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Soil pH as a strong driver of plant species distribution in alpine-nival ecotone of the Central Caucasus

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Key words: community assembly, regional patterns of species distribution, the climate and bedrock, environmental gradient.

Ključne besede: sestava združbe, regionalni vzorec razširjenosti vrst, klima in kamnina, okoljski gradient.

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Abstract

Soil pH can be a strong driver of species distributions in general, however, its role in alpine-nival ecotone is little known. We compared the composition of plant species of two locations located 25 km apart from each other, one near Mt. Kazbegi and another near Mt. Gudauri (Georgia). These locations have similar abiotic environments but significantly different soil pH levels. The sampled communities were located at 3000 m a.s.l., which in the Central Caucasus corresponds to the alpine-nival ecotone. North- *versus* south-facing slopes were sampled with a standardized stratified-random design. Soil samples were collected from the same vegetation sampling plots. The analysis of climate data from available databases showed that these two locations were climatically similar but distinguishable in soil pH values. In total, 74 species were recorded, of which the relatively frequent 33 species (those with a frequency of occurrence ≥10) were used for multivariate statistical analyses. The floristic similarity between the locations was low. Ordination axis 1, which was primarily linked to soil pH and, to a lesser extent, vegetation cover, accounted for nearly all the variation in the Canonical Correlation Analysis (CCA) ordination. Our results suggest that soil pH is a key factor in community assembly in the alpine-nival ecotone of the Central Caucasus.

Izvleček

pH tal je lahko pomemben dejavnik razširjenosti vrst, vendar je njegova vloga v nivalnem ekotonu slabo poznana. Primerjali smo sestavo rastlinskih vrst na dveh lokacijah, oddaljenih 25 km, eno v bližini gore Kazbegi in drugo pri gori Gudauri (Gruzija). Lokaciji imata podobne abiotske dejavnike, a se značilno razlikujeta v pH tal. Vzorčene združbe so na 3000 m nad morjem, kar v centralnem Kavkazu predstavlja alpinsko-nivalni ekoton. Vzorčili smo severna in južna pobočja s standardiziranim stratificirano-naključnim vzorčenjem. Talne vzorce smo vzeli na istih ploskvah, kjer smo vzorčili vegetacijo. Analiza klimatskih podatkov iz obstoječih podatkovnih baz je pokazala, da sta vzorčni lokaciji podobni v klimatskih razmerah, razlikujeta pa se v pH tal. Zabeležili smo 74 vrst, od katerih smo 33 bolj pogostih (s frekvenco ≥10) uporabili za multivariatno statistično analizo. Floristična podobnost med lokacijama je bila majhna. Ordinacijska os 1, ki je povezana s pH tal in manj s pokrovnostjo vegetacije, pojasni skoraj vso variacijo Kanonične korelacijske analize (CCA). Rezultati kažejo, da je pH glavni dejavnik pri sestavi rastlinskih združb v alpinsko-nivalnem ekotonu v centralnem Kavkazu.

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Introduction

Soil pH is often considered the most proximal among other soil characteristics for explaining plant distributions (Chytrý et al., 2003; Körner, 2003). Indeed, it was shown to be an important predictor of alpine plant species richness (Vonlanthen et al., 2006) that can regulate the structure and function of ecosystems (Braun-Blanquet & Jenny, 1926; Chytrý et al., 2007; Ji et al., 2014), plant growth (Van Breemen & Finzi, 1998), microbial activity stability (Robson, 1989; Kemmitt et al., 2006). In general soil pH is considered an important ecological variable in alpine areas, which along with other ecological factors determines plant species distribution (Körner, 2003). At the same time, the solid knowledge of the key processes that drive high-mountain plant distributions and community structure is especially important in the context of global change, as steep environmental gradients across alpine-nival landscapes with abrupt shifts in plant distribution and abundance can offer best sites for studying and monitoring the effects of climate change on vegetation over short time scales (Frei et al., 2010; Grabherr et al., 2010; Gottfried et al., 2012). This idea is realized by the Global Observation Research Initiative in Alpine Environments (GLORIA), which represents a network of research areas in the alpine-nival ecotone across mountain systems, including the Central Great Caucasus, and already has reported the changes in species distribution caused by climate (Gigauri et al., 2013, 2014, 2016, 2021; Erschbamer et al., 2013; Nakhutsrishvili et al., 2013; Abdaladze et al., 2015).

