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# Phytodiversity of Relict Steppe Enclaves in the Urals: Experience in Comparative Assessment

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**Abstract**—Unique mountain-steppe ecosystems in the Southern Urals have retained a high level of species and cenotic diversity, despite fragmentation and isolation. Specific features of these ecosystems are described.

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**Key words:** vegetation, steppes, biological diversity, the Urals.

The study of biological diversity and development of measures aimed at its conservation have priority in modern biological science. The urgency of relevant problems is emphasized in a number of international agreements, including the Convention on Biological Diversity adopted by the UN General Assembly in 1992 and ratified by the Russian Federation in 1994 (Convention..., 1994). In this context, it is especially important to further develop and improve methods for assessing biological diversity and to perform such assessments in order to create a basis for of the system of ecological monitoring.

Mountain-steppe ecosystems are among unique natural objects to be studied with respect to biological diversity and its conservation. First of all, they are a natural reserve of the gene pool and cenotic characteristics of steppe vegetation, which is threatened with extinction both in the mountains and in the plains, as well as a natural standard that is invaluable to scientists reconstructing the developmental history of the animal world of mountain countries. In addition, they are of great educational and aesthetic significance and play a major environment-forming role. Against the background of increasing unification of vegetation and its deprivation of regional aspects and original features, protection of the mountain-steppe ecosystem from the invasion of alien plant species and destruction of their unique floristic and cenotic system is of primary importance.

## STUDY REGION, OBJECTS, AND METHODS

The purpose of our studies in the Southern Urals was to assess the floristic diversity of three unique enclaves of steppe vegetation on massifs Vishnevye Gory, Egoza and Sugomak, and Il'men. These massifs are components of the Il'men–Vishnevye Gory com-

plex of magmatic and metamorphic rocks (Varlakov et al., 1998) that extends in the north–south direction for 150 km east of the axis of the Ural Ridge.

Vishnevye Gory is a low ridge (average elevations of about 400 m a.s.l.) composed mainly of miaskites. In places, serpentinites are exposed on the surface. Mounts Egoza (609 m a.s.l.) and Sugomak (591 m a.s.l.), which adjoin each other and are located between Vishnevye Gory and Il'men, consist mainly of serpentinites. The southernmost Il'men massif includes the Il'men Ridge itself (highest elevation, 747 m a.s.l.) and several lower ridges representing its northward extension. It is composed mainly of miaskites and, in places, amphibolites, with serpentinites occurring in the eastern foothills. The study region is in the subzone of pre-forest–steppe pine and birch forests of the boreal forest zone. The mountains are covered with pine (*Pinus sylvestris*) forests (in places, with Siberian larch, *Larix sibirica*) and derivative pine–birch forests (*Pinus sylvestris*, *Betula pendula*, and *B. pubescens*).

In each of the three enclaves, we analyzed the complete floristic composition of vascular plants, described all constituent plant communities, and developed their classification. The areas of the enclaves were determined, and trends in the distribution of plant communities over the ecological profile were revealed. A comparative analysis of these data was performed using the xerophytization index  $I_x$  (the proportion of mesoxerophytes and xerophytes in the ecological structure of communities) and the Sørensen–Csekanowski coefficient. In the case of the Il'men enclave, the results of our previous study (Gorchakovskii and Zolotareva, 2004) were included in the analysis.

**Table 1.** Taxonomic diversity of steppe enclaves

Enclave	Area, ha	Species density (number of species per hectare)	Number of taxa		
			families	genera	species
Vishnevy Gory	37.4	5.29	37	129	198
Egoza	6.4	21.56	33	102	138
Il'men	29.5	7.93	38	137	234
Total in three enclaves	73.3	4.13	44	168	303

### PHYTODIVERSITY AT THE SPECIES LEVEL

Table 1 shows main parameters of species diversity in the enclaves. In the aggregate, their flora comprises 303 species of 168 genera and 44 families. The highest species diversity is characteristic of the Il'men enclave; then follow the Vishnevy Gory and Egoza enclaves. The same applies to the genus and family levels. The index of species density (the number of species per hectare) depends on both species richness and the area of the enclaves. With respect to its value (inversely proportional to the enclave area), the Egoza, Il'men, and Vishnevy Gory enclaves follow each other in decreasing order.

