


# IMPACT OF DOMINANTS ON THE SPECIES RICHNESS AND COMPOSITIONAL DISSIMILARITY OF HIGH MOUNTAIN PLANT COMMUNITIES OF THE WESTERN CAUCASUS (CAUCASIAN STATE NATURE RESERVE, RUSSIA)

Valeriy V. Akatov<sup>1,2,\*</sup> , Tatyana V. Akatova<sup>1</sup>, Sergey G. Chefranov<sup>2</sup>, Tatyana G. Eskina<sup>1</sup>

<sup>1</sup>Caucasian State Nature Reserve, Russia

<sup>2</sup>Maikop State Technological University, Russia

\*e-mail: akatovmgti@mail.ru

Received: 20.04.2021. Revised: 07.09.2021. Accepted: 07.09.2021.

Climate warming may cause not only a reduction in the area of high-mountain vegetation, but also a change in the abundance of many species, including dominant ones, which may have additionally negative consequences for plant communities. Therefore, our knowledge how dominants affect high-mountain plant communities at different spatial scales is important to predict changes in their species richness in the future. In this study, we aimed to answer the following questions: i) How does the species richness of high-mountain plant communities of the Western Caucasus depend on the participation of dominant species? ii) Can this relationship be explained on the basis of the «energy diversity» hypothesis? iii) Do dominants affect the degree of similarity (or difference) in the species composition of plant communities located in different habitats? The research was carried out in the Caucasian State Nature Reserve, Russia. The objects of study were seven homogeneous sites of plant communities dominated by *Alchemilla retinervis*, *A. oxysepala*, *Geranium gymnocaulon*, *Carex capillifolia*, *Inula grandiflora*, *Calamagrostis arundinacea*, *Epilobium angustifolium*. Within each of them, biomass samples were taken from 25–30 plots of 0.25 m<sup>2</sup>, which were then disassembled by species and weighed. The participation of dominants (the degree of dominance) was assessed through the ratio of their biomass and biomass of samples as a whole. The results show that, first, most of the studied high-mountain plant communities are characterised by a close relationship between the relative participation of the dominant and the species richness in small plots. Secondly, this connection can be explained on the basis of the «energy-diversity» hypothesis. This means that the size of the species pool of plant communities with different degrees of dominance should be approximately the same. Thirdly, the plant communities with relatively high participation of dominants are characterised by a slightly higher degree of compositional dissimilarity than plant communities with low participation. We have concluded that dominants have a predominantly local effect on the species richness of high-mountain plant communities in the Western Caucasus. However, an increase in their participation leads to a decrease in the occurrence of many accompanying species, and, accordingly, can make these species more vulnerable to the effects of other factors.

**Key words:** accompanying species, biomass, dominants, herbaceous communities, species pool, species richness, species similarity

## Introduction

The Caucasus is located on the border of moderate and subtropical climate zones, moderate damp European and dry Asian regions and therefore it is characterised by extremely various climatic conditions (Gvozdetskiy, 1963). For the last 40 years an increase of average and maximum temperatures in summer and autumn has been observed in the Western Caucasus (Kostianoy et al., 2021). In the same period, there was a positive trend in the Normalised Difference Vegetation Index (NDVI) variability (Lebedev et al., 2021), an upward displacement of the distribution boundary of *Betula pubescens* var. *litwinowii* (Doluch.) Ashburner & McAll. (timberline) and some deciduous species of trees (*Acer platanoides* L., *Ulmus glabra* Huds., and *Acer pseudoplatanus* L.), as well as an increase in the occurrence in alpine plant communities of some species more typical of the subalpine zone (Akatov & Akatova,

2020). According to the scenario considered by Panov (2000), summer and winter temperatures will become approximately 2°C and 4°C higher, respectively, by the year 2050. In this case, the upper forest border should shift upwards 200–300 m (Panov, 2000), while the area of high-mountain plant communities and, accordingly, their species richness should be significantly reduced. In addition, climate warming may cause a change in abundance of many species, including dominant ones, which may have additional negative consequences for the vegetation (Hillebrand et al., 2008). Therefore, the knowledge how dominants affect high-mountain plant communities at various spatial scales is important to predict changes in their species richness in the future.

It has been suggested that the regional consequences of the impact of dominants on local species richness (alpha diversity) of plant communities may depend on how much the accompanying

plant species differ from each other in resistance to this factor (Powell et al., 2011, 2013; Akatov et al., 2018). So, according to the «energy-diversity» hypothesis (Wright, 1983; Srivastava & Lawton, 1998), the higher participation of dominants in the formation of plant communities (degree of dominance, Berger-Parker index based on Berger & Parker, 1970; Magurran, 1988), the less resources remained to other (accompanying) species, the lower their total production, the smaller number of such species will be present on sites of these plant communities. This mechanism assumes that dominants displace other species from sites of plant communities not selectively (random). In this case, dominants can significantly reduce the occurrence of many species, as well as the number of these species in small plots; but they will not be able to significantly change the species richness of communities as a whole (i.e. the size of their species pool) (Powell et al., 2011, 2013; Akatov et al., 2018).