However, it should be noted that there is very limited literature on soil pH in alpine and higher altitude regions (Schuster & Diekmann, 2003). Indeed, quantitative descriptions and analyses of the dependence of vegetation patterns on soil pH in high mountain systems in general and the Central Great Caucasus in particular, are rare (Körner, 2003). This is an important gap in our knowledge since usually temperate high mountain systems, among them the Caucasus, show high soil diversity owing to complex bioclimatic, bedrock, and geomorphologic conditions (Urushadze, 1989). The existing evidence suggests that soil pH can be particularly important to the spatial distribution of a rather large group of species in a variety of high-mountain habitats. For example, our recent study showed that soil pH contributed to the variable patterns of plant species distribution on the slope aspect gradient (North *versus* South) as well as along the altitudinal gradient (Jolokhava et al., 2020). Soil pH can integrate the collective effects of environmental variables such as climate (temperature, precipitation) and bedrock type (Molau, 2003; Kikvidze et al. 2020), and our previous study (Jolokhava et al. 2021) also found that soil pH can drive plant species distributions even more strongly than other environamental variables such as altitude and slope aspect.

We aimed to clarify the role of soil pH in influencing differences in plant species composition between two locations within the same mountain system (the Central Caucasus). These locations share a similar abiotic environment, including climate, bedrock, altitude, slope aspect, and inclination, except for their significantly different soil pH levels. We collected climate data from available electronic databases of these two locations to verify the similarity of their physical conditions at each location, we sampled vegetation on the slopes of contrasting aspects (North *versus* South), and analyzed species compositions and distributions among these sites using floristic similarity measures, cluster analysis, and multivariate ordination methods. Simultaneously, we measured soil pH and assessed vegetation cover, which we used as a surrogate of productivity. Our specific goal was to investigate the correlation between soil pH, plant species composition, and other environmental conditions that were indistinguishable or nearly identical.

Materials and Methods

Study area

The study was conducted in two sites: one on the slopes of Mt. Kazbegi and another at the ski resort of Gudauri (Figure 1a). The coordinates of the north and south slopes at each study site are as follows: Mt. Kazbegi: North Slope: N 42°39'39.50", E 44°33'32.14"; South Slope: N 42°39'38.42", E 44°33'33.43" and Gudauri: North Slope: N 42°39'39.50", E 44°33'32.14", South Slope: N 42°39'38.42", E 44°33'33.43". Both areas are located in the Stephantsminda District and are approximately 25 km apart.

The mountain massifs of the Kazbegi volcanic area are covered by Quaternary deposits, including glacial and river sediments, as well as rock falls. Additionally, there are significant accumulations of calcareous tuffs and travertines (Maruashvili, 1969; Nakhutsrishvili, 1971). The second most important bedrock in the study area, following volcanic, consists of flysch terrigenous and carbonate sediments from the Jurassic period. This includes primary clay slates and marlstone from the complete Jurassic, as well as limestone from the lower Cretaceous (Maruashvili, 1969; Nakhutsrishvili, 1971; Hanauer et al., 2023). The soils in this region are characterized by their acidic to weakly acidic reactions and alkaline properties (Urushadze & Ghambashidze, 2013). The soil cover mainly consists of montane forest-meadow and montane meadow