Among 303 species of the mountain-steppe flora, 103 species are common to all three enclaves, 113 species are common to Vishnevy Gory and Egoza, 155 are common to Vishnevy Gory and Il'men, and 103 are common to Egoza and Il'men; 33 species occur only in Vishnevy Gory, 13 species occur only in Egoza, and 66 species occur only in Il'men. Thus, the Il'men enclave ranks first with respect to both species diversity

and specificity of the flora; the Vishnevy Gory and Egoza enclaves rank second and third, respectively. The floras of the Vishnevy Gory and Il'men enclaves are most similar, whereas the floras of the Egoza and Il'men enclaves are least similar to each other.

Specific features of certain floras are revealed by analyzing the spectra of ten leading families with respect to the numbers of species representing them (Table 2). For estimating the degree of similarity or difference between floras on the basis of these spectra, of primary importance are the first three species (the first triad) determining the type of the flora (Khokhryakov, 2000). In the Holarctic floristic kingdom, the first two places are usually occupied by the families Asteraceae and Poaceae. For this reason, the type of flora is determined by the third member of the first triad, and its subtype is determined by the first member of the second triad. Following this procedure, we can attribute the total flora of all enclaves and, somewhat arbitrarily, the flora of Vishnevy Gory to the Fabaceae type (i.e., the southern Mediterranean–Central Asian type) and the flora of the other two enclaves to the Rosaceae (European) type and the Fabaceae subtype, with the latter category reflecting their Mediterranean–Central Asian connections.

To reveal specific features of the total flora or individual floras of the enclaves, it is expedient to consider indices characterizing relationships between taxa of different ranks within them (Table 3). The numbers of families, genera, and species are greater in Il'men, smaller in Vishnevy Gory, and still smaller in Egoza. The enclaves are also arranged in the same order with respect to the numerical ratios of genera to families and species to families. The average number of species per genus (1.8) in the total flora is approximately the same as in the flora of steppes in the Tunkinskaya Hollow

**Table 2.** Family–genus spectra of the flora of steppe enclaves

Family	Enclave						Total flora	
	Vishnevy Gory		Egoza		Il'men			
	number of species	%	number of species	%	number of species	%	number of species	%
Asteraceae	33	16.7	19	13.8	34	14.5	46	15.2
Poaceae	22	11.1	18	13	26	11.1	34	11.2
Fabaceae	17	8.6	10	7.2	20	8.5	29	9.6
Rosaceae	17	8.6	16	11.6	22	9.4	28	9.2
Caryophyllaceae	13	6.6	12	8.7	19	8.1	20	6.6
Lamiaceae	10	5.1	5	3.6	12	5.1	15	5
Scrophulariaceae	9	4.5	9	6.5	11	4.7	15	5
Brassicaceae	10	5.1	4	2.9	9	3.8	12	4
Apiaceae	4	2	3	2.2	7	3	9	3
Ranunculaceae	6	3	4	2.9	8	3.4	8	2.6

**Table 3.** Ratios between taxa of different ranks

Enclave	Numbers of families, genera, and species	Numerical ratios of		Average number of species per genus
		genera to families	species to families	
Vishnevye Gory	37; 129; 198	3.4	5.3	1.5
Egoza	33; 102; 138	3.09	4.18	1.3
Il'men	38; 137; 234	3.6	6.15	1.7
Total flora	44; 168; 303	3.8	6.9	1.8

**Table 4.** Cenotic structure of flora

Cenotic type	Enclave						Total flora	
	Vishnevye Gory		Egoza		Il'men			
	number of species	%	number of species	%	number of species	%	number of species	%
Rock	11	5.6	10	7.2	15	6.4	23	7.6
Steppe	61	30.8	50	36.2	73	31.2	89	29.4
Meadow–steppe	56	28.3	40	29.0	71	30.3	78	25.7
Forest–steppe	13	6.6	9	6.5	15	6.4	16	5.3
Forest	9	4.5	7	5.1	6	2.6	13	4.3
Forest–meadow	19	9.6	15	10.9	21	9.0	28	9.2
Meadow	19	9.6	6	4.3	28	12.0	44	14.5
Ruderal or segetal	10	5.1	1	0.7	5	2.1	12	4.0

(Peshkova, 2001) and the Kan forest–steppe (Polozhii et al., 2002).

