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Characterization of soils on consolidated limestone and its relations to grassland vegetation

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Abstract: Understanding the relations between soil features and plant responses is important for agricultural production and nature conservation. The aim of this study was to investigate the importance of the influence of soils' physical and chemical features on the composition of plant species and richness in grasslands studied on the limestone massif in eastern Serbia (Mt. Rtanj). The data set included 22 phytosociological relevés, the same number of corresponding mixed soil samples (0-10 cm depth) and 8 soil profiles. Two vegetation types were distinguished by numerical classification as *Saturejion montanae* and *Festucion valesiacae*. The results of detrended correspondence analysis (DCA) indicated that the most important soil parameters affecting species composition in dry grasslands were humus, the content of calcium, soil exchange capacity and base saturation, in addition to total acidity, pH and soil depth. The communities of both vegetation types are developed on Leptosols and Phaeozems. Under similar physical and chemical conditions of the soil, the grassland vegetation exhibits differences in floristic composition.

Keywords: Leptosol; Phaeozem; *Saturejion montanae*; *Festucion valesiacae*; DCA

INTRODUCTION

Soil is the crucial and most complex part of the ecosystem, playing important roles in sustained food and wood production, flood and erosion regulation, improvement of air and water quality and encouraging biodiversity [1]. As a natural body, soil influences all aspects of the ecosystem in combination with other environmental conditions such as climate, geomorphology, geology, flora and fauna, and human impacts.

Among many soil forming factors, vegetation is one of high importance. The physical, chemical and biological properties of soil depend on the influence of plants covering the soil and vice versa [2]. The aboveground cover is a key factor in preventing soil erosion and creating a microclimate that further influences soil microbial activity and subsequent soil fertility, affecting plant growth [3]. Plant roots have a complex impact on the physical, chemical and biological properties of soil. The underground plant layer influences soil structure and porosity by improving the soil water and air regime. Roots uptake water and nutrients from the soil and in return excrete exudates into the rhizosphere, increasing microbial enzymatic activities [4,5].

Soil characteristics determine the type and features of plant cover, including the composition of dominant species and overall floristic diversity. Soil texture, structure, moisture, pH, soil organic matter (SOM) and nutrients are the most investigated and influential soil parameters. In addition, different management practices (grazing, mowing) and land-use intensity also affect vegetation characteristics [6], which primarily refer to the occurrence and typology of different types of grassland vegetation.

Complex soil-grassland relations have been studied from different aspects [7-9]. The data on the

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influences of the main soil properties on the development of different grassland communities in the central Balkan region have been reported [10], but in-depth analyses are still missing. Since the literature of vegetation studies rarely addresses the appropriate soil taxonomy [8,10], to better understand their mutual interactions, it was necessary to classify soil types according to the World Reference Base for Soil Resources (WRB) 2015 for soil classification [11]. Although the present research targets a relatively limited area situated in the southeastern Balkans (Mt. Rtanj, eastern Serbia), where all studied sites have the same limestone parent material and the same or very similar climate conditions and narrow altitude range, the observed grassland communities differed in floristic composition. Therefore, the main goal was to identify the soil parameters with the most influence. Our study focuses on soil-grassland relations, including the influences of the main relief factors, the basic physical and chemical properties of the soil and the plant-available macro and microelements. Finally, a comparative analysis was performed between the range of the studied soil and other environmental data and the plant indicator values.

MATERIALS AND METHODS

Study area

The study was conducted on Mt. Rtanj, located in the central part of the Balkan Peninsula. The area belongs to the Carpathian-Balkan Mountain system that spreads from Romania towards eastern Serbia (Supplementary Fig. S1A). Mt. Rtanj is very distinct from other elements of the Carpathian-Balkan Mountain range due to its specific geological and tectonic characteristics. The complex geological composition originates from the Paleozoic, Mesozoic and Cenozoic periods. Compact Mesozoic limestone rocks participate in the formation of the higher horizons and are mostly limited to the peaks of the ridge [12]. The specific conical peak (Šiljak, 1565 m a.s.l.), with a very steep mountain slope inclined at different angles, dominates the entire area. The karst relief includes numerous deep pits and various forms of exhumed subcutaneous karst. The present study includes grasslands (Supplementary Fig. S1B) at an altitude range between 789 m a.s.l. and 996 m a.s.l. distributed on the northern and the southern aspects and on different slopes.

The broader region around Mt. Rtanj, including the surrounding basins and valleys, is characterized by a modified temperate-continental climate, with a pluviometric regime exposed to Mediterranean climatic influence [13]. The annual average temperature and precipitation for the 30-year period are 10.4°C and 659.6 mm, respectively [14]. The soil moisture regime was indirectly assessed based on the climatic data, i.e. the values of precipitation and potential evapotranspiration according to the Soil Survey Staff [15].

The dominant limestone substrate together with a prominent relief had a considerable influence on the composition and distribution of the flora, although the grasslands of Mt. Rtanj were scarcely studied with only a few reports so far [16]. The north-facing slopes are characterized by diverse and relatively well-developed forest vegetation (*Quercetum frainetto-cerridis* and *Abieto-Fagetum*). The wide, heavily eroded areas of the south-facing slopes are covered by dry grasslands and shrub vegetation with a rich and diverse floristic composition.