However, dominants can affect accompanying species not only by limiting the resources, but also in another way by changing environmental conditions, for instance, rag accumulation, changes in light and hydrological regimes, physicochemical properties of the soil (Rabotnov, 1983; Levine et al., 2003; Csergő et al., 2013; Bartha et al., 2014). In this case, some species may be less resistant to such effects than others. Therefore, an increase in the dominant participation should be accompanied by the disappearance of predominantly the same (less resistant) plant species from plant communities, and, accordingly, decrease in the size of the species pool of these plant communities. Moreover, this effect can be enhanced, if common plant species are more resistant, or weakened, if rare species are more resistant (Powell et al., 2011). In addition, if dominants have a stronger effect on widespread species (generalists), then an increase in their participation will lead to a decrease in species similarity between plant communities located in various habitats, and consequently to an increase in beta diversity. If species, characteristic of certain habitats (specialists), are less resistant to this factor, then a contrary situation occurs. However, these aspects of the organisation of plant communities, including high-mountain ones, remain poorly understood (Powell et al., 2011, 2013; Rejmánek et al., 2013; Stohlgren & Rejmánek, 2014).

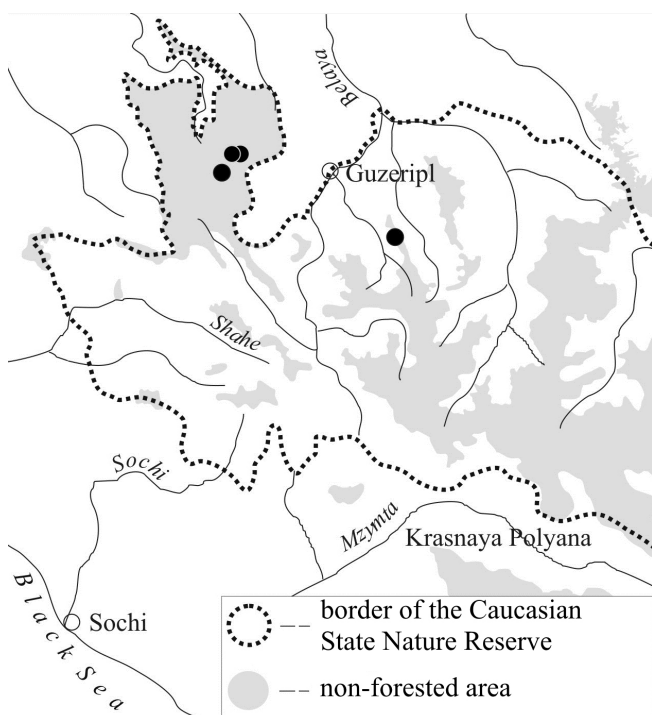
This study is aimed to assess the impact of dominants on the species richness and the degree

of dissimilarity in the species composition of high-mountain plant communities located in various habitats. We aim to answer the following questions: i) How close is the relationship between the participation of dominants and species richness in small plots of high-mountain plant communities of the Western Caucasus? ii) Can the results of the effects of dominant species on the species richness of high-mountain communities be explained on the basis of the «energy-diversity» hypothesis? iii) Do the dominants affect the degree of similarity (or difference) in the species composition of plant communities located in different habitats?

## Material and Methods

### *Study area and objects*

The study area includes two high-mountain massifs of the Western Caucasus within the Caucasian State Nature Reserve, Russia: the Oshten Mount and the Pastbishche Abago Ridge (system of the Greater Caucasus Ridge, Belaya River basin) (Fig. 1). The climate of the high-mountain zones of the study area is cold and humid with a mean temperature of August (warmest month) less than 14°C and average annual precipitation 1200 mm (Varshanina & Mitusov, 2005; Bedanokov et al., 2020). This area includes practically all range of plant communities typical to the high-mountain zones of the Western Caucasus. The subnival vegetation is fragmentary expressed at mountain tops and ridge crests more than 3000 m a.s.l. It is formed by open aggregations of lichens, mosses, and some vascular plants. The alpine belt is located in the altitude range of 2300–2800 m a.s.l. Its landscape is characterised by a combination of stony and grassy slopes, rock streams and screes, glaciers, and snowfields. The most widespread plant communities are rock plant aggregations, alpine short-grass meadows, lichen heaths, mats, and meadows. Altitudes of 1700–2300 m a.s.l. correspond to the subalpine belt. The middle-grass and high-grass meadows and thickets of evergreen shrub (*Rhododendron caucasicum* Pall.) are typical for this area (Shiffers, 1953; Onipchenko, 2002). Alpine communities of the Western Caucasus have approximately the same local species richness as plant communities of the Central Alps developing under similar ecological conditions (Onipchenko & Semenova, 1995), but they have a higher species richness than similar plant communities of the Krkonoše Mountains (Czechia), Altai and Priokhotye Region (Russian Far East), Japan and New Zealand (Onipchenko et al., 2005).



**Fig. 1.** Map of the study area (Caucasian State Nature Reserve, Western Caucasus, Russia). The black dots show locations of the study sites (Oshten Mount, 2356 m a.s.l., 2224 m a.s.l. and 1990–2000 m a.s.l.; Pastbishche Abago Ridge, 1813 m a.s.l.).