The genus spectrum of the Ural mountain–steppe flora is characterized by the prevalence of genera represented by a single species (107 genera accounting for 35.2% of the total species number), 33 genera contain two species, 12 genera contain three species, and three genera contain four species each. The group of multi-species genera is represented by *Artemisia*, *Potentilla* (11 species), *Thymus*, *Euphorbia* (seven species), *Carex* (six species), *Oxytropis*, *Campanula*, *Poa*, *Astragalus*, and *Silene* (five species). The leading positions of the genera *Artemisia* and *Potentilla* make the flora of the Ural enclaves similar to that of steppe islands in the Yenisei region (Polozhii et al., 2002). Malyshev (1972) notes that the number of species in the genus *Potentilla* increases in mountain regions with a continental climate. One more characteristic feature is the relatively high rank of the genera *Thymus* (seven species) and *Astragalus* (five species), which is accounted for by ecotopic features of habitats, on the one hand, and the presence of endemic species in these genera, on the other hand.

With respect to the spectrum of life forms, herbaceous polycarpic plants prevail in the flora of mountain–steppe enclaves, with rhizomatous or tap-rooted species occupying the leading position. Monocarpic species (annual, annual–biennial, or biennial) rank next to

them. The presence of shrubs and dwarf shrubs should be noted, although their proportion in the spectrum of life forms is insignificant.

Plants with the Eurasian type of range prevail in the flora of mountain–steppe enclaves. The proportions of European–western Asian, European–Siberian, and eastern European–Asian species are also significant. Seventeen species are endemic to the Urals and Cisural region.

The ratio of ecological plant groups in the total flora of the enclaves is as follows: xerophytes, 9.6%; meso-xerophytes, 29.4%; xeromesophytes, 36%; mesophytes, 24.1%; and hygromesophytes, 1% (xerophytization index  $I_x = 39$ ). The flora of the Egoza enclave is most xerophytic, and that of Vishnevye Gory is least xerophytic ( $I_x = 49.3$  and 40.4, respectively).

Table 4 shows the cenotic spectrum of the enclaves. It is characterized by the prevalence of steppe plants, including those of stony steppes, which are closely connected with rock outcrops and products of weathering. Meadow–steppe plants are second in abundance; then follow meadow, forest–meadow, rock, and forest–steppe species. The steppe pattern of the flora is best manifested in the Egoza enclave, where the proportion of steppe species reaches 36.2%.

The mountain–steppe flora includes 17 species endemic to the Urals and Cisural region (Table 5).

**Table 5.** Endemic and relict species in the flora of mountain-steppe enclaves

Species composition	Enclave			Total flora
	Vishnevye Gory	Egoza	Il'men	
Endemics				
<i>Astragalus clerceanus</i> Iljin et Krasch.	+		+	+
<i>Astragalus kareliniamus</i> M. Pop.	+	+		+
<i>Aulacospermum multifidum</i> (Smith) Meinsh.			+	+
<i>Dianthus acicularis</i> Fisch. ex Ledeb.	+	+	+	+
<i>Elytrigia reflexiaristata</i> (Nevski) Nevski	+	+	+	+
<i>Minuartia helmii</i> (Fisch.) Schischk.			+	+
<i>Minuartia krascheninnikovii</i> Schischk.	+	+	+	+
<i>Oxytropis approximata</i> Less.			+	+
<i>Oxytropis ponomarjevii</i> Knjasev	+		+	+
<i>Scabiosa isetensis</i> L. Mant.		+		+
<i>Scorzonera glabra</i> Rupr.	+	+	+	+
<i>Serratula gmelinii</i> Tausch.	+		+	+
<i>Silene baschkirorum</i> Jnisch.	+	+	+	+
<i>Thymus bashkiriensis</i> Klok. et Shost.	+		+	+
<i>Thymus punctulosus</i> Klok.		+		+
<i>Thymus talijevii</i> Klok. et Shost.	+	+	+	+
<i>Thymus uralensis</i> Klok.			+	+
Total endemics	11	9	14	17
Relicts				
<i>Alyssum obovatum</i> (C.A. Mey.) Turcz.	+	+	+	+
<i>Anemone sylvestris</i> L.			+	+
<i>Artemisia armeniaca</i> Lam.			+	+
<i>Artemisia frigida</i> Willd.	+	+	+	+
<i>Artemisia sericea</i> Web.	+	+	+	+
<i>Asperula petrea</i> V. Krecz.		+		+
<i>Aster alpinus</i> L.	+	+	+	+
<i>Astragalus danicus</i> Retz.	+	+	+	+
<i>Astragalus falcatus</i> Lam.	+			+
<i>Astragalus onobrychis</i> L.	+			+
<i>Campanula sibirica</i> L.	+	+	+	+
<i>Carex caryophyllea</i> Latourr.			+	+
<i>Centaurea sibirica</i> L.	+	+	+	+
<i>Clausia aprica</i> (Steph.) Korn.-Tr.	+	+	+	+
<i>Cotoneaster melanocarpus</i> Fisch. ex Blytt	+	+	+	+
<i>Echinops ruthenicus</i> Bieb.	+	+	+	+
<i>Festuca pseudovina</i> Hack. ex Wiesb.			+	+
<i>Festuca valesiaca</i> Gaudin	+		+	+
<i>Filipendula vulgaris</i> Moench	+	+	+	+
<i>Galatella angustissima</i> (Tausch) Novopokr.	+	+	+	+
<i>Galatella biflora</i> (L.) Nees.	+	+	+	+
<i>Galium ruthenicum</i> Willd.	+	+	+	+
<i>Galium verum</i> L.	+	+	+	+