Mt. Rtanj was proclaimed a Special Nature Reserve in 2019 by the Government of the Republic of Serbia. The grasslands of Mt. Rtanj are still used for grazing, but significant areas have been abandoned due to the depopulation of rural areas in southeastern Serbia, and the Balkans in general [8].

Soil and vegetation sampling and analyses

A total of 22 phytosociological relevés were collected for the purpose of studying the grassland vegetation (Supplementary Fig. S1B). The relevé sampling was carried out according to the modified Braun-Blanquet approach (cover expressed in percentage) [17,18]. We recorded all vascular plants that were present on the 10-m^2 plots, and the percentage cover values were estimated for each individual species. The nomenclature of plant taxa followed the Flora of the Republic of Serbia [19] and Flora Europaea [20]. A mixed soil sample (0-10 cm depth) was collected from five random positions for each vegetation sampling plot. Soil depth was measured at five random points using the soil depth indicator [18], and the slope gradient and the slope aspect were determined by an inclinometer and compass, respectively. GPS data were recorded for each plot. In order to identify and classify the soils of the examined sites, a total of eight representative soil profiles (Supplementary Fig. S1B) were excavated down to the depth of the consolidated rock. The soils were examined according to the FAO Guidelines for Soil Description [21]. Disturbed and undisturbed soil samples of an approximate volume of 100 cm^3 were collected from a genetic horizon. The studied soils were classified according to the international WRB 2015 classification [11].

Immediately after soil sampling, the larger clods were carefully broken up by hand in the laboratory into aggregates of 20-25 mm. After visible plant materials were removed, all soil samples were air-dried, crushed and passed through a 2-mm sieve. Soil properties were investigated using the following methods: the color for dry and moist soil was identified using the Munsell Color Chart [22]; soil texture by combining the sieving and pipette methods, with 0.1 M sodium pyrophosphate as a dispersing agent; the soil textural class according to the USDA triangle; bulk density (BD) by the core method with water retention at -33 and -1500 kPa [23]; the soil organic carbon (SOC) by the dichromate method, and a humus content=SOC × 1.72 [24]; soil pH by the potentiometric method (soil/water 1/2.5) [25]; and the total acidity (H) was determined by Kappen's method using 1 M Na-acetate solution [26]. The soil aggregate stability was evaluated based on the dry mean weight diameter (DMWD) and the wet mean weight diameter (WMWD) [27], while the structural stability index (SI) [28] was calculated to assess the risk of structural degradation. Different extraction procedures were applied to determine the plant-available content of elements [29] as follows: ammonium lactate (AL)-ammonium acetate (AAc) was used for the determination of P; AAc for Mg, Ca, K, Na, while the DTPA (diethylenetriaminepentaacetic acid)-TEA (triethanolamine) solution (buffered at pH 7.3) was used to determine the contents of microelements (Cu, Fe, Mn, Mo, Ni, Zn). The elemental content in fine soil samples subjected to different extraction procedures was determined by inductively coupled plasma optical emission spectroscopy (ICP-OES, Spectro Genesis EOP II Spectro Analytical Instruments GmbH, Kleve, Germany) with the exception of the concentrations of P, which were determined by the colorimetric molybdenum blue method at 580 nm. The cation exchange capacity (CEC) and exchangeable bases (S) were determined by 1 M AAc extraction buffered at pH 7. Base saturation (V) was calculated using S and CEC.

To obtain a better appreciation of the environmental factors that could influence the composition of the floristic community, the mean unweighted ecological indicator values (EIVs) [30] were used for light, continentality, temperature, nutrients, moisture and soil reaction. The calculations were based on the indicator values.

Statistical analysis

The multivariate cluster analysis was used in the PC-ORD 5 software [31] to obtain appropriate clusters of the phytocenological relevés. With the aim of confirming diagnostic grassland species for each cluster, the software JUICE 7.0 was used [32] with the phi coefficient as a measure of fidelity [33]. Species exhibiting phi coefficient values higher than 0.10 were considered diagnostic. Species with a cover >20% found in a minimum of 50% of the total relevés were accepted as dominant in each cluster. Species recorded in a minimum of 50% of the total relevés were considered constant.

To determine the influence of the relief and soil parameters on the species composition of different grassland plant communities, detrended correspondence analysis (DCA) was applied in the JUICE 7.0 program [32], the R-project (http://www.r-project.org), and the vegan package (http://cc.oulu.fi/~jarioksa/softhelp/vegan.html) [34]. Mean unweighted EIVs for light, continentality, temperature, nutrients, moisture and soil reaction were used in DCA with passively projected explanatory variables. Due to the small sample size and because the deviation for most variables did not exhibit a normal distribution, the comparison between relief and soil parameters of the two clusters was conducted by the non-parametric Mann-Whitney U test. The test was carried out by SPSS 21.0 software (IBM, Chicago, USA).

RESULTS

Soil characteristics

According to WRB 2015 [11], all studied soil profiles contained the SOC and mineral material as diagnostic materials, continuous rock as diagnostic properties and mollic as the only diagnostic horizon (Supplementary Table S1). Consequently, six studied soil profiles (1, 2, 3 (Supplementary Fig. S2A), 5, 6 and 8) were classified as Eutric Rendzic Leptosols (Humic, Loamic), while profiles assigned under 4 and 7 (Supplementary Fig. S2C) match the criteria of Eutric Leptic Rendzic Phaeozems (Hyperhumic, Loamic) and Eutric Leptic Chernic Rendzic Phaeozems (Loamic), respectively.