The study objects were seven homogeneous sites of plant communities dominated by a certain species: 1) one site of alpine meadow communities dominated by *Alchemilla retinervis* Buser (Oshten Mount, old glacial cirque, 2356 m a.s.l., 44.000833° N, 39.941944° E); 2) two sites of alpine communities dominated by *Geranium gymnocaulon* DC and *Carex capillifolia* (Decne.) S.R.Zhang (Oshten Mount, slope, 2224 m a.s.l., 44.011111° N, 39.955556° E); 3) one site of subalpine communities dominated by *Inula grandiflora* Willd. (Oshten Mount, slope, 1990 m a.s.l., 44.013889° N, 39.974444° E); 4) two sites of subalpine communities dominated by *Calamagrostis arundinacea* (L.) Roth and *Alchemilla oxysepala* Juz. (Oshten Mount, slope, 2000 m a.s.l., 44.017778° N, 39.974444° E); 5) one site of subalpine meadows dominated by *Epilobium angustifolium* L. (Pastbishche Abago Ridge, slope, 1813 m a.s.l., 43.935556° N, 40.221667° E).

The studied plant communities were formed under different conditions. Thus, the plant communities of the alpine belt are subjected to lower temperatures than the subalpine communities. Besides, the floristic composition of both alpine and subalpine plant communities is controlled by the snow cover duration, in relation with variation in mesorelief. Thus, alpine grasslands dominated by

*Alchemilla retinervis* and *Geranium gymnocaulon*, and subalpine plant communities dominated by *Inula grandiflora* develop on habitats with considerable snow accumulation. Alpine plant communities dominated by *Carex capillifolia* are formed on convex slopes with a small amount of snow, where the winter soil temperatures are very low. Meadows dominated by *Calamagrostis arundinacea*, *Alchemilla oxysepala* and *Epilobium angustifolium* occupy the most favourable slopes, where the winter snow accumulation is moderate. At the same time, *Epilobium angustifolium* prefers habitats, which are periodically disturbed by wild ungulates.

### Field sampling

We used the above-ground biomass as a surrogate measure of the production of plant communities according to García et al. (1993), Bhattarai (2017), Ma et al. (2010). The biomass of plant communities was sampled in 2019 and 2020 in the period when the herbaceous layer was at a peak of development. Within the selected sites of plant communities, 25–30 plots (0.5 × 0.5 m) were laid. The major part of the samples was collected in a regular pattern along linear transects including ten 0.25 m<sup>2</sup> plots each. Others were collected in series of five to ten samples per site. In the second case, variants of plant communities with a high and low projective cover of dominant species were selected. In total, we took 195 above-ground biomass samples. In each 0.25 m<sup>2</sup> plot we determined: 1) dry above-ground biomass of the plant communities in general in grams ( $W$ ) and only dominant ( $W_d$ ) and accompanying species ( $W_s$ ); 2) the degree of dominance or participation of dominant ( $D = W_d/W$ ); 3) number of species ( $S$ ) and number of accompanying species ( $S_s$ ). In addition, for each series of samples as a whole, the total number of species ( $N$ ) and total number of accompanying species was determined ( $N_s$ ). Vascular plant nomenclature is based on the database of POWO (<http://www.plantsoftheworldonline.org/>).

### Analysis methods

The analysis of the factual data included the following procedures. For each site, the nature (sign) and closeness of the relationship between the values of the following parameters were assessed: 1)  $D$  and  $S_s$ ; 2)  $D$  and  $W_s$ ; 3)  $W_s$  and  $S_s$ ; 4)  $D$  and  $S_r$ , where  $S_r$  are residues of the variation

in  $S_s$  after excluding the influence of the biomass of accompanying species ( $W_s$ ) on values of  $S_s$  ( $S_r = S_s - S_e$ ). For this purpose, we used the Spearman rank correlation coefficient ( $R$ ). It makes it possible to measure the degree of association between characteristics, irrespective of the distribution law and form of relationship. The  $S_e$  values were determined on the basis of linear or power-law regression models of the  $S_s$  ( $W_s$ ) ratio. If the impact of dominants on the species richness of micro-sites of plant communities is negative and significant and can be explained on the basis of «energy-diversity» hypothesis, it should be expected that: 1) the relationship between values of  $D$  and  $S_s$ , as well as  $D$  and  $W_s$  will be significant negative; 2) the relationship between  $W_s$  and  $S_s$  will be significant positive; 3) the relationship between  $D$  and  $S_r$  will be absent.

If the ratio between the participation of a dominant and the number of accompanying species is determined only by the amount of resources available to them (non-selective displacement of species), the probability of the presence of each species in the groups of samples with LPD and HPD, but with equal total biomass of accompanying species (due to the different number of samples in groups) must be the same. Accordingly, the ratio of the number of detected species of the plant community and ones not found in these groups of samples should also be approximately the same. To test this assumption for each of the seven sites, we (1) formed groups of five biomass samples with LPD and determined the total biomass of accompanying species for them. Then, we (2) formed groups of samples with HPD, in which the total biomass of accompanying species approximately corresponded to the values of this characteristic in groups of samples with LPD. Finally, we (3) compared the total number of species in the groups of samples with LPD and HPD, but having approximately the same total biomass of accompanying species. The ratio of the number of accompanying species found ( $N'_s$ ) and not found ( $N_s - N'_s$ ) in samples with LPD was considered as expected for samples with HPD. The statistical significance of differences in these ratios was assessed using the  $\chi^2$  test.

To estimate the influence of dominants on the degree of dissimilarity in the species composition of the plant communities located in different habitats, we calculated the values of Sørensen coefficient between all sites, separately for groups of

biomass samples with LPD and HPD according to the formula:

$$K_s = \frac{2C}{A+B},$$

where A and B are the number of species in ten samples with respectively the lowest and the highest participations of this species selected in the compared sites, and C is the total number of species in the groups of samples of compared sites.

