

Intra- and Inter-Cultivar Variability of Lavandin (*Lavandula* × *intermedia* Emeric ex Loisel.) Landraces from the Island of Hvar, Croatia

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Abstract: Lavandin (*Lavandula* × *intermedia* Emeric ex Loisel.) was brought to the Island of Hvar (Croatia) in the 1920s, coinciding with the beginning of large-scale cultivation of lavandin in France. Although the cultivation of lavandin and the production of essential oils are of great importance worldwide, the genetic diversity of lavandin has been little studied. We performed an AFLP-based genetic analysis that included the landraces ‘Bila’ and ‘Budrovka’ and two lavandin cultivars from France ‘Grosso’ and ‘Abrialis’, as well as the parental species of the hybrid (*L. angustifolia* and *L. latifolia*). Distance-based cluster analysis revealed the existence of the third landrace, named ‘Budrovka Sveti Nikola’. This result was confirmed by the model-based cluster analyses implemented in STRUCTURE and BAPS, where the optimal number of clusters was three. ‘Budrovka’ clearly separated from all other samples, while ‘Bila’ and ‘Budrovka Sveti Nikola’ showed some degree of admixture, indicating ancestral polyclonality. The landrace ‘Bila’ showed higher polymorphism than ‘Budrovka’ and ‘Budrovka Sveti Nikola’. Analysis of molecular variance (AMOVA) showed that genetic diversity (56.63%) was higher within landraces than among (43.37%). This research will provide a basis for conservation of the Island landraces and will help in the establishment of a high-quality regional brand.

Keywords: AFLP; ‘Budrovka’; ‘Bila’; molecular analysis; traditional cultivars



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1. Introduction

The genus *Lavandula* (lavender; Lamiaceae) includes 39 species and 16 interspecific hybrids that are grouped into three subgenera and eight sections [1–5]. *Lavandula* × *intermedia* Emeric ex Loisel. (lavandin) occurs in the Alps, south-east France, as a spontaneous hybrid of *Lavandula angustifolia* Mill and *Lavandula latifolia* Medic [3]. These two species and their hybrid are the main sources of lavender essential oils in the world [2,6], for which global demand continues to increase [7]. As lavandin is of interest for industrial essential oil production, it is widely cultivated and is the most commonly grown lavender, dominating global lavender oil production [1].

Lavandin was brought into cultivation between 1909 and 1912. Full-scale cultivation of lavandin in southern France began in the 1920s [1]. Interestingly, cultivation of lavandin in Croatia also began in the 1920s on islands Hvar and Vis [8]. Lavandin is an iconic plant species of the Island of Hvar, Croatia, where it has been cultivated for decades and gradually brought prosperity to the Island and it is deeply intertwined into the tradition of the community. Cultivation began in 1926 on the western side of the Island [8,9] and then spread eastward. In 1966, 80 tons of lavender oil were produced on the Island of Hvar, which was 90% of the production in the former Yugoslavia and about 10% of the world

lavender production. The lavandin was exported mainly to Europe: France, Belgium and Germany, and then to the United States, Japan, South America and Africa [10].

On the Island of Hvar, Devetak [9], during his research in 1946–1947, found about 40 hectares under lavandin cultivation, which he called ‘Obična’ (Croat. obično = ordinary), while the growers called it ‘Domaća’ (Croat. domaće = domestic). He found the same lavandin on the Island of Vis as remnants from the cultivation that was abandoned in 1946. The name ‘Domaća’ is still used for this landrace on the eastern side of the Island of Hvar, while in the western part of the Island it is called ‘Bila’ (Croat. dial. bilo = white) and in the centre of the Island it is called ‘Levonda’ (Croat. dial. levonda = lavender). At the meeting of The Working Group of Lavandin Producers on 18 March 2021, the producers decided on a unified name for this cultivar—‘Bila’. During his research in 1947, Devetak [11] found another lavandin on one of the terraces belonging to the Budrović family. He described this lavandin as blue because it had distinctly blue flowers and dark green leaves. This lavandin did not form additional shoots during vegetation and the flower stalks were easily broken. The name for this landrace is ‘Budrovka’ (name derived from the surname Budrović), also called ‘Plava lavanda’ (Croat. plava lavanda = blue lavender), ‘modrulja’ or ‘morulja’ (Croat. modro = (dark) blue) and ‘čorna’ (Croat. dial. čorno = black). Devetak proposed to introduce this lavandin into cultivation, as he found that its essential oil was of better quality than that of ‘Bila’ [8,9,11]. Its wider production started in 1949. At that time on Island of Hvar 96% of the lavandin grown was ‘Bila’ and 4% was ‘Budrovka’ [9]. Nowadays, both landraces are grown on the Island of Hvar. These landraces have been studied morphologically and biochemically in the past [8,9,12].