The soil structure and water properties related to soil quality and plant growth are shown in the Supplementary Table S2. The obtained results (WMWD/DMWD=0.7±0.1 mm on average) indicated a very stable soil structure for all investigated soil profiles. Since SI value was above 19%, the soil structure was determined as extremely stable and without the risk of degradation. Water retention at -33 kPa showed high values (exceeding 35%). Values at -1500 kPa were estimated as relatively high (exceeding 23.1%). Shallow soil depth is linked with moderate water storage capacity (186.2-333.8 m^3·ha). Precipitation values exceeded potential evapotranspiration in the period between October-February (Supplementary Fig. S3). Potential evapotranspiration was higher than the precipitation in March, but the actual evapotranspiration is still equal to the potential one because of the utilization of the previously accumulated water recharge. Consequently, a water deficit is expected in the period from June to October.

The analyzed physical and chemical soil properties in mixed soil samples for each plot relevé are presented in Supplementary Table S3 and Supplementary Table S4. All soils were moderately acid to neutral, characterized by a silt clay loam and silt loam, and with high values of humus, CEC and base saturation.

Considering that the soils have developed on compact limestone, the soil samples contained a high content of plant-available calcium and were well-supplied with potassium and magnesium. The phosphorus content was in the low range, which is in accordance with the classification parameters [35,36]. The studied soils were generally well-supplied in plant-available microelements except for molybdenum, which was in the deficiency range [35,37].

Vegetation characteristics

A total of 200 plant species were determined within the studied grassland plots. The results of the cluster analysis allowed the grouping of the relevés into two clusters as follows:

Cluster 1: *Saturejion montanae* (Supplementary Fig. S2B). The cluster was represented by 14 relevés, and diagnostic species were: *Artemisia alba, Carex humilis, Melica ciliata, Satureja montana* ssp. *kitaibelii,* and *Stipa pulcherrima*. *Artemisia alba* was the constant and dominant species in the herb layer.

Cluster 2: *Festucion valesiacae* (Supplementary Fig. S2D). The number of relevés for this cluster was 8, and the species with phi coefficient values higher than 0.10 were: *Stachys officinalis, Dianthus carthusianorum, Elymus repens, Filipendula vulgaris, Helianthemum nummularium, Knautia arvensis, Rhinanthus rumelicus, Thymus odoratissimus,* and *Trifolium alpestre. Festuca valesiaca* was the species recorded in more than 50% relevés. The herb layer is dominated by *Festuca valesiaca* and *Orlaya grandiflora.*

Saturejion montanae vegetation has an open structure, the plants are of a shrubby form, low height and prostrate, while *Festucion valesiacae* plants are typical herbaceous species and this type of vegetation is characterized by a closed structure.

Vegetation-environment relationships

The DCA analysis enabled the indication of relief and soil variables important for plant cluster grouping (Fig. 1A). The humus, S and CEC, in addition to the vegetation cover were the most important factors determining the floristic composition of grasslands on the study area. The first ordination axis was negatively correlated with the humus indicator value (r=-0.60; P=0.001), while a positive correlation was found for the vegetation cover (r=0.91; P=0.001). The humus content influences the grouping of *Saturejion montanae* plants, while the parameter vegetation cover influenced the

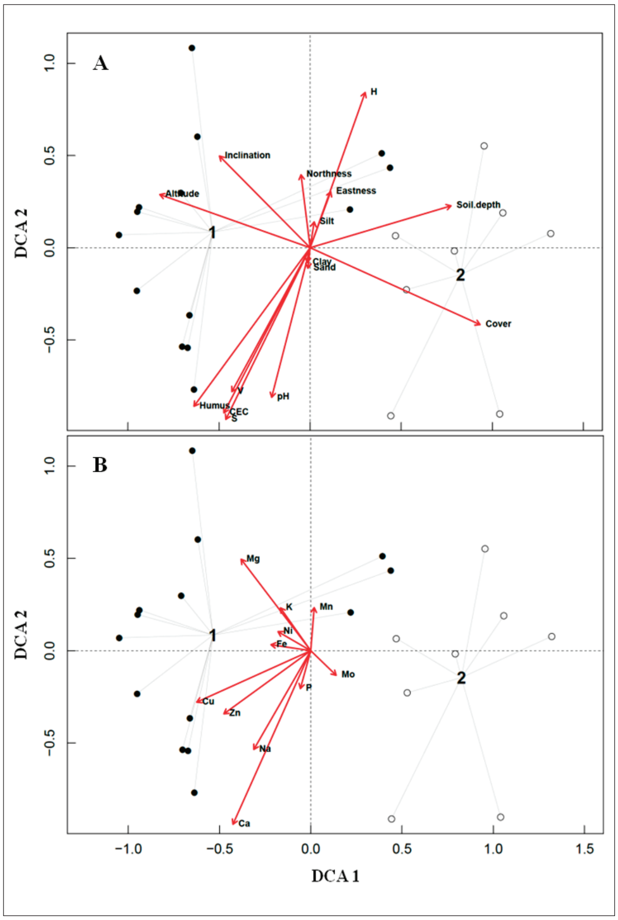

Fig. 1. Detrended correspondence analysis (DCA) ordination diagram on the relevés from grassland communities in relation to soil and relief factors (**A**) and the plant-available macro- and microelements (**B**). Clusters: 1 – *Saturejion montanae*; 2 – *Festucion valesiacae*.