Higher values of this coefficient indicate less dissimilarity (higher similarity) between sites (groups of samples). We suggest that if dominants do not have a permanent effect on  $K_s$  values, then the species similarity of sample groups with LPD and HPD is on average approximately the same. The significance of the difference between  $K_s$  values was assessed using the Wilcoxon rank sum test. The principal component analysis (PCA) was used to visualise the patterns of (dis)similarity of plant communities with LPD and HPD. Ordination was performed on the basis of data on the presence and absence of species in the samples using PAST 3.16 (Hammer et al., 2001). Seventy biomass samples (seven groups of ten samples) with LPD, as well as 70 samples with HPD, were the subject of this analysis.

## Results

General characteristics of the studied communities are presented in Table 1. It shows that subalpine meadows dominated by *Inula grandiflora* and *Epilobium angustifolium* have the highest average productivity. Among plant communities of the alpine belt, grasslands dominated by *Alchemilla retinervis* and *Geranium gymnocaulon* are the most productive. Plant communities dominated by *Carex capillifolia* have a lower productivity. In addition, this type is the least productive among all studied plant communities. An average higher degree of dominance ( $D$ ) is characterised by alpine plant communities with dominance of *Alchemilla retinervis* and *Carex capillifolia*. A lower degree of dominance was found in subalpine meadows dominated by *Calamagrostis arundinacea*, followed by other plant communities. At the same time, the  $D$  values in communities of all types vary in a wide range. Table 1 also indicates that species richness is the highest in plant communities of subalpine meadows dominated by *Alchemilla oxysepala*. This parameter has lower values in plant communities of the alpine belt, with dominance of *Geranium gymnocaulon*, and subalpine belt, with *Epilobium angustifolium* dominance, followed by other plant communities.

**Table 1.** Characteristics of the studied high-mountain plant communities of the Western Caucasus

Dominant (some typical) species	n	W	D	S	N
		mean ± SE (min–max)	mean ± SE (min–max)	mean ± SE (min–max)	
<i>Geranium gymnocaulon</i> DC. ( <i>Carum meifolium</i> Boiss., <i>Primula amoena</i> M.Bieb., <i>Potentilla erecta</i> (L.) Raeusch.)	25	72.9 ± 6.4 (28.4–150.4)	0.63 ± 0.04 (0.13–0.93)	15.1 ± 0.7 (9–23)	41
<i>Alchemilla retinervis</i> Buser ( <i>Pedicularis nordmanniana</i> Bunge, <i>Chaerophyllum rubellum</i> Albov, <i>Myosotis alpestris</i> F.W.Schmidt)	25	104.2 ± 4.2 (62.2–135.4)	0.75 ± 0.04 (0.24–0.97)	7.7 ± 0.7 (3–16)	28
<i>Carex capillifolia</i> (Decne.) S.R.Zhang ( <i>Vaccinium vitis-idaea</i> L., <i>Carex tristis</i> M.Bieb., <i>Ranunculus breynianus</i> Crantz)	25	32.9 ± 1.5 (21.3–48.5)	0.72 ± 0.04 (0.23–0.95)	8.2 ± 0.6 (4–14)	28
<i>Inula grandiflora</i> Willd. ( <i>Campanula latifolia</i> L., <i>Pedicularis atropurpurea</i> Nordm., <i>Trollius ranunculinus</i> (Sm.) Stearn)	30	165.7 ± 7.3 (104.4–281.8)	0.53 ± 0.04 (0.18–0.92)	9.9 ± 0.4 (5–14)	26
<i>Epilobium angustifolium</i> L. ( <i>Dactylis glomerata</i> L., <i>Brachypodium sylvaticum</i> (Huds.) P.Beauv., <i>Silene vulgaris</i> (Moench) Garcke)	30	229.9 ± 13.1 (106.7–349.1)	0.51 ± 0.04 (0.17–0.86)	12.8 ± 0.5 (9–20)	41
<i>Alchemilla oxysepala</i> Juz. ( <i>Carex brevicollis</i> DC., <i>Solidago virgaurea</i> L., <i>Cota macroglossa</i> (Sommier & Levier) Lo Presti & Oberpr.)	30	139.1 ± 8.5 (51.4–198.7)	0.57 ± 0.03 (0.21–0.81)	22.2 ± 0.8 (16–32)	58
<i>Calamagrostis arundinacea</i> (L.) Roth ( <i>Vicia tenuifolia</i> subsp. <i>subalpina</i> (Grossh.) Zernov, <i>Carex mingrelica</i> Kük., <i>Cephalaria gigantea</i> (Ledeb.) Bobrov)	30	196.7 ± 12.0 (92.2–306.7)	0.64 ± 0.04 (0.21–0.94)	9.3 ± 0.6 (5–17)	39

Note: n – number of samples; W – dry above-ground biomass of the entire plant communities (g/0.25 m<sup>2</sup>); D – degree of dominance; S – species richness per 0.25 m<sup>2</sup>; N – total number of species in a series of samples; SE – standard error.