It is known that landraces are characterized by intrinsic genetic diversity that evolve through the influence of natural selection and producers. This allows landraces to adapt to changing environmental conditions, which is a major problem for agriculture, and justifies their in situ conservation, for which detailed genetic analysis is a prerequisite [13]. Despite the large commercial production and historical value, to our knowledge, no information is available on the genetic diversity of lavandin landraces. Moreover, the genetic diversity of *Lavandula* species and cultivars has been poorly studied despite their importance in global essential oil production except for the evidence that the EST-SSRs developed in the research of Adal et al. [2] can discriminate among cultivars and *Lavandula* species.

We have performed molecular analyses to assess inter- and intra-cultivar variability of lavandin landraces from islands Hvar and Vis, which have been cultivated by farmers for almost a century. We chose molecular AFLP markers because of their high-resolution power [14,15]. The goal of this research was to gain insight into the diversity and genetic structure of *L. × intermedia* landraces, which represent valuable genetic material adapted to specific environmental conditions.

2. Materials and Methods

2.1. Plant Material

A total of 42 samples were included in the study. We collected lavandin landraces on two Croatian islands Hvar and Vis, located in central Dalmatia. Thirteen samples of the lavandin landrace ‘Budrovka’ (S08–S20) we collected at five locations on the Island of Hvar. We collected 22 samples of the lavandin landrace ‘Bila’, 15 from the Island of Hvar (S21–S36, from five locations) and 6 from the Island of Vis (S37–S42, from three locations). Although our primary goal was to analyze lavandin from the Island of Hvar, we included the samples from the Island of Vis to verify that they are the same clonal landrace, because there is a story that lavandin from the Island of Vis was brought to the Island of Hvar. Whenever possible, three samples were taken from the same field. Samples of English (*L. angustifolia*; S01) and broad-leaved lavender (*L. latifolia*; S02) were included in the molecular analysis along with samples of French lavandin (*L. × intermedia*) cultivars ‘Abrialis’ (S03, S04) and ‘Grosso’ (S05–S07). List of samples and collection sites are given in the Table S1.

2.2. AFLP Analysis

Total genomic DNA was extracted from 20 mg of silica gel dried leaves using a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). We performed AFLP analysis according to the method described by Vos et al. [16] with several modifications [17]. Four primer combinations were selected for amplification: FAM-*EcoRI*-ACA + *MseI*-CAC, NED-*EcoRI*-AGA + *MseI*-CAC, VIC-*EcoRI*-ACG + *MseI*-CGA and PET-*EcoRI*-AGC + *MseI*-CGA. The AFLP alleles were detected with an ABI3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA).

2.3. Data Analysis

Amplified fragments (between 50 and 500 bp) were scored for the presence (1) or absence (0) of homologous bands to create binary matrices using GeneMapper 4.0 software (Applied Biosystems, Foster City, CA, USA). Pairwise genetic distances were calculated using Dice's distance coefficient [18], and the cluster analysis was performed by the neighbor-joining (NJ) method as implemented in PAST v. 2.01 [19]. Statistical support of the branches was tested with bootstrap analysis using 10,000 replicates [20].

Molecular diversity of the samples of Croatian *L. × intermedia* landraces was assessed by calculating the percentage of polymorphic loci (%P), the number of private loci (N_{pr}), Shannon's information index (I ; [21,22]) and average Dice's similarity coefficient among samples within landraces (S_{Dice}). To test the significance of the differences in the Shannon's information index (I) and the average Dice's similarity coefficient (S_{Dice}) among 'Budrovka', 'Budrovka Sveti Nikola' and 'Bila', the Kruska-Wallis test (among all landraces) and the Wilcoxon rank sum test (between all possible landrace pairs) were performed using the NPAR1WAY procedure in SAS v. 9.4 (SAS Institute, Cary, USA) [23]. Similarly, the differences in I and S_{Dice} between 'Bila' samples from Island of Hvar and Island of Vis were tested using the Wilcoxon rank sum test.