grouping of *Festucion valesiacae*. The first ordination axis was negatively correlated with the factors of altitude (r=-0.94; P=0.01) and inclination (r =-0.71; P=ns) resulting in the *Saturejion montanae* grouping, while the soil depth factor showed a positive correlation in the clustering of the *Festucion valesiacae* (r=0.96; P=0.020). The second axis correlated well with most of the investigated variables, including: S (r=-0.90; P=0.001); CEC (r=-0.88; P=0.001); humus (r=-0.80; P= 0.001); H (r=-0.94; P=0.009); V (r=-0.87; P=0.004) and pH (r=-0.96; P=0.012). Furthermore, other variables were well correlated with the second axis as well, such as northness (r=0.99), eastness (r=0.93), sand (r=-0.99), silt (r=0.99) and clay (r=-0.98).

The second DCA ordination analysis was based on the content of the soil elements (Fig. 1B). The *Festucion valesiacae* cluster was formed under the influence of molybdenum and manganese contents, while the rest of the studied elements had an influence on the formation of the *Saturejion montanae* cluster. The significant variable for the *Saturejion montanae* grouping was Ca, corresponding to the second DCA axis (r=-0.91; P=0.001). In addition, Mg (r=0.79), Na (r=-0.86), K (r=0.81), P (r=-0.96) and Mn (r=0.99) corresponded to the second DCA axis, but they did not have any influence on the separation of the two clusters. The first DCA axis was correlated with the content of Cu (r=-0.91), Fe (r=-0.99), Mo (r=0.72), Ni (r=-0.86) and Zn (r=-0.81), but no statistically significant values were observed.

Statistical analyses showed that there were no significant differences in soil characteristics, except in the soil depth, while the two relief parameters (altitude and aspect) differed significantly between the two clusters (Supplementary Table S5, Fig. 2).

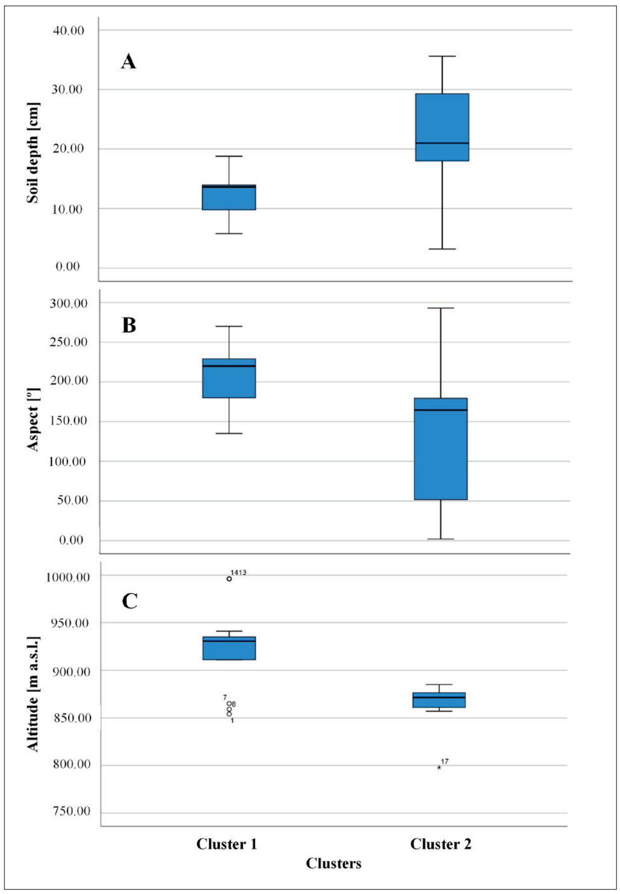

Fig. 2. Box plots of means, standard deviation and 95% confidence intervals of soil depth (**A**); aspect (**B**) and altitude (**C**) for Cluster 1 (*Saturejion montanae*) and Cluster 2 (*Festucion valesiacae*) based on the Mann-Whitney U test.

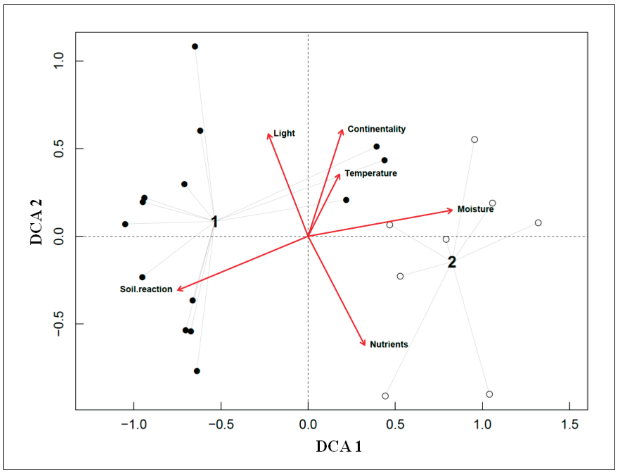

Fig. 3. Detrended correspondence analysis (DCA) ordination diagram of grassland vegetation in relation to the ecological indicator values. Clusters 1 – *Saturejion montanae* and 2 – *Festucion valesiacae.*

The DCA ordination figure based upon EIVs (Fig. 3) shows that the most important ecological factors influencing the diversity and variability in the floristic composition of the grassland vegetation were the soil reaction and light for the *Saturejion montanae*, and the moisture, nutrient content, temperature and continentality for the *Festucion valesiacae* vegetation type.

