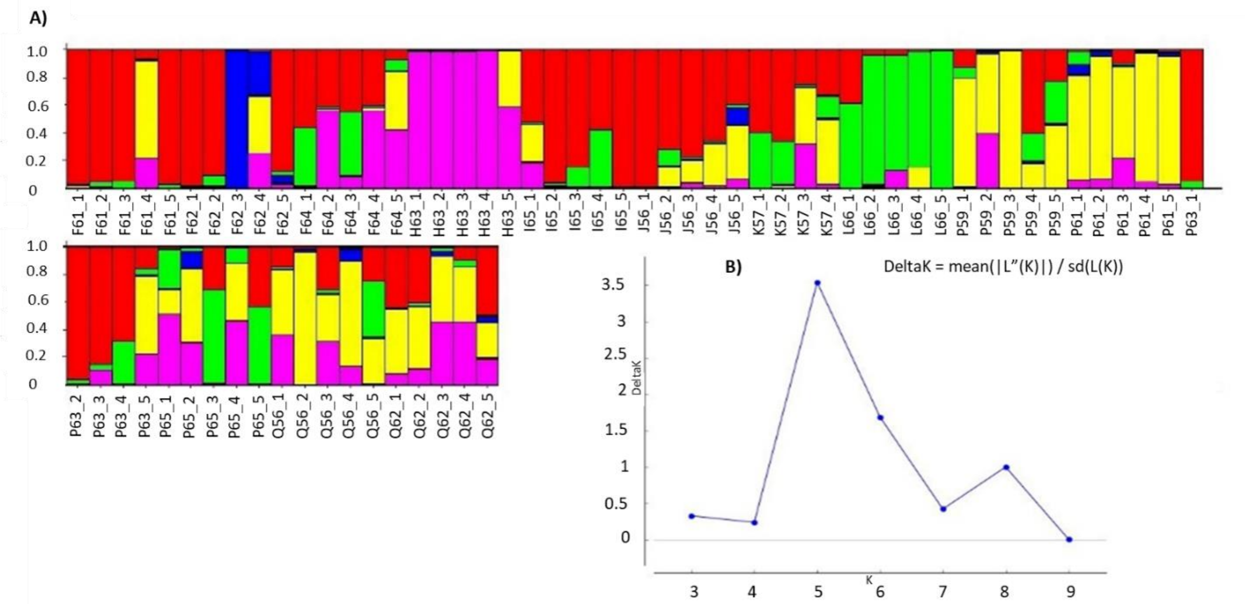

Fig. 4: A) Genetic structure for 14 populations of *Telekia speciosa* inferred by STRUCTURE software B) ΔK generated by STRUCTURE according to [7].

Available studies suggest that the phylogeographical structure of subalpine species across their European distribution is markedly less pronounced than that observed in most alpine species, thus serving as a representative case study for the history of mountain flora characterized by broader elevational amplitudes [31, 32]. The results of the present study align with this hypothesis; notably, they revealed a lack of strong phylogeographical structure in the mountain species, *Telekia speciosa*, an observation that is particularly surprising given the species' current distribution across disjunct areas of the SE Carpathians (Fig. 1).

The striking genetic similarity among both populations and individuals inhabiting the Eastern and Southern Carpathians may be interpreted as indirect evidence supporting a common origin for the populations in these geographical regions and indicating a relatively consistent exchange of genetic material, as no significant geographical barriers exist between the Southern and Eastern Carpathians [29]. Moreover, even the most geographically isolated populations of *T. speciosa* from the Apuseni Mountains (populations no. 13–14 in Fig. 1) exhibited minimal genetic distinctions. For instance, individuals from population K57, sampled from Muntele Mare in Valea Ierii, Apuseni Mountains (no. 13; Table 1 and Fig. 1), are found to intermingle genetically with individuals from populations belonging to the southern and the eastern segments of the SE Carpathians (Fig. 2).

The observed weak geographical genetic structure within the Carpathians (Fig. 2) suggests that the populations constituting the current range of this species have not endured prolonged isolation. This pattern may be elucidated by the distinctive vegetation history during the last glaciation in this region. Unlike the Alps, the Carpathians were not entirely enveloped by glaciers during the Quaternary glaciations; it has been estimated that the snowline during the Würm glaciation was situated at approximately 1,700–1,800 meters in altitude [23]. As the lower massifs and valleys remained unglaciated [19], various groups of plants—including alpine species—might have persisted *in situ* within deep valleys, exhibiting localized vertical shifts rather than extensive migrations across larger regions [32]. Palynological and paleobotanical evidence have indicated that certain tree species, such as spruce (*Picea*) and birch (*Betula*), occupied glacial refugia within the Carpathian valleys [17].