Table 5. (Contd.)

Species composition	Enclave			Total flora
	Vishnevye Gory	Egoza	Il'men	
<i>Genista tinctoria</i> L.	+	+	+	+
<i>Goniolimon speciosum</i> (L.) Boiss.	+	+		+
<i>Gypsophila altissima</i> L.	+	+	+	+
<i>Helictotrichon desertorum</i> (Less.) Nevski	+	+	+	+
<i>Helictotrichon schellianum</i> (Hack.) Kitag.	+	+	+	+
<i>Hieracium virosum</i> Pall.	+		+	+
<i>Koeleria cristata</i> (L.) Pers.	+	+	+	+
<i>Linaria debilis</i> Kuprain.	+	+		+
<i>Lychnis sibirica</i> L.	+	+	+	+
<i>Thlaspi cochleariforme</i> DC.		+		+
<i>Onobrychis sibirica</i> (Sirj.) Turcz. Ex Grossh.	+	+	+	+
<i>Onosma simplicissima</i> L.	+	+	+	+
<i>Orostachys spinosa</i> (L.) C.A. Mey.		+	+	+
<i>Oxytropis pilosa</i> (L.) DC.			+	+
<i>Oxytropis songorica</i> (Pall.) DC.			+	+
<i>Oxytropis spicata</i> (Pall.) O. et B. Fedtsch.			+	+
<i>Patrinia sibirica</i> (L.) Juss.			+	+
<i>Phleum phleoides</i> (L.) Karst.	+	+	+	+
<i>Phlomoides tuberosa</i> (L.) Moench	+		+	+
<i>Poa stepposa</i> (Kryl.) Roshev.			+	+
<i>Polygala sibirica</i> L.	+		+	+
<i>Potentilla nivea</i> L.			+	+
<i>Potentilla sericea</i> L.	+	+	+	+
<i>Salvia stepposa</i> Shost.			+	+
<i>Saussurea controversa</i> DC.	+			+
<i>Schivereckia hyperborea</i> (L.) Berkutenko	+	+	+	+
<i>Sedum hybridum</i> L.			+	+
<i>Seseli ledebourii</i> G. Don fil.	+	+	+	+
<i>Silene repens</i> Patrin	+	+	+	+
<i>Spiraea crenata</i> L.	+	+	+	+
<i>Stipa capillata</i> L.	+	+	+	+
<i>Stipa dasyphylla</i> (Lindem.) Trautv.	+	+	+	+
<i>Stipa pennata</i> L.	+	+	+	+
<i>Stipa zalesskii</i> Wilensky			+	+
<i>Thalictrum foetidum</i> L.	+	+	+	+
<i>Thesium arvense</i> Horvatovszky		+	+	+
<i>Thesium refractum</i> C.A. Mey.	+	+	+	+
<i>Thymus marschallianus</i> Willd.	+		+	+
<i>Thymus mongolicus</i> (Ronn). Ronn.			+	+
<i>Thymus petraeus</i> Serg.			+	+
<i>Verbascum phoeniceum</i> L.	+		+	+
<i>Veronica spicata</i> L.	+	+	+	+
<i>Vincetoxicum albowianum</i> (Kusn.) Pobed.	+	+	+	+
Total relicts	47	42	59	66

**Table 6.** Phytodiversity at the level of syntaxa

Enclave	Number of syntaxa*			
	vegetation subtype	formation	group of associations	association
Vishnevy Gory	4 + 1	5 + 2	8	17 + 7
Egoza	4	8	10	18
Il'men	4 + 1	7 + 1	13	20 + 2
Total in three enclaves	4 + 1	11 + 2	26	54 + 9

\* Added values refer to taxa of indeterminate rank (thickets of steppe shrubs).