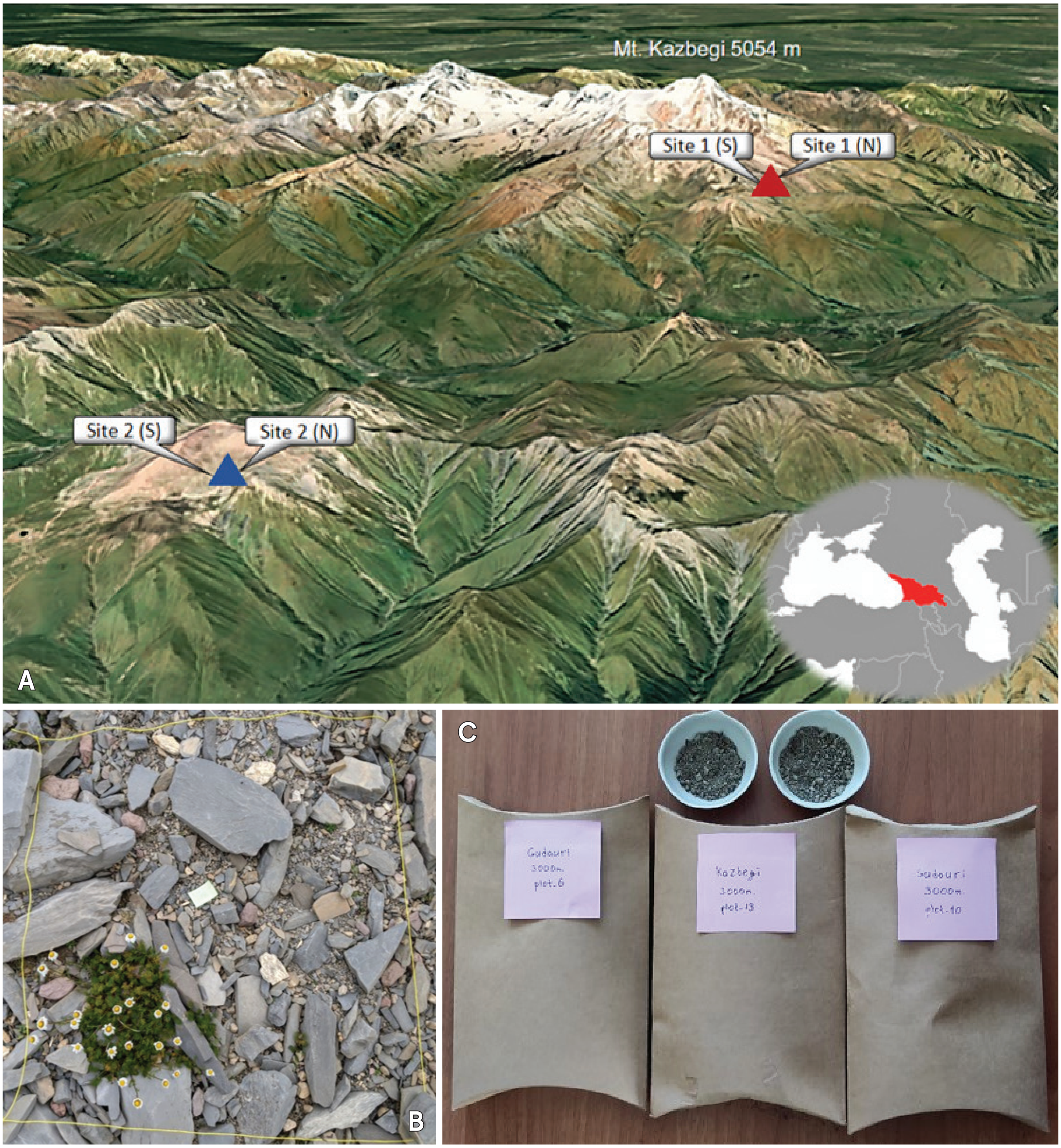

Figure 1: Approximate locations of study areas on the slopes of the Central Great Caucasus: A – Kazbegi (red triangle) and Gudauri (blue triangle) sites; B – 1m × 1m sampling plot; C – soil samples for laboratory analysis.

Slika 1: Približna lokacija preučevanih območij na pobočjih srednjega Kavkaza: A – Kazbegi (rdeči trikotnik) in Gudauri (modri trikotnik); B – vzorčna ploskev 1m × 1m; C – talni vzorci za laboratorijske analize.

soils of more than ten types, sub-types, and genera (Urushadze, 1997; Urushadze & Kvrivishvili, 2014; Urushadze et al., 2015). The climate is moderately humid with relatively dry, cold winters and long, cool summers. The climate between 2600 and 3400 m a.s.l. is moderately humid with no real summer. The average temperature from January to February reaches -14 °C. Snow cover persists for 7–8 months and is rather deep (200 cm). Snow remains throughout the year in depressions. Strong westerly winds prevail. The mean temperature of July and August hardly reaches 10 °C. Snow, night, and morning frost are frequent in summer at about 3000 m. Weather changes often and quite rapidly during the day (Nakhutsrishvili, 2004; Abdaladze et al., 2015, Erschbamer et al., 2015).

The flora of the Kazbegi district includes 1112 species of vascular plants, which make up 27% of the total number of plants (about 4100 species) recorded in Georgia (Gagnidze, 2005). The potential tree line in the Kazbegi region occurs at an altitude of ca. 2650 m with well-developed alpine meadows above. These meadows form a continuous cover till ca. 3000 m a.s.l., the higher the vegetation becomes patchy and forms alpine-nival ecotone. (Nakhutsrishvili, 2013; Nakhutsrishvili & Abdaladze, 2017).

Sampling design and data collection

We established sampling plots at each study site on the slopes of opposite aspects (North *versus* South), at 3000 m a.s.l. The altitude and slope aspects were determined using a GPS device (Etrex Summit TM, Garmin, Switzerland). The slope angle (inclination) was measured by a compass-clinometer (Recta DP 6TM, Switzerland).

Within each study site, which covered an area of approximately 200 m², we randomly placed 20 sampling plots, each measuring 1 m × 1 m (see Figure 1b). The distance between the plots was maintained at a minimum of 4 to 5 meters. Within each plot, we recorded all plant species present and estimated the vegetation projective cover in percentage terms through visual assessment. Additionally, we calculated the frequency of occurrence for each species by counting how often each species was present across the sampling plots. For plant species names, we followed the International Plant Names Index (IPNI).

Within each sampling plot (1 m × 1 m), soil samples were collected from a depth of 0–20 cm using a Gouge auger (Tan, 2005). From the center of each sampling plot (measuring 1 m × 1 m), soil samples were collected from a depth of 0–20 cm using a Gouge auger (TAN, 2005). A total of 80 samples, one from each plot, were stored in polyethylene bags (Figure 1c); next, we dried the samples at 35 °C, sieved it through a 2-mm sieve, and took it to the laboratory to determine the pH of the soil. Soil pH was determined in 1 : 2.5 Soil/Water suspension using a pH meter (WTW Benchtop pH Meter InoLab® Multi 9310 IDS, Xylem Analytics, Germany) with a glass electrode (Jackson, 2005).