An analysis of molecular variance (AMOVA) [24] was used to partition the total variance among and within 'Budrovka', 'Budrovka Sveti Nikola' and 'Bila' landraces; and between and within 'Bila' from the Island of Hvar and 'Bila' from the Island of Vis. The variance components were tested using 10,000 permutations in Arlequin v3.5.2.2 [25].

The genetic structure of the samples of Croatian *L. × intermedia* landraces was inferred using Bayesian model-based clustering as implemented in STRUCTURE v. 2.3.4 [26] and BAPS v. 6 [27,28]. In STRUCTURE, a burn-in period of 200,000 followed by 1,000,000 Markov chain Monte Carlo (MCMC) replications was used for clustering under the admixture model and assuming independent allele frequencies for each of 30 runs over the assumed number of clusters ($K = 1$ to 11). The optimal number of clusters was determined using the methods of Evanno et al. [29] and Puechmaille [30] as implemented in Structure Selector [31] which integrates the Clumpak program [32] used to merge data from independent runs. BAPS was run 30 times for each K from one to 10. The results of the mixture analysis served as input for the admixture analysis [33], which was run with default settings.

3. Results and Discussion

Four AFLP primer combinations yielded a total of 378 polymorphic markers in a set of 42 *Lavandula* specimens. Our research started with the assumption that we collected two landraces from the Island of Hvar: 'Bila' and 'Budrovka'. Local lavandin growers helped us to distinguish one from another. Data analyses using the Dice's distance coefficient (Table 1) and the cluster neighbor-joining analysis (Figure 1) showed that we have been dealing with two groups of 'Budrovka'. The group of five specimens (S16–S20) that were collected in the valley below peak Sveti Nikola (Saint Nicholas) separated from the other group collected in the surrounding of Velo Grablje (S13–S15), Zastrazišće (S10–S12), Oštro glovo (S09) and Krušovica (S08). Considering that 'Budrovka' is the name given by Devetak [9,11] to the lavandin found in vicinity of Velo Grablje, we concluded that samples S8–S15 are true 'Budrovka'. To the group S16–S20 we gave the name 'Budrovka Sveti Nikola'. All further analyses we pursued with three landraces; 'Budrovka', 'Budrovka Sveti Nikola' and 'Bila'.

Table 1. Molecular diversity of *Lavandula × intermedia* landraces from islands Hvar and Vis, Croatia.

No.	Landrace	n	%P	N _{pr}	I ^a	S _{Dice}
1	'Budrovka'	8	56.87	21	0.445 ^b	0.855 ^a
2	'Budrovka Sveti Nikola'	5	48.47	1	0.408 ^b	0.818 ^c
3	'Bila'	22	76.34	11	0.547 ^a	0.838 ^b
	P(KW)				***	**
3.1	- 'Bila', Island of Hvar	16	73.28	7	0.513 ^a	0.851 ^a
3.2	- 'Bila', Island of Vis	6	51.15	0	0.419 ^b	0.843 ^a
	P(KW)				*	ns

n—number of samples, %P—percentage of polymorphic loci, N_{pr}—number of private loci, I—Shannon's information index (Different letters in the same column indicate significant differences between values), S_{Dice}—average Dice's similarity coefficient among samples, P(KW)—significance of Kruskal-Wallis test: ^{ns} $p > 0.05$, * $0.05 < p < 0.01$, ** $0.01 < p < 0.001$, *** $p < 0.001$.