According to Gorchakovskii's (1969) classification, they belong to the rock–mountain steppe group. In addition, there are 66 relict species. According to the same classification, some of them (e.g., *Sedum hybridum*, *Orostachys spinosa*, *Clausia aprica*, *Patrinia sibirica*, and *Potentilla sericea*) are rock and mountain-steppe species of Asian origin that came to the Urals in the Late Pleistocene or Early Holocene, and other species are relicts of invasion or the steppe plant complex to the north during general warming in the second half of the Middle Holocene.

PHYTODIVERSITY AT THE CENOTIC LEVEL

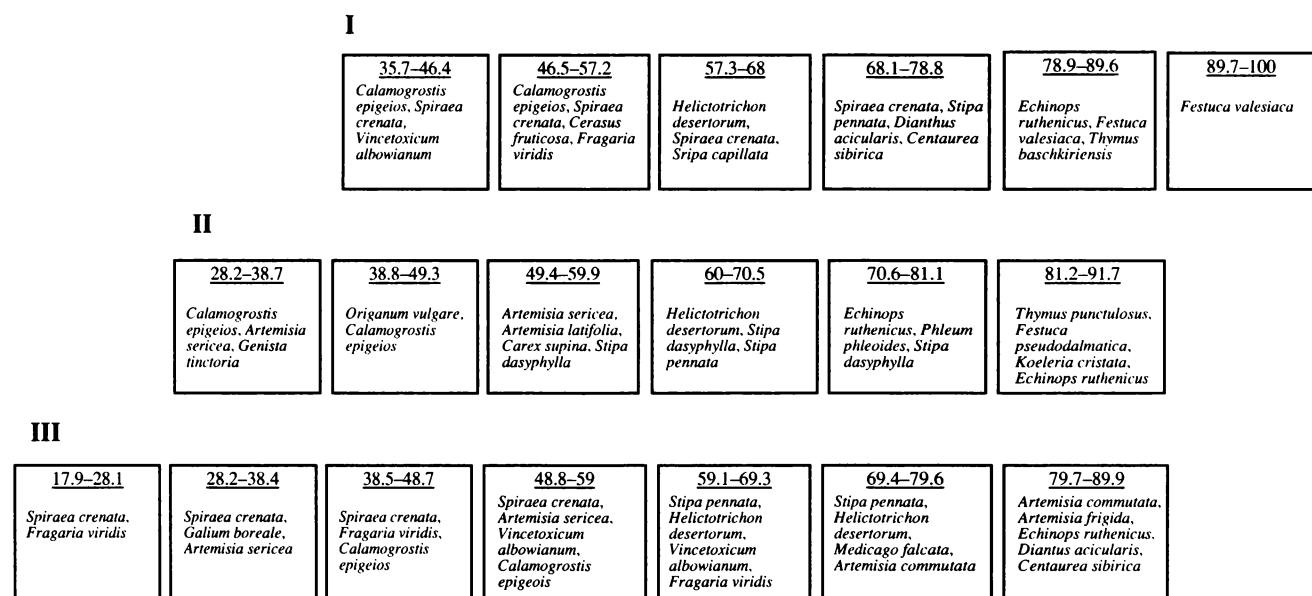
The diversity of vegetation in the steppe enclaves (Table 6) may be reduced to four subtypes: stony steppes, true steppes ("classic" steppes represented in the typical form on the Russian Plain), brush steppes, and meadow steppes. Thickets of steppe brush, which have no definite taxonomic rank, form a separate category that is close to these subtypes. The Il'men and

Egoza enclaves are characterized by higher diversity at the levels of formations and groups of formations, with Il'men ranking first also at the level of associations. Cenotic diversity of the entire flora of the enclaves is very high (54 associations of 26 groups).