Data analyses

Climatic data (1992-2022) on monthly precipitation and mean monthly temperatures of the eastern (Kazbegi and Gudauri) parts of the Central Great Caucasus were obtained from the Meteoblue database (https://content.meteoblue.com/en/content/view/full/2559) and assessed the similarity of climate between two study sites (Hubálek & Horáková, 1988, Townend, 2013).

From the sample data, we constructed a combined community matrix that included location, aspect, soil pH and plant cover (independent variable), and species with their frequencies of occurrence. Using this matrix, we calculated mean values per plot for soil pH, vegetation cover, and species richness and compared these values between sampling sites using the Kruskal-Wallis H test using IBM SPSS 21 software (IBM Analytics, Armonk, U.S.A.).

We employed cluster analysis and Canonical Correspondence Analysis (CCA) to compare species compositions among the plots and sites. Only 33 most frequent species (frequency of occurrence ≥10) were included in these analyses. Cluster analysis was based on the Bray-Curtis distance (Beals, 1984; Anderson et al., 2011). The CCA ordination included soil pH and plant cover in the secondary matrix. The goodness-of-fit of the obtained ordination was assessed using a permutation test with 999 permutations.

Results

The climatic character appeared to be indistinguishably similar between the Kazbegi and Gudauri sites (data collected from online databases, Figure 2). This similarity was to be expected, as the altitude of these sites is above the influence of the Great Caucasus watershed on climate, and air masses move freely between these sites, which are not far from each other. Vegetation cover was variable, the difference being statistically significant between aspects but not sites. On the contrary, soil pH differed strongly between sites but not aspects (Figure 3).

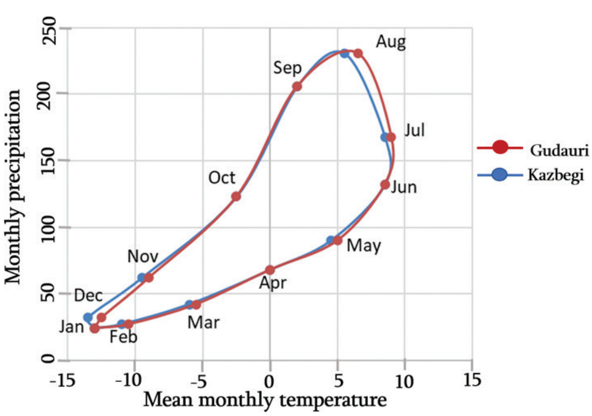

Figure 2: Mean monthly temperatures and monthly precipitation at the two study sites (Kazbegi and Gudauri, the Central Caucasus).
Slika 2: Povprečna mesečna temperatura in mesečne padavine na dveh preučevanih lokacijah (Kazbegi in Gudauri, centralni Kavkaz).

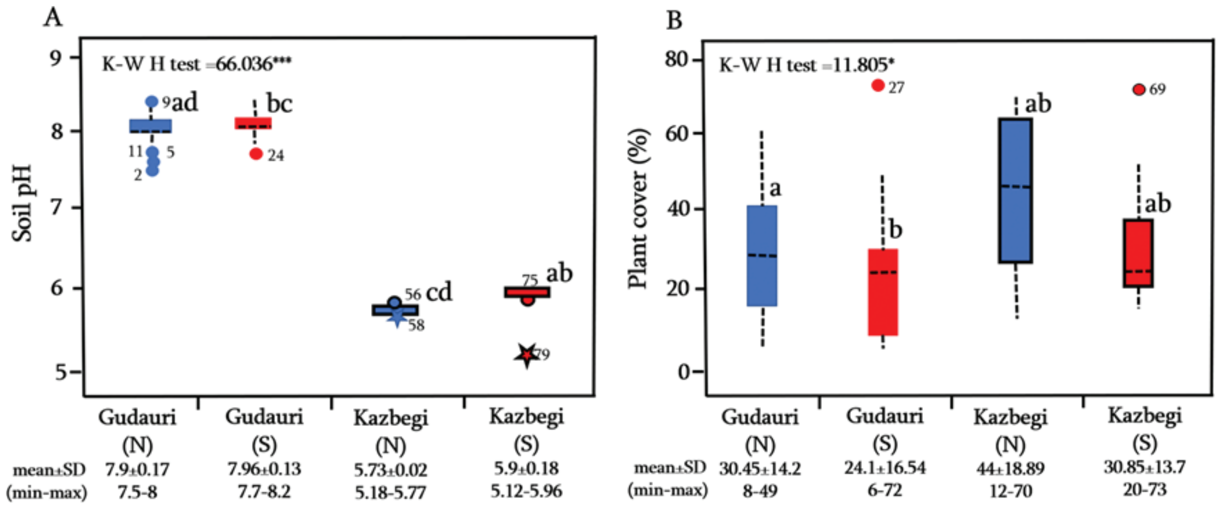

Figure 3: Soil pH (A) and plant cover (B) at the two study sites. The mean rank multiple comparisons between each pair of study sites were performed with the Kruskal-Wallis *H* test; the same letters next to each boxplot indicate significant differences among the mean ranks between pairs of study sites at $p \leq 0.001$.