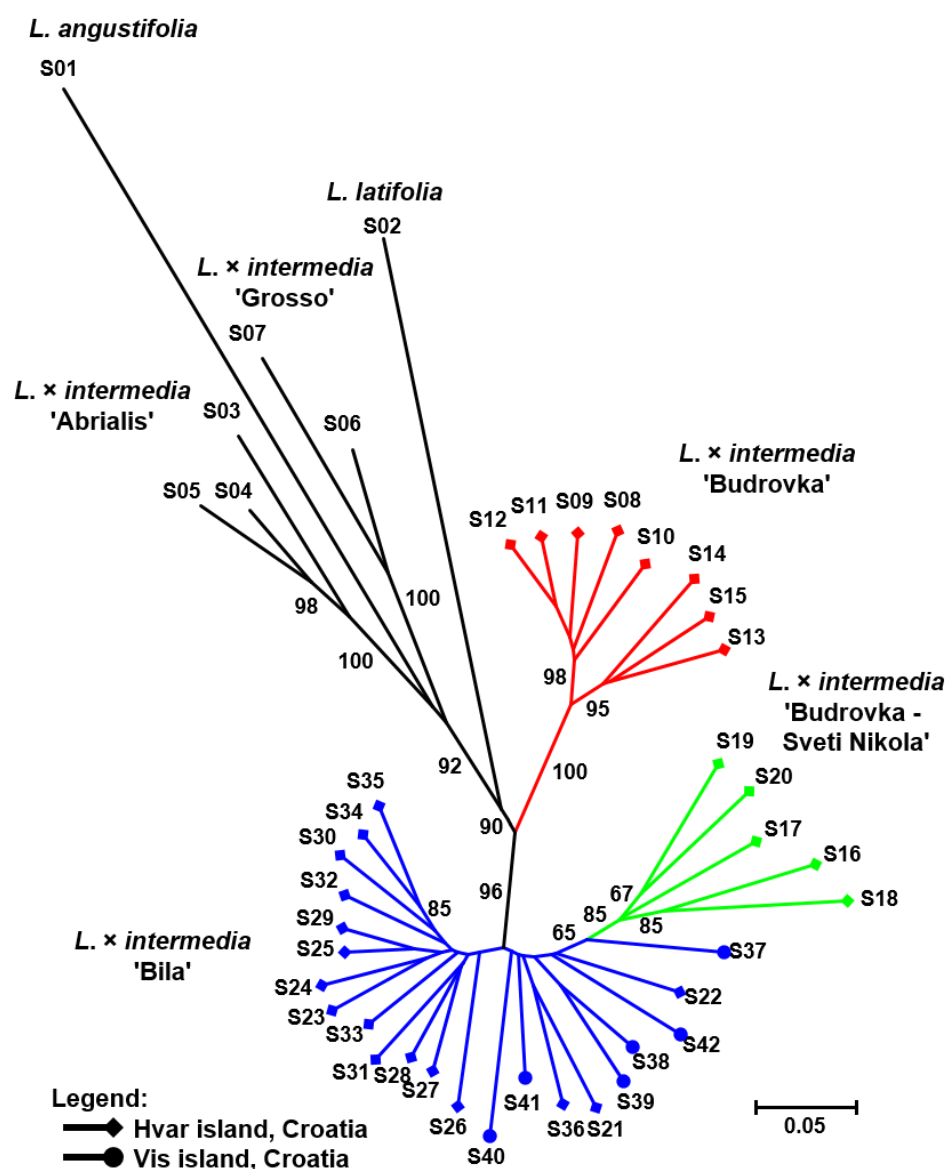


Figure 1. Unrooted neighbor-joining tree based on AFLP marker data of the two *Lavandula × intermedia* landraces from Croatia ('Budrovka', 'Bila'), two *L. × intermedia* cultivars ('Abrialis', 'Grosso') and two progenitor species (*L. angustifolia*, *L. latifolia*). Samples of the landrace 'Budrovka' from Sv. Nikola, Island of Hvar are referred to as 'Budrovka Sveti Nikola'. Bootstrap support values above 50% (1000 replicates) are indicated above the branches.

Table 1 shows the results of the analysis of the molecular diversity of *Lavandula* × *intermedia* landraces from the islands of Hvar and Vis, Croatia. The landraces ‘Budrovka’ and ‘Budrovka Sveti Nikola’ had significantly lower Shannon’s information index than ‘Bila’, while ‘Budrovka’ had significantly higher Dice’s similarity than ‘Budrovka Sveti Nikola’ and ‘Bila’. Farmers started to grow the clone ‘Budrovka’ to a greater extent after the cultivation recommendation of 1949 [8,9], but ‘Bila’ still dominates. ‘Budrovka’ had a much higher number of private loci (21) than ‘Budrovka Sveti Nikola’ (11) and ‘Bila’ (1). This was to be expected, as ‘Budrovka’ is clearly different from ‘Budrovka Sveti Nikola’ and ‘Bila’ (Figure 1), while ‘Budrovka Sveti Nikola’ and ‘Bila’ are genetically much closer to each other. This was also evident from the AMOVA’s pairwise ϕ_{ST} values between the landraces (see below; Table 3).