Table 7 characterizes the cenotic diversity of steppe enclaves in more detail. Stony and meadow steppes are more diverse in the Egoza enclave; true steppes, in the Il'men enclave, and brush steppes, in the Vishnevy Gory enclave. Steppe communities show a series of transitions from the most xerophilic (stony steppes with  $I_x = 70-100$ ) to more mesophilic communities (thickets of steppe brush with  $I_x = 23.9-60$ ).

A comparative analysis of ecotones (Fig. 1) shows that the Vishnevy Gory enclave is shifted toward the most xerophilic links ( $I_x = 89.7-100$ ) and lacks the most mesophilic components, the Il'men enclave is shifted toward mesophilic links ( $I_x = 17.9-28.1$ ), and the Egoza enclave occupies an intermediate position.

To estimate similarity (interrelatedness) of the steppe complexes according to the Sørensen–Cse-



**Fig. 1.** Ecotones of the vegetation of (I) Vishnevy Gory, (II) Egoza, and (III) Il'men enclaves and dominant plant species in individual links. Figures show values of the xerophytization index ( $I_x$ ).

**Table 7.** Main parameters of vegetation in steppe enclaves

Parameter	Stone steppe			True steppe			Meadow steppe
	V	E	I	V	E	I	V
Number of associations	15	21	13	6	15	33	2
Coverage of herbaceous layer, %	40–80 (61.3)	20–75 (45.5)	20–50 (31.7)	40–80 (61.7)	50–90 (66)	22–77 (51.8)	70–90 (80)
Coverage of shrub layer, %	0	0	0	0	0	0	0
Number of species in community	19–44 (30.5)	16–40 (28.9)	23–42 (31.9)	16–38 (25.7)	32–54 (40.2)	23–55 (35)	39–42 (40.5)
Xerophytization index, %	70.2–100 (82.5)	72.5–90.9 (82.3)	74.1–89.3 (80.8)	62.5–82.1 (74)	50–77.8 (64.5)	50–81.5 (66.3)	35.7–46.2 (40.9)
Parameter	Meadow steppe		Brush steppe			Thickets of steppe brush	
	E	I	V	E	I	V	I
Number of associations	4	1	8	2	5	11	6
Coverage of herbaceous layer, %	70–95 (86.3)	85	50–70 (58.8)	50–90 (70)	68–95 (78.6)	50–90 (67.3)	40–85 (65)
Coverage of shrub layer, %	0	0	8–40 (27.3)	25–30 (27.5)	8–40 (21.6)	50–80 (60.9)	40–90 (53.3)
Number of species in community	37–41 (39)	72	24–71 (45.8)	50–56 (53)	23–67 (37)	20–71 (41.5)	35–69 (57.3)
Xerophytization index, %	28.2–46.3 (39.2)	37.5	45.5–80 (61.1)	35.7–68 (51.9)	17.9–73.9 (53.9)	38–74.2 (55.8)	23.9–60 (44.8)

Note: Letters refer to (V) Vishneve Gory, (E) Egoza, and (I) Il'men enclaves.

kanowski coefficient, we plotted a dendrite that included all phytocenoses described in the enclaves (Fig. 2). It has two main clusters: cluster I comprises thickets of steppe brush, brush steppes, and the most mesophilic steppe phytocenoses (fragments of meadow steppes), and Cluster II comprises communities of true and stony steppes. Cluster II, in turn, divides into two smaller clusters in which correlation pleiads combine communities with similar species composition from the same habitat. Thus, large clusters reflect ecological connections of the vegetation, while correlation pleiads reflect specific features of steppe communities in individual habitats. Stony steppe communities are segregated to the greatest extent, as it is precisely these communities that include species characteristic of a certain enclave.