Slika 3: pH tal (A) in pokrovnost rastlin (B) na dveh preučevanih območjih. Povprečne primerjave ranga med vsemi pari preučevanih območij smo naredili s Kruskal-Wallisovim *H* testom; iste črke ob diagramih prikazujejo značilne razlike med povprečnimi rangi pri $p \leq 0,001$.

We recorded 74 plant species in total through our sampling campaign (see supplementary material Table S1). For our analyses, we used the 33 most frequent species (frequency of occurrence ≥10). Community structure was different both in species richness and composition, the similarity of species composition between the sites being remarkably low (Figure 4, Bray-Curtis index = 0.398). Species composition between aspects was more similar, less so at Kazbegi (Bray-Curtis index = 0.440) than at Gudauri (Bray-Curtis index = 0.580). These differences appeared to be statistically highly significant (p < 0.0001 for sites, aspects, and their interaction, by Permanova test; Table 1).

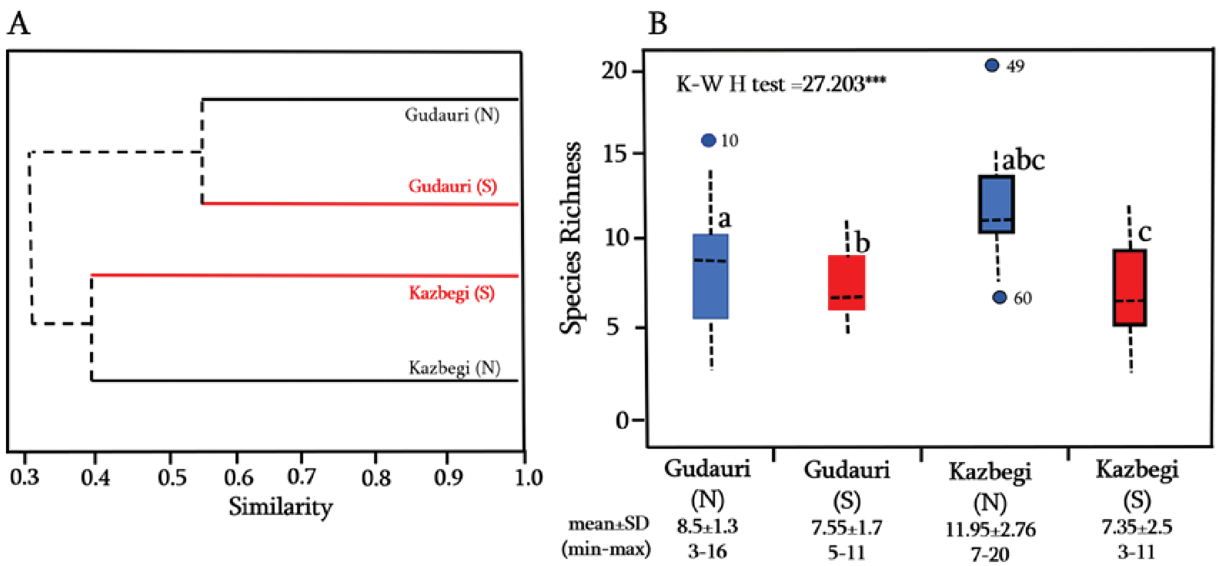

Figure 4: Cluster analysis of the floristic similarity among the two study sites: A – Bray Curtis similarity (Cophen. Corr. = 0.98); B – box plots representing the species richness for each site. The mean rank multiple comparisons of species richness between each pair of study sites were performed with the Kruskal-Wallis *H* test; the same letters next to each boxplot indicate significant differences among the mean ranks between pairs of study sites at $p \leq 0.001$.

Slika 4: Klastrska analiza floristične podobnosti med dvema preučevanima območjema: A – Bray Curtis podobnost (Cophen. Corr. = 0,98); B – grafikon kvantilov predstavlja vrstno pestrost za posamezno območje. Primerjave povprečnih rangov vrstne pestrosti med območjema smo naredili s Kruskal-Wallisovim *H* testom; črke ob grafikonih predstavljajo značilne razlike med povprečnimi rangi parov preučevanih območij pri $p \leq 0,001$.