DISCUSSION

It is established that the mutual relationships of soil, vegetation and climate are very complex, determining the formation at the climax vegetation stage [8]. Among the ecological factors responsible for the vegetation type appearance and its related floristic composition, the relief (mainly the inclination and the altitude) and climate (the temperature and the precipitation) are frequently addressed [6,38,39]. The following soil characteristics were reported as the most influential: soil pH and/or base saturation [8,40-42], SOM [42], soil texture [8,42], structure [6] and soil depth [38]. In our study, altitude was the main relief variable important for cluster grouping (Fig. 1A), while humus, S, CEC, available Ca, H, soil depth and pH were the most important soil parameters affecting the species composition of grassland ecosystems (Fig. 1A, B).

The soil samples investigated in this study originate from a relatively small area and are spread across a narrow range of altitude (200 m), inclination (18°) and aspect (2-293°). The Mann-Whitney U test indicated that significant differences exist depending on the altitude and the aspect between soils and the corresponding vegetation of the two clusters, while the DCA highlighted altitude and inclination as the relief parameters important for cluster separation.

The researched soils developed on the same Mesozoic consolidated limestone and exhibit similar physical and chemical properties as confirmed by the Mann-Whitney U test. Soil depth was the only soil characteristic that significantly differed between the soils of the two clusters, and it was a significant factor for cluster separation, as shown by the DCA analysis.

Under similar physical and chemical conditions of soil and under different soil depth and relief features (altitude and aspect), the grassland vegetation exhibits differences in floristic composition resulting in the formation of two different vegetation types. The significant diversity of the steppe grasslands is represented by the *Saturejion montanae* and *Festucion valesiacae* alliances. The sub-Mediterranean-subcontinental steppe alliance *Saturejion montanae* is a Balkan endemic alliance spread across eastern Serbia and Bulgaria [43]. The grassland vegetation of *Saturejion montanae* inhabited higher altitude sites of a moderate slope position and shallower soils, while the species of *Festucion valesiacae* preferred the somewhat deeper soils developed on lower altitudes and sites with gentle inclinations. It is well accepted that soils on steeper slopes (*Saturejion montanae* dry grasslands) are more exposed to soil erosion and surface water runoff, which in turn results in shallower depth and less water infiltration. By contrast, soils on flatter terrains (vegetation type of the *Festucion valesiacae*) are not exposed to erosion processes and there is less surface water runoff. Therefore, these soils are deeper and water infiltration is higher. Higher water infiltration means higher water flow and bases eluviation, and thus the pH and base saturation in these soils decrease. Also, better moisture conditions induce humus decomposition (mineralization), resulting in lower humus content.

All samples of investigated soils expressed high water retention values. Nevertheless, it was shown that shallower soil depth mainly caused low to moderate water storage capacity. Additionally, the estimated soil moisture regime indicated the problem of water deficit in the summer season. Moreover, altitude may also have influenced climatic conditions and the soil moisture regime [44]. Although all the studied plot samples were collected in a relatively narrow altitude belt of about 200 m a.s.l., some higher altitudes are related to sharper microclimatic conditions and steeper slopes. All these factors have a statistically significant effect on the separation of the open xerophytic vegetation of the *Saturejion montanae* cluster.

It is a known fact that grassland vegetation richness and composition are strongly influenced by the soil's macro and micronutrients [6,39,40,45]. In addition to the effects of the relief and soil conditions shown in the present study, the plant-available macro- and microelements have also influenced the cluster separation. Ca had the greatest impact on the separation of the *Saturejion montanae*, followed by Mg, Na, and K; P also influenced the *Saturejion montanae* grouping, partly due to the higher humus content. Most of the microelements affected the grouping of the *Saturejion montanae*, while Mo and Mn influenced the separation of the *Festucion valesiacae*. Higher soil moisture and acidity levels favor the increasing content of plant-available forms of Mn and Mo. The acidic soils of semi-natural meadows have been shown to be poor in most of the macro- and microelements, apart from Mn [46].

There were no differences in the classification of soils corresponding with the vegetation plots according to the performed WRB 2015 [11]. The RSGs of Leptosols and Phaeozems were present in both clusters. It was expected that Leptosols, being shallower, will be found in *Saturejion montanae* sites and Phaeozems in the *Festucion valesiacae*. The Phaeozem in the *Saturejion montanae* sites was found on higher altitudes but it appeared on some flatter slopes where soil depth was above 25 cm.