The landrace ‘Budrovka Sveti Nikola’ showed the lowest polymorphism (48.47%), the lowest Dice’s similarity (0.818) and the lowest genetic diversity ($I = 0.408$). It is genetically close to ‘Bila’ from the Island of Vis (Figure 1, Table 3). This is an interesting case of ancestral polyclonality (Figure 2) and homonymy at the same time. There have been many cases where some European cultivars have been misidentified because they were morphologically similar [34]. In 1910, Dr. Jakov Giakoni brought 10,000 plantlets of *L. angustifolia* from Barrême, Alpes-de-Haute, France, to the Island of Vis. Among them were also some plantlets of *L. × intermedia* [8,9,35]. It is likely that the two landrace clones ‘Bila’ and ‘Budrovka Sveti Nikola’ derived from this set of seedlings originating from a similar set of parents (Figure 2).

The results of the analysis of molecular diversity of ‘Bila’ samples from the Island of Hvar and the Island of Vis showed that ‘Bila’ from Hvar had a higher percentage of polymorphic loci (%P) than ‘Bila’ from Vis. Furthermore, ‘Bila’ from Hvar had seven private alleles, while ‘Bila’ from Vis had none. Genetic diversity, expressed by the Shannon’s information index (I), was significantly higher in ‘Bila’ from Hvar (0.513) than in ‘Bila’ from Vis (0.419), while the difference in the average Dice similarity coefficient (S_{Dice}) was not significant. ‘Bila’ on the Island of Hvar was grown continuously for almost a century, and higher occurrences of somatic mutations could be attributed to the frequent production of new plants, which has resulted in higher values of genetic variation parameters. On the Island of Vis, there was no continuity in the cultivation of ‘Bila’, neither high production of lavandin as on the Island of Hvar. It is abandoned now except for a few fields. The lack of propagation may have contributed to the maintaining of low clonal diversity [36]. Similarly, to the landrace ‘Bila’, the intra-cultivar variability and clustering of accessions were also detected in the Portuguese olive cultivar ‘Galega vulgar’ from different regions [37] and in the Italian grapevine cultivar ‘Malvasia nera’ [4].

All three clonal landraces showed a certain degree of intra-clonal polymorphism through AFLP molecular analyses. The intra-cultivar variability of a particular vegetatively propagated landrace depends on many different factors, including a number of historical events [37]. Somatic mutations could be an important source of genetic variation in clonally propagated plants [38]. Intra-cultivar variability has been demonstrated in many different clonally propagated species: olive [36,37,39,40], grapevine [4,14,41], agave [42,43] and pineapple [44].

The parental species *L. latifolia* and *L. angustifolia* were separated from the other samples with high bootstrap value, with *L. latifolia* being closer to explored landraces (Figure 1). Hind et al. [5] using DNA barcoding and Adal et al. [2] using EST-SSRs showed closer relationship of *L. × intermedia* with *L. angustifolia*.

Analysis of molecular variance (AMOVA) confirmed the results of the neighbor-joining analysis regarding the relationships between ‘Bila’, ‘Budrovka Sveti Nikola’ and ‘Budrovka’ (Table 3). It showed in Table 2 that genetic diversity (56.63%) was greater within landraces than among landraces (43.37%). The highest ϕ_{ST} value between each pair of landrace clones (interpreted as the inter-clonal average distance between any two clones) was found between ‘Budrovka’ and ‘Budrovka Sveti Nikola’ ($\phi_{ST} = 0.577$), while the lowest value was found between ‘Budrovka Sveti Nikola’ and ‘Bila’ ($\phi_{ST} = 0.176$) from the island of Vis. The

ϕ_{ST} value between two groups of 'Bila' samples (from islands Hvar and Vis) was the lowest ($\phi_{ST} = 0.145$) (Table 3). All ϕ_{ST} values were highly significant ($p < 0.0001$) (Table 2).