Table 1: Results of PERMANOVA based on Bray-Curtis similarity testing. SS = Sum of sqrs, df = degrees of freedom, MS = mean-squares, F = pseudo-F-value, p = permutational P-value. Unique permutations of the test statistic obtained under 999 permutations.

Tabela 1: Rezultati analize PERMANOVA na osnovi testa podobnosti Bray-Curtis. SS = vsota kvadratov, df =stopnje prostosti, MS = povprečje kvadratov, F = psevdo-F-vrednost, p = permutacijska P-vrednost. Edinstvene permutacije testne statistike so dobljene z 999 permutacijami.

Source	SS	df	MS	F	p
Site	3.44	1	3.44	17.31	0.0001
Aspect	2.81	1	2.81	14.14	0.0001
Interaction	1.38	1	1.38	6.93	0.0001
Residual	15.12	76	0.2	-	-
Total	22.76	79	-	-	-

Alopecurus glacialis was particularly dominant on both the north (N) and south (S) slopes at the Kazbegi location (Table S1). At the Gudauri location, the most abundant species were *Tripleurospermum subnivale* on the north (N) slope and *Campanula collina* on the south (S) slope. *Saxifraga moschata* was also fairly abundant at all four sites but more frequent at the Gudauri location. Frequent species also included *Carum caucasicum, Cerastium polymorphum,* and *Gentianella caucasea*, though these were present only at the Gudauri location.

The Cartesian Coordinate System exposed that the spatial distribution of plots was strongly influenced by plant cover and soil pH (Figure 5). The distribution of soil pH across the sample plots is presented in supplementary material, specifically in Table S2. Ordination with the CCA conformed to these results as it revealed strong differences between the locations (Kazbegi *versus* Gudauri), while the aspects were less distant (Figure 6). The CCA ordination appeared to be statistically highly significant ($p < 0.0001$), but, remarkably, almost all variation was explained by Axis 1, associated with increasing pH and decreasing plant cover. Species were also clearly distributed along this gradient (Figure 7).

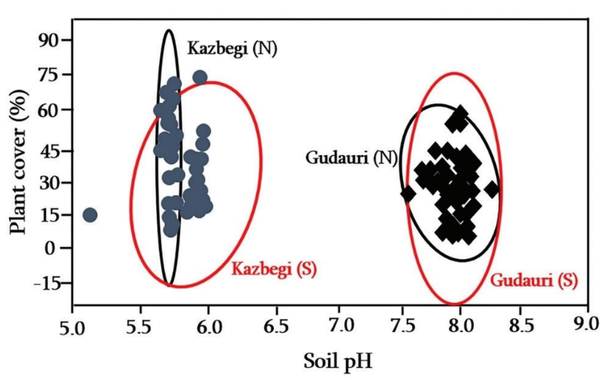

Figure 5: Soil pH and vegetation cover of the sampling plots: each symbol represents a 1m × 1m plot (20 plots per site) encircled by the 95% confidence interval. The two study sites clearly differentiate in soil pH but not by vegetation cover.

Slika 5: pH tal in pokrovnost vegetacije na vzorčnih ploskvah: vsak simbol predstavlja ploskev 1 m × 1 m (20 ploskev na preučevano lokacijo), obkroženo s 95% intervalom zaupanja. Dve preučevani območji se jasno ločita v pH tal, a ne v pokrovnosti vegetacije.

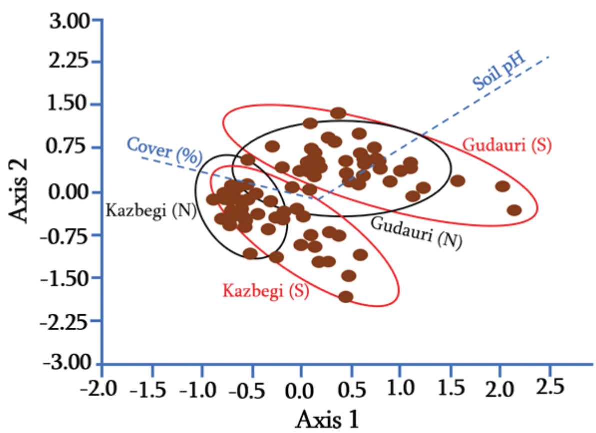

Figure 6: CCA ordination diagram of the sampling plots encircled by a 95% confidence interval; plant cover (%) and soil pH were used as environmental variables. Axis 1 explains 99.86% of the variation.

Slika 6: CCA ordinacijski diagram vzorčnih ploskev, obkrožen s 95 % intervalom zaupanja; pokrovnost rastlin (%) in pH tal sta uporabljena kot okoljski spremenljivki. Os 1 pojasni 99,86 % variacije.