Comparison of the obtained parameters and ecological indexes [30] used for DCA analyses showed that soil reaction was most critical for the separation of *Saturejion montanae*, and soil moisture (influenced by soil depth) for *Festucion valesiacae.* Furthermore, soil depth was a crucial factor for nutrient estimation, as shown by Pignatti [30], if deeper soils imply a higher nutrient storage, which resulted in the nutrients' influence on *Festucion valesiacae* separation. Despite this, the obtained macro- and micronutrients, expressed in mass percentage, influenced *Saturejion montanae* separation.

CONCLUSIONS

Investigations performed on the limestone massif of Mt. Rtanj confirmed the impact of environmental factors and soil properties on the grassland vegetation composition. Two clusters were distinguished: *Saturejion montanae* and *Festucion valesiacae.* There were no statistically significant differences in soil characteristics except for soil depth, while the two relief parameters (altitude and aspect) differed significantly between the two clusters. Altitude and inclination were the main relief variables and humus, CEC, base saturation and soil pH were the most important soil variables, influencing the grouping of *Saturejion montanae*. On the other hand, the significant factors for *Festucion valesiacae* were the vegetation cover, soil depth and total acidity. Apart from Mo and Mn, all other plant-available macro- and microelements also impacted the grouping *Saturejion montanae*, but only Ca did so significantly. According to the WRB 2015 soil classification, RSGs of Leptosols and Phaeozems were present in both clusters. Soil reaction and soil moisture were the two ecological indices that correlated with the experimental parameters obtained by the soil laboratory and corresponding DCA analyses, which in turn confirmed the validity and rationale of using ecological indexes in addressing the soil-vegetation relationships.

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funding acquisition, JB, AĐ, ZD. All authors have read and agreed to the published version of the manuscript.

Conflict of interest disclosure: The authors declare no conflict of interest.

Data availability: The vegetation data in this paper is part of the Vegetation Database of Grassland Vegetation of Serbia with Svetlana Aćić as custodian. This database is a participating database of a single public data repository of vegetation-plot observations of the European Vegetation Archive (EVA) and is available at: http://euroveg.org/eva-database-participating-databases

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SUPPLEMENTARY MATERIAL

Supplementary Table S1. The measured relief parameters of the examined pedology profiles and the results of the analyzed soil properties required for WRB 2015 soil classification.

Profile	Depth (cm)	Altitude (m a.s.l.)	Inclination (°)	Aspect	Color (dry)	Color (moist)	Textural class (USDA)	Soil organic carbon (%)	Base saturation (%)
1	0-18	908	3	W	10 YR 3/2	10 YR 2/2	SiCL	6.57	92.9
2	0-24	904	2.5	W	10 YR 3/2	10 YR 2/2	SiCL	6.18	90.3
3	0-20	905	16	S	10 YR 3/4	10 YR 2/2	SiCL	5.83	94.7
4	0-22	1030	9	SW	10 YR 3/1	10 YR 2/1	SiCL	6.83	93.1
	22-40				10 YR 3/3	10 YR 2/1	SiCL	6.60	96.7
5	0-22	978	3	SW	10 YR 3/2	10 YR 2/2	SiCL	5.94	95.7
6	0-18	943	5	SW	10 YR 3/2	10 YR 2/2	SiCL	7.78	96.3
7	0-29	922	7	SE	10 YR 3/2	10 YR 2/2	SiCL	5.25	82.5
	29-50				10 YR 3/2	10 YR 3/2	SiCL	4.32	84.2
8	0-20	899	2	SE	10 YR 2/2	10 YR 2/1	SiCL	7.00	94.3

W – west; S – south; SW – southwest; SE – southeast; SiCL – silty clay loam

Supplementary Table S2. The soil structure and water properties of the examined soil profiles.

Profile	Depth (cm)	DMWD	WMWD	WMWD/DMWD	Structural stability index (%)	Water retention (%)		Soil water storage ($m^3 \cdot ha$)
		(mm)				-33	-1500	
						(kPa)		
1	0-18	3.81	2.63	0.691	30.8	40.4	29.6	194.0
2	0-24	4.11	2.54	0.620	31.2	36.3	27.8	204.0
3	0-20	4.21	2.54	0.603	33.5	35.2	25.9	186.2
4	0-22	4.06	2.04	0.501	38.0	36.6	28.0	190.1
	22-40	3.54	2.89	0.817	37.9			
5	0-22	3.43	2.73	0.796	29.0	38.3	27.0	248.6
6	0-18	3.37	2.51	0.744	42.7	ND	ND	ND
7	0-29	4.50	3.34	0.742	27.0	38.1	26.6	333.8
	29-50	5.53	2.92	0.527	19.0			
8	0-20	3.02	1.92	0.637	40.0	35.0	23.1	237.8

DMWD – dry mean weight diameter; WMWD – wet mean weight diameter; DMWD/WMWD – ratio; ND – not detected

Supplementary Table S3. Basic physical and chemical properties in mixed soil samples for each plot relevé.