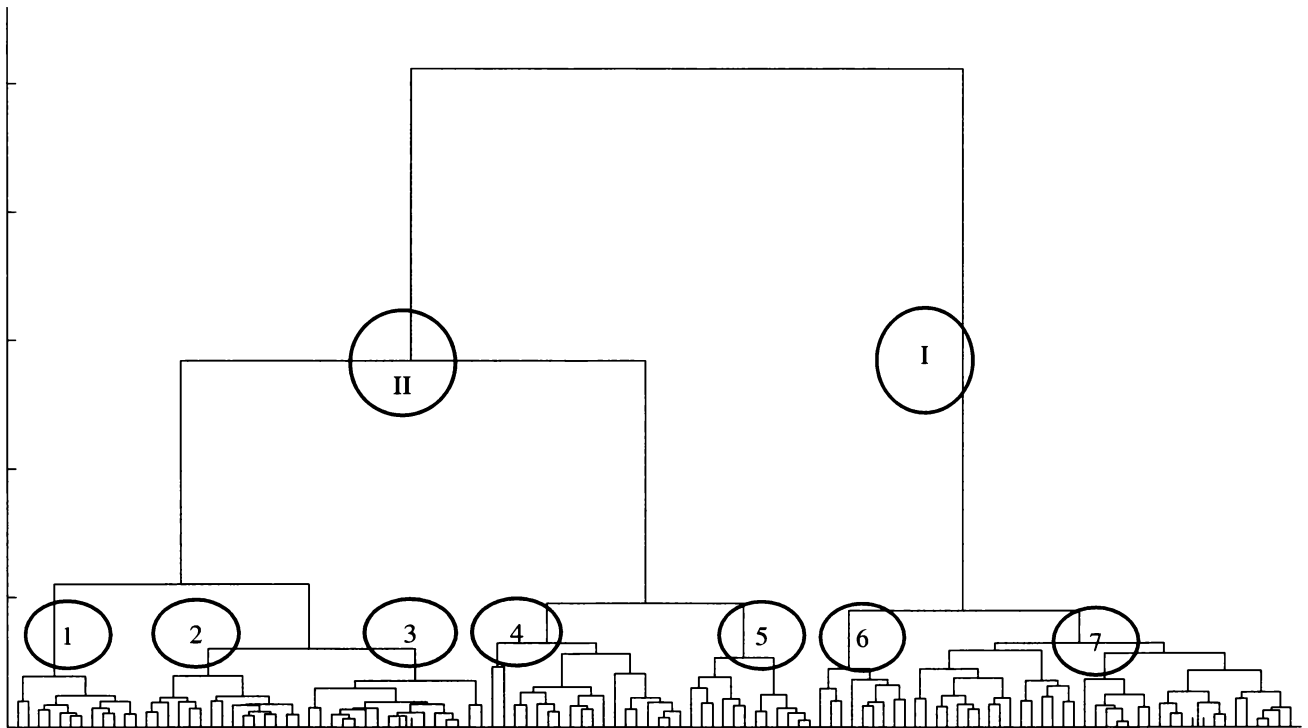
Cluster I consists of two large pleiads, with one of them representing the least floristically segregated communities of three habitats that form different combinations. Mesophilic brush steppes and thickets of steppe brush grow in areas with more temperate conditions, which accounts for the presence of widespread meadow, meadow-forest, and meadow-steppe plants in their composition. This is why segregation of this group with respect to location is weakly manifested. Never-

theless, the Vishneve Gory pleiad is distinct within cluster I, as it includes *Cerasus fruticosa* communities and certain species that are absent from brush thickets of the Il'men enclave.

Cluster II consists of five correlation pleiads that form two groups, with phytocenoses of Mount Egoza and Il'men Ridge in one group and phytocenoses of the Vishneve Gory massif in the other. Correlation pleiad 1 combines stony steppes on mounts Sugomak and Egoza dominated by *Festuca pseudodalmatica* (the most xerophilic communities). Correlation pleiad 2 combines more mesophilic communities dominated by *Echinops ruthenicus*, *Phleum phleoides*, and *Helictotrichon desertorum*. It is connected with the pleiad of stony steppes on the Il'men Ridge (pleiad 3) in which *Artemisia frigida*, *Festuca valesiaca*, and *Dianthus acicularis* are dominant.

Pleiad 4 combines the most xerophilic brush steppes and sheep's fescue (*Festuca valesiaca*) stony steppes on the Vishneve Gory massif. Finally, pleiad 5 combines stony and true steppes of Mount Karavai, part of the Vishneve Gory massif. Their segregation is explained by unique microclimatic conditions characteristic of its steep slopes and anthropogenically affected areas.