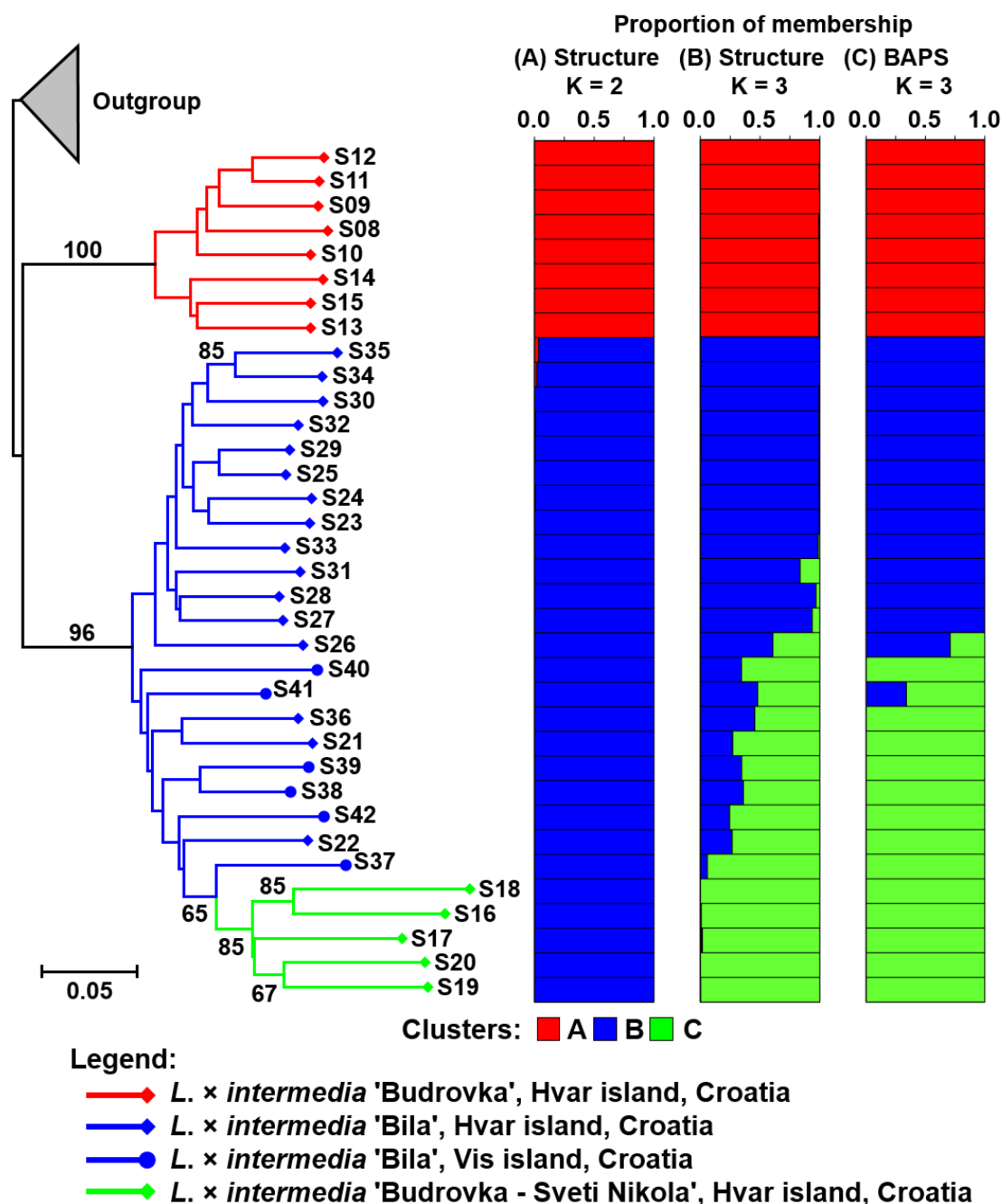


Figure 2. The neighbor-joining tree of the three *Lavandula × intermedia* landraces from Croatia ('Budrovka', 'Budrovka Sveti Nikola', 'Bila') and the proportions of membership in each cluster as obtained by STRUCTURE at K = 2 (A) and K = 3 (B) and BAPS at K = 3 (C). The tree is rooted by two *L. × intermedia* cultivars ('Abrialis', 'Grosso') and two progenitor species (*L. angustifolia*, *L. latifolia*).

Table 2. The results of AMOVA analysis of Croatian *Lavandula* × *intermedia* landraces: the partition of the total molecular diversity (A) among and within ‘Budrovka’, ‘Budrovka Sveti Nikola’ and ‘Bila’, and (B) between and within ‘Bila’ from the Island of Hvar and ‘Bila’ from the Island of Vis.