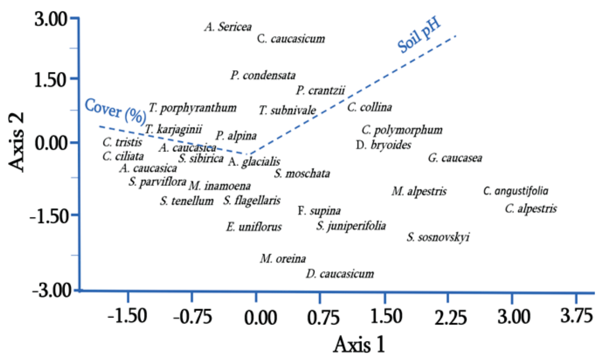

Figure 7: CCA ordination diagram of plant species composition between two study sites (Gudauri and Kazbegi) in alpine-nival ecotone (3000 m a.s.l.) in the Central Caucasus; plant cover (%) and soil pH are used as environmental variables (Species full names are given in Table 1).

Slika 7: Ordinacijki CCA diagram sestave rastlinskih vrst med dvema preučevanima območjema (Gudauri in Kazbegi) v alpinsko-nivalnem ekotonu (3000 m nmv) v centralnem Kavkazu; pokrovnost rastlin (%) in pH tal sta uporabljena kot okoljski spremenljivki (rastlinska imena so enaka kot v Tabeli 1).

Discussion

The climate and bedrock at Kazbegi and Gudauri locations where we sampled vegetation and soil were virtually the same, but soil pH was notably different and, therefore, we attribute the observed differences in plant community structure mainly to the differences in soil pH between these two locations. Soil pH also differed between slope aspects within the same locations; however, these differences were small and were clearly overridden by much stronger differences between the locations. Species richness and composition analyses corroborated well the differences found in soil pH resulting in stronger differentiation between the locations than between northern *versus* southern slopes within each sampling location. Generally, species richness was notably higher at the Kazbegi site than at the Gudauri site, and northern slope communities were slightly richer as compared to those on southern slopes. Finally, the distribution of both plots and the species in the ordination space (CCA) were driven by soil pH. All in all, our results strongly support our expectation that in temperate high mountains, or at least at alpine-nival ecotone of the central Caucasus, soil pH mediates the relations of plants with climate variables and bedrock, and thus can be a better predictor of species distributions than geographical (altitude), topographical (aspect) or climate variables (Jolokhava et al., 2020, 2021). The important question is why soil pH is so variable in a climatically and geologically similar region. One factor that we did not control and can be an important determinant of this variation is the time elapsed after the last volcanic activity in this region, which might happen at different times at different locations (e.g. Skhirtladze, 1958; Milanovsky & Koronovsky, 1973; Adamia et al., 2010).

The Greater Caucasus is part of the Alpine (Mediterranean) geosynclinal belt (Gamkrelidze, 1986). The main watershed range and adjoining lateral ridges are composed mainly of crystalline rocks and shale. The tectonic activity of the area enhances erosion processes (Tsereteli et al., 2016; Ismail-Zadeh et al., 2020). In areas where weathering and vegetation activity have had less time to develop young soils on basic rocks, the characteristics of the soil primarily reflect the properties of the parent rock, giving it an embryonic quality (Foth, 1951; Jenny, 1994; Egli et al., 2001; Poulenard & Podwojewski, 2006). As previously mentioned, the study area is partially of volcanic origin. Consequently, andesite, dacite, lava, tuff, and residual loam from andesite-dacite are the common parent materials for soils in the Kazbegi region. This may help explain the varying pH values of the soil, as Kazbegi is characterized by moderately acidic reactions, in contrast to Gudauri. Additionally, soil pH can also be sensitive to topography owing to the different exposure to the sun (Jenny, 1941; Chytrý et al., 2007; Bürli et al., 2020). Our previous research at the Kazbegi location indicated that slightly more acidic soils occur on northern slopes, which also correspond to a different composition of plant communities. This aligns with findings from Jolokhava et al. (2020), which suggest that slope aspect preference is a relatively consistent characteristic of plants. The alpine-nival ecotone is particularly sensitive to climate change (Pauli et al., 2003; Parmesan & Yohe, 2003; De Frenne et al., 2013). Soil pH plays a dual role: it acts as a strong filter for community reassembly and is also influenced by climate change. Will global warming accelerate soil formation or, conversely, degrade existing soils? Where can we expect to see these opposing effects? How might these changes impact species composition? Currently, we can only speculate on the answers to these questions, which highlights the need for further intensive studies on soil pH as a significant driver of species distribution patterns along ecological gradients, particularly in mountainous regions. Additionally, exploring the relationships between species richness and soil pH in areas with similar climate, vegetation, and geology may help uncover regional differences that have not been recognized in broader studies.

Conclusions

1 Our results show that soil pH is a key factor in community assembly in the alpine-nival ecotone of the Central Caucasus. Therefore, soil pH should be routinely incorporated in the gradient analyses of alpine plant communities, particularly at and above the alpine-nival ecotone.