Sample	Sand 2-0.05 mm	Silt 0.05-0.002 mm	Clay <0.002 mm	Humus (%)	pH H_2O	Total acidity	Exchangeable bases	CEC	Base saturation (%)
	(%)					($cmol \cdot kg^{-1}$)			
1	2.32	66.9	30.8	14.5	7.25	1.78	57.8	59.6	97.0
2	1.88	72.2	25.9	13.0	6.59	4.12	45.7	49.8	91.7
3	4.01	65.3	30.7	9.93	6.42	3.60	42.6	46.2	92.2
4	1.27	69.8	29.0	15.1	6.71	2.75	54.9	57.7	95.2
5	0.83	75.4	23.8	18.1	6.52	3.82	51.4	55.2	93.1
6	8.70	67.1	24.2	11.6	7.32	1.27	45.3	46.5	97.3
7	2.19	73.5	24.3	12.2	6.73	2.41	44.2	46.6	94.8
8	7.95	63.8	28.2	14.7	6.8	3.20	50.1	53.3	94.0
9	2.87	66.3	30.8	15.9	6.28	4.94	49.6	54.6	90.9
10	5.27	71.9	22.8	19.4	7.14	1.63	58.7	60.4	97.3
11	4.21	71.6	24.2	14.7	6.62	3.38	42.7	46.1	92.7
12	2.69	71.5	25.8	13.6	6.41	4.22	41.6	45.8	90.8
13	3.83	65.9	30.2	16.4	6.56	3.44	51.3	54.7	93.7
14	3.83	65.9	30.2	16.4	6.56	3.44	51.3	54.7	93.7

Supplementary Table S3. continued

15	4.86	68.6	26.6	18.8	6.92	1.72	55.3	57.0	97.0
16	3.31	68.9	27.8	15.5	6.74	2.75	46.0	48.7	94.4
17	2.74	71.6	25.7	13.2	6.42	3.89	45.2	49.1	92.1
18	1.53	71.2	27.3	15.9	6.59	2.98	46.7	49.7	94.0
19	2.33	68.8	28.8	15.0	6.33	4.47	45.7	50.2	91.1
20	2.31	67.9	29.8	14.0	6.28	4.70	42.9	47.6	90.1
21	2.61	69.8	27.6	11.9	5.58	8.48	29.5	38.0	77.7
22	1.85	71.8	26.4	7.58	5.63	6.53	22.3	28.8	77.3

CEC – soil exchange capacity

Supplementary Table S4. Elements content in mixed soil samples for each plot relevé.

Sample	Mg	Na	Ca	K	P	Cu	Fe	Mn	Mo	Ni	Zn
	(mg·kg^{-1})										
1	152.2	24.8	11103.5	355.9	11.9	1.28	27.7	124.9	0.027	0,749	1,92
2	169.4	21.3	8684.2	286.0	8.42	1.27	24.6	142.2	0.017	0.732	1.70
3	157.9	22.2	8131.0	217.7	5.19	1.49	25.9	116.0	0.016	0.653	0.678
4	151.8	27.5	10570.2	261.9	8.60	1.34	27.0	99.6	0.020	0.885	2.34
5	197.7	14.4	9815.2	235.7	17.5	1.45	35.8	117.8	0.021	0.960	3.20
6	107.2	10.6	8694.6	335.4	16.4	1.24	23.7	51.8	0.019	0.611	2.47
7	220.6	14.3	8276.3	356.5	7.25	1.45	24.2	95.6	0.020	1.11	1.93
8	169.2	14.6	9632.0	196.1	7.64	1.43	28.9	89.2	0.024	0.886	1.33
9	269.1	17.6	9253.0	411.5	20.8	1.80	43.7	212.4	0.042	1.30	4.04
10	200.0	16.0	11266.6	262.6	24.3	1.50	31.7	111.3	0.036	0.893	4.17
11	217.0	17.7	8039.5	252.1	12.7	1.07	24.6	113.5	0.027	0.570	1.68
12	281.4	14.2	7696.0	261.2	9.52	1.26	29.0	104.7	0.025	0.535	2.02
13	225.6	15.4	9743.9	249.0	6.55	1.47	30.8	106.2	0.031	0.998	1.84
14	225.6	15.4	9743.9	249.0	6.55	1.47	30.8	106.2	0.031	0.998	1.84
15	306.4	72.8	10342.0	281.6	10.2	2.53	46.7	138.5	0.040	1.55	4.33
16	226.5	40.8	8617.0	322.5	9.12	2.27	42.4	158.9	0.020	1.44	2.82
17	271.2	10.8	8409.2	319.4	14.8	1.41	31.8	86.3	0.026	0.852	2.28
18	427.2	54.9	8403.0	361.2	15.9	2.91	50.1	180.9	0.020	1.54	5.97
19	266.3	16.9	8565.4	231.0	9.25	1.28	36.5	132.4	0.033	1.22	2.24
20	240.8	14.2	8056.0	201.8	8.73	1.07	32.5	138.0	0.033	1.24	1.48
21	271.8	17.7	5285.4	292.1	9.52	1.50	43.7	215.6	0.041	2.14	3.07
22	184.1	11.1	3998.5	264.2	7.11	1.31	47.1	108.4	0.027	1.25	0.672