Table 2 shows the relationships between values of 1) D and S<sub>s</sub>; 2) D and W<sub>s</sub>; 3) W<sub>s</sub> and S<sub>s</sub>; 4) D and S<sub>r</sub>. It can be seen that in most plant communities, both alpine and subalpine belts (dominated by *Alchemilla oxysepala*, *Calamagrostis arundinacea*, *Inula grandiflora*, *Alchemilla retinervis*, and *Carex capillifolia*), there is a negative significant (p < 0.05) relationship between D and S<sub>s</sub>, as well as between D and W<sub>s</sub>, a positive significant (p < 0.05) relationship between W<sub>s</sub> and S<sub>s</sub> and, finally, there is non-significant relationship between D and S<sub>r</sub>. Thus, our results indicate that in these plant communities, the higher participation of dominants, the lower biomass of accompanying species, and the lower species richness. After excluding the influence of the W<sub>s</sub> parameter on the S<sub>s</sub> values, the relationship between D and S<sub>s</sub> disappears. This indicates that the impact of these dominants on the species richness of most alpine and subalpine plant communities can be explained on the basis of the «energy-diversity» hypothesis. Only in plant communities with a high *Geranium gymnocaulon* participation, the relationship between W<sub>s</sub> and S<sub>s</sub> is non-significant, while it is negative significant (p < 0.05) between D and S<sub>r</sub>.

Table 3 presents data on the average species diversity of individual samples and the total number of species in their groups formed on the basis of two features: participation of dominants (LPD and HPD) and equal total (for sample groups) biomass of accompanying plant species due to the various numbers of samples

per group. Groups with LPD consisted of five samples, while groups with HPD consisted of 8–18 samples. Table 3 shows that the average number of species in samples with LPD is expectedly higher than the average number of species with HPD by 1.2–1.9 times. However, the total number of species in the compared sample groups differs to a much lesser extent and in different directions. Only in plant communities with a high *Geranium gymnocaulon* participation, the number of species was significantly lower (p < 0.05) than in plant communities with a low participation of this dominant species. In total 143 species were found in all 195 samples, 118 of which were identified in 35 samples, with LPD (average D = 0.27 ± 0.02 taken from an area of 8.75 m<sup>2</sup>), and 123 species were identified in 95 samples, with HPD (average D = 0.77 ± 0.02 taken from an area of 23.75 m<sup>2</sup>). In these two groups of samples, the difference in the ratios between N'<sub>s</sub> and (N<sub>s</sub> - N'<sub>s</sub>) is non-significant (χ<sup>2</sup><sub>3,84</sub> = 1.45, p = 0.05). Thus, the ratio of the areas of plant communities with the highest and lowest participation of dominants, but with an equal number of species, is approximately 2.7 : 1.0.

The average values of Sørensen coefficient of species similarity were 0.23 ± 0.03 (n = 22) between the groups of samples with LPD, and 0.17 ± 0.02 (n = 22) between the groups of samples with HPD. This means that they do not differ considerably. At the same time, among 22 pairwise-related K<sub>s</sub> variants in 16 cases, the

values of this coefficient were higher between groups of samples with LPD (sum of ranks is 233) and only in six cases with HPD (sum of ranks is 20). This difference is statistically significant (Wilcoxon Rank Sum Test,  $W_{50} = 20$ ,  $p = 0.01$ ). Fig. 2 shows results of the ordination of biomass samples with LPD and HPD. In both cases, samples dominated by different species form clearly distinguishable groups. At the same time, groups of samples with LPD, taken on sites of subalpine communities, are located in the diagram field closer to each other than groups of samples with HPD.

Fig. 3 shows the number of species present in biomass samples taken in plant communities of only one type, or simultaneously in plant communities of two or more types. The groups of samples with HPD, in comparison with groups of samples with LPD, are charac-

terised by a higher number of species found in plant communities of only one type and a lower number of species found simultaneously in several types of high-mountain plant communities. In all groups of samples with LPD, 127 plant species were identified, while 110 species in groups of samples with HPD, and 134 species in all 140 samples. Comparison of the species occurrence in plant communities of different types with LPD and HPD showed that 66 species have an equal occurrence; 35 species have a higher occurrence in plant communities with LPD; 20 species are present only in one group of samples with LPD, but were not found in any group of samples with HPD; six species have a higher occurrence in plant communities with HPD; seven species are present only in one group of samples with HPD, but were not found in any group of samples with LPD.

**Table 2.** Spearman correlation coefficients between  $S_s(D)$ ,  $W_s(D)$ ,  $S_s(W_s)$  and  $S_r(D)$  and dominant species in the studied high-mountain plant communities of the Western Caucasus