2 As any other gradient analyses conducted on vegetation, our work also has clear implications for studies on climate change. In particular, our work suggests that the patterns of species redistribution that might happen owing to global warming cannot be well understood unless soil pH will be included as a factor.

Research data availability

The data used in this study are available from the corresponding author upon reasonable request.

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Supplementary material

Table S1. Distribution of species abundance (countable stems) on the northern and southern slopes of Gudauri and Kazbegi regions in the Central Caucasus.

Species	Study Area				
	Gudauri (N)	Gudauri (S)	Kazbegi (N)	Kazbegi (S)	Total
Alchemilla caucasica	4		12	6	22
Alchemilla chlorosericea			1	4	5
Alchemilla sericea	22	28	6	2	58
Alopecurus glacialis	25	39	84	62	210
Anemonastrum fasciculatum	6	1			7
Antennaraia caucasica			81	9	90
Anthemis iberica				1	1
Anthemis marschalliana	1				1
Botrichium lunaria				1	1
Campanula biebersteiniana			4		4
Campanula ciliata			28		28
Campanula collina	9	83			92
Carduus nutans		1			1
Carex dacica			4		4
Carex tristia	1		48	1	50
Carum caucasicum	10	10			20
Cerastium polymorphum	12	11			23
Chamaenerion angustifolium	1				1
Cirsium ciliatum		1			1
Cirsium obvallatum			1		1
Colpodium versicolor			17		17
Corydalis alpestris	6	9			15
Corydalis angustifolia		13			13
Daphne glomerata			1		1
Delphinium caucasicum			3	25	28
Draba bryoides	7	8			15
Dryopteris oreades			1		1
Erigeron uniflorus		1	15	16	32
Festuca supina	3	13	1	43	60
Festuca varia	8				8
Gentiana angulosa	1	7			8
Gentianella caucasea	18	21			39
Hieracium ruprechtii			3		3
Jurinea filicifolia			1		1
Leontodon hispidus	1	8			9
Luzula spicata			1		1
Minuartia inamoena			1	18	19
Minuartia oreina			13	1	14
Myosotis alpestris	2	8	1	3	14
Nardus stricta			3		3
Pedicularis condensanta	6	17	9		32
Pedicularis crassirostris	4	1			5
Poa alpina	36	10	62	7	115
Potentilla crantzii	17				17
Potentilla gelida		2		5	7
Potentilla reptans	2	1			3
Primula algida	4	6			10

Species	Study Area				
	Gudauri (N)	Gudauri (S)	Kazbegi (N)	Kazbegi (S)	Total
Saxifraga exarata	5	2			7
Saxifraga flagellaris		4	19	11	34
Saxifraga juniperifolia	6		12		18
Saxifraga kartilaginea				1	1
Saxifraga moschata	14	49	41	40	144
Saxifraga scleropoda			1		1
Saxifraga sibirica	29		67	19	115
Scrophularia minima				8	8
Sedum stevenianum			6		6
Sedum tenellum			31		31
Senecio sosnovskyi	6			5	11
Senecio taraxacifolius			1		1
Sibbaldia parviflora			53	9	62
Silene pigmaea			4		4
Taraxacum officinale	2	1			3
Taraxacum porphiranthum	4	6	9	7	26
Taraxacum stevenii			2		2
Tephroseris karjagini		2		11	13
Trifolium polyphyllum			4		4
Tripleurospermum subnivale	68	56	45	11	180
Trisetum spicatum			1		1
Veronica chistosa			4		4
Veronica gentianoides			1		1
Veronica telephiifolia			6		6
Viola minuta			2		2
Ziziphora puschkinii			1	9	10
Ziziphora subnivalis			6		6

Table S2. Soil pH in the sample plots on the northern and southern slopes of Gudauri and Kazbegi regions in the Central Caucasus.

Sampling plots (1 m × 1 m size)	Study Area			
	Gudauri (N)	Gudauri (S)	Kazbegi (N)	Kazbegi (S)
1	7.95	7.80	5.74	5.96
2	7.55	7.95	5.71	5.96
3	7.90	8.0	5.72	5.90
4	7.80	7.7	5.73	5.94
5	7.60	7.95	5.74	5.95
6	7.95	7.95	5.71	5.92
7	7.90	7.90	5.74	5.94
8	7.90	7.90	5.73	5.90
9	8.20	8.20	5.74	5.94
10	8.0	8.0	5.74	5.96
11	7.65	7.65	5.74	5.93
12	7.90	7.90	5.74	5.96
13	7.90	7.90	5.73	5.93
14	8.0	8.0	5.74	5.93
15	7.85	7.85	5.73	5.85
16	8.0	8.0	5.77	5.94
17	8.05	8.05	5.72	5.93
18	7.90	7.90	5.67	5.94
19	7.90	7.90	5.73	5.12
20	8.05	8.05	5.74	5.94