**Fig. 2.** Dendrite reflecting the degree of similarity in species composition between steppe phytocenoses according to the Sørensen–Czekanowski coefficient: (I) cluster comprising brush steppes and thickets of steppe brush, (II) cluster comprising stony and true steppes: (1) steppes on mounts Egoza and Sugomak dominated by *Festuca pseudodalmatica*; (2) steppes on mounts Egoza and Sugomak dominated by *Echinops ruthenicus*, *Phleum phleoides*, and *Helictotrichon desertorum*; (3) Steppes on the Il'men ridge dominated by *Artemisia frigida*, *Festuca valesiaca*, and *Dianthus acicularis*; (4) brush and sheep's fescue (*Festuca valesiaca*) steppes on the Vishnevy Gory massif; (5) steppes on Mount Karavai; (6) thickets of steppe brush on the Vishnevy Gory massif; and (7) mesophilic thickets of steppe brush, brush steppes, and meadow steppes of all three steppe enclaves.

## DISCUSSION

Mountain steppes are relatively ancient, as their formation began in the end of the Pliocene. In the course of climatic change and consequent transformation of plant cover in the Pleistocene and Holocene, steppe vegetation periodically expanded or receded. One of the relatively recent periods of its expansion in the Ural Mountains coincided with warming in the second half of the Middle Holocene. Upon subsequent cooling, however, it gave way to forest vegetation, which occupied a major part of the former steppe area. This resulted in fragmentation of steppe vegetation, which disintegrated into a number of enclaves located several dozens of kilometers apart. These enclaves usually represented variants of stony steppes with adjoining more mesophilic plant communities.

Although the mountain-steppe enclaves considered in this study occupy a small area (less than 100 ha), their species richness (303 vascular plant species) is comparable to that of steppe islands in southern Siberia, whose area reaches several tens or even hundreds of square kilometers. Thus, the floras of the Ol'khon and Ubsunur steppes consist of 342 and 361 species, respectively (Peshkova, 2001); the steppe flora of the

Tunkinskaya Hollow, 323 species; and the flora of the Kan forest–steppe, 362 species (Polozhii et al., 2002).

In the course of the aforementioned climatic changes during the Pleistocene and Holocene, the steppe flora in enclaves of the Southern Urals retained its essential components and characteristic spectrum of plant communities due primarily to physicochemical properties of the rock substrate (serpentinites, amphibolites, and products of their weathering) making it unsuitable for the growth of trees. Of major significance was also the fact that these communities included species with different properties that belonged to different ecological and cenotic groups (steppe, meadow–steppe, meadow–forest, and other groups). This accounted for an increase in species diversity in the zone of contact between xerophilic and mesophilic communities (the boundary effect) and provided the possibility of plant migration from one community to another and displacement of plant communities within the ecotone against the background of cyclic climatic changes, with the core of the steppe floristic complex remaining intact even under the least favorable conditions.

To a certain degree, enclaves of steppe vegetation in the Southern Urals have been exposed to anthropogenic

impact (recreation, tourism, and livestock grazing). As a consequence, 26 alien species (anthropophytes) appeared and three species of apophytes improved their positions in steppe communities.

A comparison of our data with the results of previous studies shows that changes occurred in the vegetation of the Egoza enclave during the past few decades. Sochava (1945) described several spots of "brush-herb mountain steppe" dominated by *Cerasus fruticosa*, *Rosa cinnanomea*, and some other species near the ridge connecting mounts Egoza and Sugomak. Today, only separate groups of steppe brush remain there. The retreat and virtual disappearance of shrubs since 1945 may be attributed both to the expansion of forest vegetation and to the effect of frequent fires on the slopes of these mountains. Moreover, Sochava found *Asperula petraea* and Gorchakovskii (1969) found *Orostachys spinosa* on Mount Egoza, but both species have disappeared since then.

### CONCLUSIONS

The unique natural complex of mountain steppes in the Southern Urals largely retained its initial structure, although its area is small and fragmented. This complex has a high phytocenotic diversity manifested at both the species level (alpha-diversity) and the cenotic level (beta-diversity).

The constituent plant communities are characterized by high species richness (up to 72 species in the meadow steppe) and include many typical steppe plants and, which is especially important, a large number of endemic or relict species.

Transformation of habitats under increasing anthropogenic impact creates the risk of destruction of mountain-steppe ecosystems and loss of the gene pool and cenotic characteristics of their plant component. First of all, this concerns the most vulnerable endemic species with their narrow specialization (adaptation to

growth on a stony substrate rich in calcium). It is necessary to take urgent measures aimed at phytodiversity monitoring and conservation in this natural complex, which, in some aspects, is a botanical-geographic paradox.

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