In parallel, other tall-herb species, including *Cicerbita alpina* [29], *Ranunculus platanifolius* [30], and *Doronicum austriacum* [32], have displayed analogous phylogeographical patterns within the SE Carpathians. Similar patterns have also been observed in populations of *Fagus sylvatica* that span a broad altitudinal range in the SE Carpathians [1]. The genetic patterns identified in *T. speciosa* correspond with findings for other high-mountain species within the Carpathians [24, 34], although levels of genetic divergence among *T. speciosa* groups are generally lower than those found in alpine species. Nonetheless, it is noteworthy that low levels of genetic differentiation among populations are documented even in high-alpine plants, such as *Carex curvula* [21]. The lack of genetic structure observed in the anemophilous *Carex curvula* within the SE Carpathians has been attributed to the influence of its biological characteristics, particularly its wind-mediated pollination and dispersal mechanisms [21]. The mode of dispersal likely constitutes a significant driver of the observed genetic patterns, directly impacting genetic variability levels [34]. The discrepancies in genetic patterns observed between two tall-herb species, namely *Campanula alpina* [25, 26] and *Ranunculus platanifolius*, may be attributable to differing dispersal modes (anemochory versus gravity) [30].

Telekia speciosa is characterized as a tall plant primarily pollinated by insects, capable of producing an abundant quantity of lightweight achenes featuring a small pappus that facilitates long-distance dispersal through wind [16]. In addition to anemochory, the species exhibits anthropochorous traits [37], and even occasional downstream transport of seeds by adjacent rivers [G. Coldea, personal observation]. Occasional long-distance dispersal of seeds could have facilitated gene flow between geographically distant regions, contributing to low genetic isolation. The genetic structure revealed for *T. speciosa* is consistent with the presence of local, isolated centres of occurrence for this species in different parts of the Carpathians.

The phylogeographical structure displayed by *T. speciosa* is notably weaker than that of more ecologically constrained plant species, suggesting that this tall-herb species might had the potential for long-term persistence across expansive altitudinal gradients in isolated mountain ranges, including the lowlands that interconnect these ranges during glacial periods [30]. Consequently, the populations of *T. speciosa* may have endured climatic oscillations within their respective regions, with their migrations being more closely aligned with shifting elevations than with extensive movements across the Carpathians.

Conclusions

The main conclusion of this study is that the genetic variation observed in *Telekia speciosa* is relatively evenly distributed throughout its distribution range, with limited discrete population structuring detected within the species.

Authors' Contributions: The contributions of authors to the manuscript are as follows: conceptualization: GC; field work: DȘ, ZRB; analytical investigation: IB, DȘ; data curation: DȘ, IB; formal analysis: DȘ, IB; funding acquisition: DȘ; investigation: DȘ, IB, ZRB; methodology: DȘ, IB; project administration: DȘ; writing - original draft: IB, DȘ; writing - review and editing: DȘ, IB, ZRB, and GC. All authors read and approved the final manuscript.

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DIVERSITATEA GENETICĂ ȘI STRUCTURA POPULAȚIONALĂ A SPECIEI MONTANE *TELEKIA SPECIOSA* (ASTERACEAE) ÎN CARPAȚII DE SE

(Rezumat)

Studiul prezintă o analiză moleculară bazată pe tehnica AFLP cu scopul elucidării filogeografiei speciilor din categoria ierburilor înalte. Obiectul studiului l-a reprezentat specia *Telekia speciosa*, care este o componentă tipică a comunităților ierboase subalpine din munții Europei.

Analizele moleculare au fost conduse în direcţia identificării unui set de markeri AFLP suficient de polimorfi pentru a determina structura populațională a speciei analizate. Ulterior, pe baza datelor AFLP obținute, au fost realizate analize de diversitate genetică intra- și interpopulațională, analiza varianței moleculare (AMOVA), scalare metrică multidimensională (PCOA), precum și analize de structură a populațiilor (STRUCTURE).

Toate analizele efectuate au indicat o structurare filogeografică slabă. Aceasta poate fi datorată faptului că diferitele părți ale ariei de distribuție a speciei nu au fost izolate pentru o perioadă lungă de timp. Potențiale cauze pentru această lipsă de izolare ar fi capacitatea ridicată a speciei de a se dispersa anemocor, precum și particularitățile ecologice ale speciei, acestea permițând supraviețuirea ei în timpul glaciațiunilor Cuaternarului în văi împădurite de-a lungul râurilor din lanțuri muntoase relativ joase.

Concluzia principală a studiului este că variația genetică observată la specia *Telekia speciosa* este distribuită relativ uniform pe toată aria sa de răspândire.

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