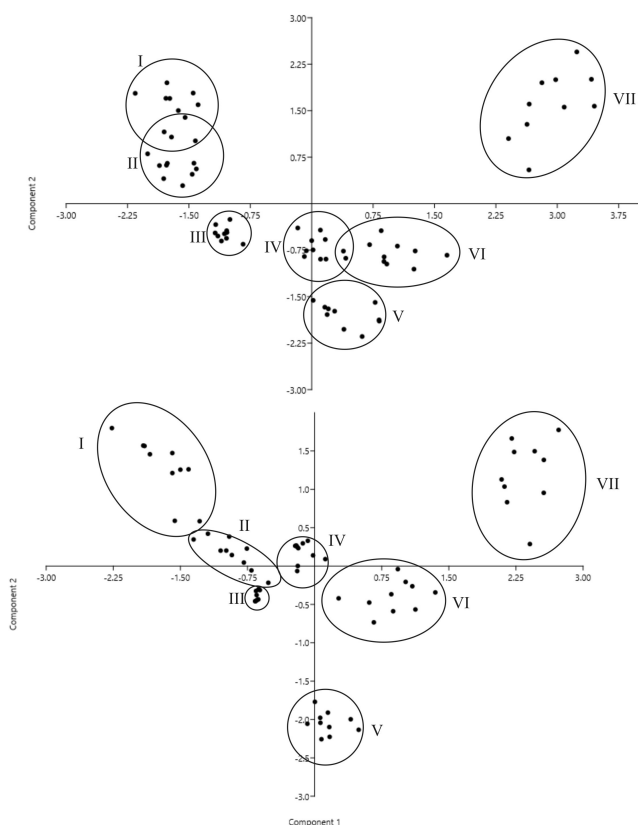
Dominant species of the studied plant communities	$n$	$S_s(D)$	$W_s(D)$	$S_s(W_s)$	$S_r(D)$
<i>Geranium gymnocaulon</i>	25	-0.495*	-0.705*	-0.134	-0.509*
<i>Alchemilla retinervis</i>	25	-0.788*	-0.980*	0.809*	-0.352
<i>Carex capillifolia</i>	25	-0.839*	-0.915*	0.805*	-0.235
<i>Inula grandiflora</i>	30	-0.645*	-0.898*	0.752*	-0.100
<i>Epilobium angustifolium</i>	30	-0.423*	-0.662*	0.207	-0.303
<i>Alchemilla oxysepala</i>	30	-0.733*	-0.836*	0.585*	-0.335
<i>Calamagrostis arundinacea</i>	30	-0.565*	-0.880*	0.551*	-0.190

Note:  $n$  – number of samples;  $D$  – average degree of dominance for the sample;  $W_s$  – total biomass of accompanying species in groups of samples (g/0.25 m<sup>2</sup>);  $S_s$  – average number of accompanying species for the sample; \* – values of statistically significant ( $p < 0.05$ ) Spearman correlation coefficients.

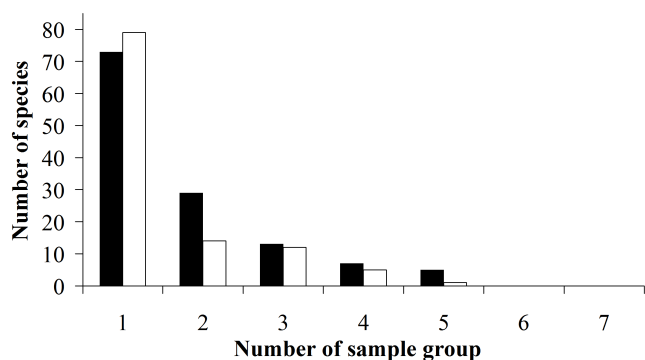
**Table 3.** The number of accompanying plant species in sample groups with different participation of dominants, but having approximately an equal total biomass of accompanying species due to the various number of samples in the groups. Samples were taken from seven high-mountain plant communities in the Western Caucasus

Dominant species	$N_s$	Low participation of the dominant					High participation of the dominant				
		$n$	$D$	$W_s$	$S$	$N'_s$	$n$	$D$	$W_s$	$S$	$N'_s$
<i>Geranium gymnocaulon</i>	42	5	0.44	40.6	19.4	35	10	0.77	40.5	13.2	29*
<i>Alchemilla retinervis</i>	27	5	0.39	61.4	11.4	24	17	0.85	61.5	6.8	21
<i>Carex capillifolia</i>	27	5	0.42	35.5	12.8	23	16	0.83	35.4	6.7	21
<i>Inula grandiflora</i>	25	5	0.22	114.3	11.8	20	13	0.74	114.6	7.8	19
<i>Epilobium angustifolium</i>	40	5	0.22	664.2	12.2	26	8	0.71	661.4	10.3	25
<i>Alchemilla oxysepala</i>	57	5	0.27	74.5	28.0	49	13	0.74	74.4	18.5	47
<i>Calamagrostis arundinacea</i>	38	5	0.25	210.3	11.6	22	18	0.77	210.3	8.1	28

Note:  $n$  – number of samples in groups;  $D$  – average degree of dominance per sample;  $W_s$  – total biomass of accompanying species in groups of samples (g/0.25 m<sup>2</sup>);  $S_s$  – average number of accompanying species per sample;  $N_s$  – total number of accompanying species in the series of samples;  $N'_s$  – number of accompanying species found in groups of samples with different participation of the dominant (HPD vs. LPD); \* – the ratio of  $N'_s$  and  $(N_s - N'_s)$  in the groups of samples with HPD is lower than in the groups of samples with LPD, and this difference is statistically significant ( $\chi^2$  test) ( $p < 0.05$ ).



**Fig. 2.** Ordination of high-mountain plant communities of the Western Caucasus with low degree of dominance, LPD (upper diagram), and high degree of dominance, HPD (bottom part). The analysis was performed by the method of principal components (PCA) based on data on presence and absence of species in samples. Samples taken from certain sites of plant communities are circled with lines as follows: I – dominated by *Geranium gymnocaulon*, II – dominated by *Alchemilla retinervis*, III – dominated by *Carex capillifolia*, IV – dominated by *Inula grandiflora*, V – dominated by *Epilobium angustifolium*, VI – dominated by *Alchemilla oxysepala*, VII – dominated by *Calamagrostis arundinacea*.