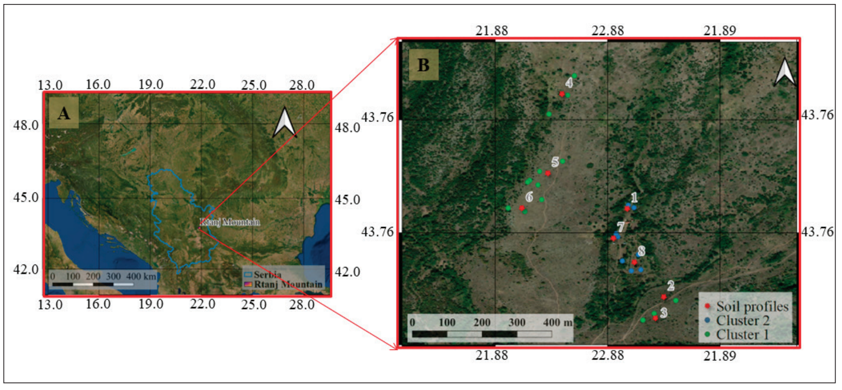
Supplementary Table S5. Soil and relief properties for Cluster 1 (*Saturejion montanae*) and Cluster 2 (*Festucion valesiacae*).

Relief and soil properties	Unit of measurement	Cluster 1	Cluster 2	*p* values
Soil depth	(cm)	12.20±3.75	21.93±10.02	0.004*
Altitude	(m a.s.l.)	922.6±42.94	862.6±27.48	0.008*
Inclination	(°)	8.07±5.01	5.00±1.83	0.402
Aspect	(°)	209.7±36.10	135.8±97.88	0.010*
Sand 2-0.05 (mm)	(%)	3.14±1.81	3.68±2.33	0.764
Silt 0.05-0.002 (mm)	(%)	69.73±3.31	68.68±2.38	0.570
Clay <0.002 (mm)	(%)	27.13±2.35	27.64±2.99	0.664
Humus	(%)	15.23±1.88	12.98±3.58	0.059
pH (H_2O)	pH	6.60±0.169	6.49±0.690	0.525
Total acidity	(cmol·kg^{-1})	3.36±0.824	4.06±2.54	0.616
Exchangeable bases	(cmol·kg^{-1})	48.29±4.33	43.10±12.49	0.297
Soil exchange capacity	(cmol·kg^{-1})	51.65±4.13	47.16±10.43	0.365

Supplementary Table S5. continued

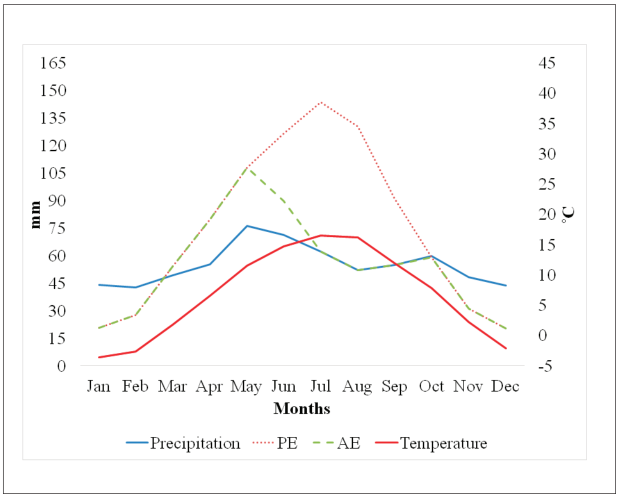
Base saturation	(%)	93.44±1.71	90.00±8.23	0.616
Mg	(mg·kg^{-1})	239.9±70.20	197.6±58.65	0.238
Na	(mg·kg^{-1})	25.10±18.37	16.70±4.98	0.525
Ca	(mg·kg^{-1})	9087.5±898.40	8137.6±2517.21	0.441
K	(mg·kg^{-1})	288.8±58.46	270.1±54.95	0.616
P	(mg·kg^{-1})	11.11±4.51	11.56±6.14	0.920
Cu	(mg·kg^{-1})	1.65±0.536	1.33±0.152	0.297
Fe	(mg·kg^{-1})	33.60±8.71	33.60±8.37	0.868
Mn	(mg·kg^{-1})	125.2 ±37.19	124.8±45.25	0.664
Mo	(mg·kg^{-1})	0.026±0.008	0.029±0.009	0.238
Ni	(mg·kg^{-1})	1.03±0.329	1.09±0.498	1.000
Zn	(mg·kg^{-1})	2.67±1.30	2.09±1.19	0.441

Statistically significant differences (P≤0.05) are denoted by asterisk (*); mean±standard deviation values are presented for each soil property.



Supplementary Fig. S1. Study area: **A** – the geographical position of Mt. Rtanj; **B** – phytosociological relevés and soil profiles. Clusters: 1 – *Saturejion montanae;* 2 – *Festucion valesiacae*

Supplementary Fig. S2. The studied soils and vegetation. **A** – Leptosols (profile number 3); **B** – *Saturejion montanae* inhabited higher altitudes at sites of a moderate slope position and on the shallower soils; **C** – Phaeozems (profile number 7); **D** – *Festucion valesiacae* prefer deeper soils developed on the lower altitudes and on sites with a gentle inclination.



Supplementary Fig. S3. Mean monthly precipitation, potential (PE) and actual (AE) evapotranspiration (in mm) and soil temperature (in °C), based on hydrometeorological data [14] and the Soil Survey Staff method [15].