Analysis	Source of Variation	df	Variance Components	% Total Variation	ϕ_{ST}	$P(\phi_{ST})$
(A)	Among landraces	2	25.44	43.37	0.434	<0.0001
	Within landraces	32	33.27	56.63		
(B)	Between islands	1	5.44	14.50	0.145	0.0004
	Within islands	20	32.08	85.50		

Table 3. AMOVA’s pairwise ϕ_{ST} values among Croatian *Lavandula* × *intermedia* landraces.

No.	Landrace	Landrace			
		1	2	3.1	3.2
1	‘Budrovka’		***	***	***
2	‘Budrovka Sveti Nikola’	0.577		***	**
3.1	‘Bila’, Island of Hvar	0.480	0.337		***
3.2	‘Bila’, Island of Vis	0.531	0.176	0.145	

Below diagonal: pairwise ϕ_{ST} values; above diagonal: $P(\phi_{ST})$ values; significance level: ** significant at $p < 0.01$, *** significant at $p < 0.001$.

When the value of ΔK was calculated using STRUCTURE according to the method of Evanno et al. [28] the optimal solution was $K = 2$ ($\Delta K = 1054.01$), followed by $K = 3$ ($\Delta K = 611.65$) (Figure S1). In agreement with the results of distance-based clustering (Figure 1), cluster A at $K = 2$ consisted of ‘Budrovka’ samples, while cluster B contained the rest of the samples, including both ‘Budrovka Sveti Nikola’ and ‘Bila’ samples (Figure 2). At $K = 3$, all samples of ‘Budrovka Sveti Nikola’ were assigned to the newly formed cluster C ($Q = 75\%$), together with all samples of ‘Bila’ from the Island of Vis, but also with three samples (S21, S22, S36; Figure 2) from the Island of Hvar, while cluster B contained the rest of ‘Bila’ samples from the Island of Hvar. However, the Q-values (proportion of cluster membership) of all ‘Bila’ samples assigned to cluster C were lower than 75% indicating a high admixture level [45], with the exception of samples S37 (Čojno poje, Island of Vis) and S42 (Vela gomila, Island of Vis). Moreover, by calculating a set of parameters (MedMedK, MedMeaK, MaxMedK and MaxMeaK) proposed by Puechmaille [29] the optimal number of clusters was clearly set to three (Figure S2). Similarly, the genetic structure characterized by BAPS revealed $K = 3$ as the best partition (Figure 2) with a probability of 100% and a log marginal likelihood of -4346.33 . The cluster composition in BAPS was identical to that of STRUCTURE, while the Q-values of all ‘Bila’ samples assigned to cluster C were higher than 75%, except for S41 (Podšpilje, Island of Vis), the only sample with admixed ancestry.

The Neighbor-Joining tree, STRUCTURE and BAPS (Figures 1 and 2) placed together samples of ‘Bila’ from Island of Hvar (S21, S22 and S36) with ‘Bila’ from Island of Vis. The samples S21 and S22 (Krušvica) we collected from old bushes that remained of an old plantation. Presumably that is the reason they are more similar to those for which we assume were original clones. We collected sample S36 together with samples S34 and S35 from the Zastržišće plantation on the Island of Hvar. This plantation was established in 1960s from the plantlets from Velo Grablje that obviously did not have the same clonal source.

This study provides insight into intra- and inter-cultivar variability of lavandin landraces from the islands of Hvar and Vis that could serve as a motivation for further molecular studies of this economically important species. Reliable and accurate genetic identification will provide a solid basis for the implementation of conservation measures for the landraces, which is a great challenge for the future. The study also paves the way for the establishment of a high-quality regional brand that should go beyond local importance. As a further step, the studies of the essential oil chemical profiles of lavandin landraces are crucial.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy12081864/s1>, Figure S1. Determination of the optimal number of clusters based on the results of STRUCTURE using ΔK [29]. Figure S2. Determination of the optimal number of clusters based on the results of STRUCTURE using MedMedK, MedMeaK, MaxMedK and MaxMeaK [30]. Table S1. *Lavandula* samples and collecting sites.

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Data Availability Statement: Data supporting reported results are available from the corresponding author on reasonable request.

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