**Fig. 3.** The number of species present in biomass samples taken in high-mountain plant communities of the Western Caucasus of only one type, or simultaneously in plant communities of two or more types. Black columns indicate groups of samples with LPD, and white columns shows groups of samples with HPD. In this analysis, we used 70 biomass samples with LPD and 70 samples with HPD (ten samples with the lowest degree of dominance and ten samples with the highest degree of dominance, taken from each plant community).

### Discussion

Our results show that, first, most of the studied high-mountain plant communities are characterised by a close relationship between the relative participation of the dominant and the species richness in small plots, which can be explained on the basis of the «energy-diversity» hypothesis. Secondly, the similar biomass of accompanying species in sample groups with HPD and LPD (due to the various numbers of samples in groups) supports a similar number of such species. This is also consistent with the «energy-diversity» hypothesis. Thirdly, an increase in the participation of dominants leads to a decrease in the species occurrence. It is related to both widespread (generalists) and relatively rare, growing in plant communities of only certain types (specialists). This process leads to some increase in the degree of dissimilarity in the species composition of plant communities located in various habitats. Thus, our results suggest that the accompanying species mostly differ little from each other in resistance to dominants. Consequently, an increase in the participation of dominants leads to the exclusion of mainly different species from small plots of plant communities (random extinction). Accordingly, the size of the species pool of plant communities with different dominance degrees should be approximately the same. As a result, the increase in the participation of dominants should not lead to the complete extinction of some species in relatively large sites of plant communities. Therefore, on larger sites of plant communities with a high degree of dominance, the same number of species can potentially grow as on their small sites with a low degree of dominance, if the biomass of accompanying species on these sites is approximately the same. In our case, the ratio of the area of such sites is on average 2.7 : 1.0. However, the consequence of the increase in the participation of dominants is a decrease in the occurrence of many high-mountain plant species. They will become more vulnerable to effects of other factors, including environmental fluctuations, a reduction in both area and fragmentation of plant communities. Thus, the increase in the participation of dominants affects the species richness of high-mountain plant communities in the same way as a decrease in the area of these plant communities.

At the same time, in plant communities of alpine grasslands dominated by *Geranium gymnocaulon*, the connection between  $D$  and  $S_s$  is relatively weak, while it is absent between  $W_s$  and  $S_s$ , but the relationship between  $D$  and  $S_r$  is moderately negative (statistically significant). In plant communities with a high participation of *G. gymnocaulon*, a certain biomass

of accompanying species supports a smaller number of such species than in plant communities with LPD. This may mean that the relationship between the participation of *G. gymnocaulon* and the species richness of plant communities cannot be explained on the basis of the «energy-diversity». This circumstance is unexpected. According to data of Onipchenko et al. (1998, 2020), obtained at the alpine station «Malaya Khatipara» (Teberda State Nature Reserve, Western Caucasus), *G. gymnocaulon* is characterised by a relatively large area and mass of leaves, large seeds, and a relatively low growth rate, which corresponds to the C-strategy. At the same time, we are not aware of the *G. gymnocaulon* ability to considerably alter its habitats. We assume that on the studied sites of this plant community, the species richness is determined not so much by the degree of *G. gymnocaulon* participation in comparison with other factors, such as the snow cover depth. However, the influence of this factor on the species richness and composition of the plant community could not be estimated during the sampling period (August). Therefore, to test this assumption, special studies are needed.

In general, the data presented in our study are consistent with results of similar studies of plant communities of other types. In particular, we have previously analysed the relationship between the degree of dominance, the density of individuals (or shoots), and the number of species on the sample plots of forest stands and plant communities of riverine shallows in the Western Caucasus (Akatov et al., 2018). Data collection was carried out in basins of the River Malaya Laba, River Belaya, River Pshada, River Shepsi, River Shakhe, River Sochi, River Mzymta and others in the altitude range of 10–2100 m a.s.l., including the Protected Areas (e.g. Caucasian State Nature Reserve, Sochi National Park, Bolshoy Tkhach Natural Park, Maykop Sanctuary). The results showed that in both types of plant communities, the connection between  $D$  and  $S_s$  is moderately negative (statistically significant), but it is absent between  $D$  and  $S_r$ . In addition, we have compared the species richness, species constancy, and the size of the species pool of forest stands with LPD and HPD (Akatov, 2018). We found that forest stands with LPD are characterised by a higher species richness and higher species constancy than stands with HPD. At the same time, the size of the species pool of these plant communities, with some exceptions, turned out to be similar.

Moreover, we considered this issue by the example of six sites of plant communities dominated by the alien species *Solidago canadensis* L., found in various habitats (Belaya River valley, Western Cau-

casus, 190–210 m a.s.l.) (Akatov et al., 2021). The results showed that *S. canadensis* significantly reduces the number of accompanying species in microplots of plant communities. However, the sites of plant communities with a high and low dominance of *S. canadensis*, containing a similar total biomass of accompanying species (due to different area), include, on average, a similar number of such species. It was concluded that the size of the species pools of plant communities with high and low degrees of dominance of *S. canadensis* is approximately the same.

Unfortunately, we are not aware of some other studies devoted to the analysis of the relationship between the degree of dominance and species richness in plant communities based on the «energy-diversity» hypothesis. At the same time, the results obtained using other approaches provide arguments both in favour and against the viewpoint that dominant species can reduce the species diversity of relatively large areas of vegetation (Hejda et al., 2009; Powell et al., 2011, 2013; Stohlgren & Rejmánek, 2014). Overall, however, information on this issue is very limited. Moreover, as objects of study, these authors used plant communities that are most often colonised by alien plant species. In particular, in some studies devoted to the impact of alien dominants on the species richness of plant communities (Gaertner et al., 2009; Powell et al., 2011; Rejmánek et al., 2013), it was shown that invasions rarely cause regional species extinction, although they often reduce diversity in small areas of plant communities.

## Conclusions

Our results show that an increase in the participation of dominants leads to a decrease in the local species richness, as well as to some increase in compositional dissimilarity of high-mountain plant communities of Western Caucasus. However, our results also show that dominants are not able to considerably affect the species richness of alpine plant communities, if their area is sufficiently large. At the same time, an increase in their participation leads to a decrease in the occurrence of many accompanying species and, accordingly, can make these species more vulnerable to the effects of other factors, such as environmental fluctuations. It can be assumed, that the negative role of these factors can significantly increase in the event of climatic changes in the region and, as a result, a significant reduction in the area and fragmentation of high mountain vegetation.

## Acknowledgements

We thank Sergey Trepets (Caucasian State Nature Reserve, Russia) for the technical assistance in preparing the manuscript,



Evgeniya Eskinina (Krasnodar, Russia) for revising the English, and the Russian Foundation of Fundamental Research for financial support (grants No. 16-04-00228 and 20-04-00364).

## References

- Akatov V.V. 2018. The composition, species richness and species pool size of mono- and oligodominant forest stands of the Western Caucasus. *Vegetation of Russia* 32: 3–18. DOI: 10.31111/vegus/2018.32.3 [In Russian]
- Akatov V.V., Akatova T.V. 2020. Contemporary changes of the vegetation in the mountainous Adygea as the reflection of global processes. In: M.K. Bedanokov, S.A. Lebedev, A.G. Kostianoy (Eds.): *The Republic of Adygea Environment*. Vol. 106. Cham: Springer. P. 413–441. DOI: 10.1007/698\_2020\_493
- Akatov V.V., Akatova T.V., Chefranov S.G. 2018. Degree of dominance and species richness in plant communities with high and low intensity of interspecies competition. *Biology Bulletin Reviews* 8(6): 389–400. DOI: 10.1134/S207908641805002X
- Akatov V.V., Akatova T.V., Chefranov S.G. 2021. Impact of *Solidago canadensis* L. on species diversity of plant communities at different spatial scale. *Russian Journal of Biological Invasions* 12(1): 1–10. DOI: 10.1134/S2075111721010021
- Bartha S., Szentes Sz., Horváth A., Házi J., Zimmermann Z., Molnár Cs., Dancza I., Margóczy K., Pál R., Purger D., Schmidt D., Óvári M., Komoly C., Sutyinszki Zs., Szabó G., Csathó A.I., Juhász M., Penksza K., Molnár Zs. 2014. Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands. *Applied Vegetation Science* 17(2): 201–213. DOI: 10.1111/avsc.12066
- Bedanokov M.K., Chich S.K., Chetyz D.Y., Trepet S.A., Lebedev S.A., Kostianoy A.G. 2020. Physicogeographical Characteristics of the Republic of Adygea. In: M.K. Bedanokov, S.A. Lebedev, A.G. Kostianoy (Eds.): *The Republic of Adygea Environment*. Vol. 106. Cham: Springer. P. 19–55. DOI: 10.1007/698\_2020\_637
- Berger W.H., Parker F.L. 1970. Diversity of planktonic foraminifera in deep-sea sediments. *Science* 168(3937): 1345–1347. DOI: 10.1126/science.168.3937.1345
- Bhattacharai K.R. 2017. Variation of plant species richness at different spatial scales. *Botanica Orientalis* 11: 49–62. DOI: 10.3126/botor.v11i0.21033
- Csergő A.M., Demeter L., Turkington R. 2013. Declining diversity in abandoned grasslands of the Carpathian Mountains: do dominant species matter? *PLoS ONE* 8(8): e73533. DOI: 10.1371/journal.pone.0073533
- Gaertner M., Breeyen A.D., Hui C., Richardson D.M. 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: A meta-analysis. *Progress in Physical Geography* 33: 319–338. DOI: 10.1177/2F0309133309341607
- García L.V., Marañón T., Moreno F., Clemente L. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. *Journal of Vegetation Science* 4: 417–424. DOI: 10.2307/3235601
- Gvozdetkiy N.A. 1963. *Caucasus. Essay on the Nature*. Moscow: Publishing house of geographical literature. 264 p. [In Russian]
- Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9.
- Hejda M., Pyšek P., Jarošík V. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97(3): 3393–3403. DOI: 10.1111/j.1365-2745.2009.01480.x
- Hillebrand H., Bennett D.M., Cadotte M.W. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89(6): 1510–1520. DOI: 10.1890/07-1053.1
- Kostianoy A.G., Serykh I.V., Lebedev S.A., Kostianaya E.A., Varshanina T.P. 2021. Regional climate change in the Republic of Adygea. In: M.K. Bedanokov, S.A. Lebedev, A.G. Kostianoy (Eds.): *The Republic of Adygea Environment*. Vol. 106. Cham: Springer. P. 311–357. DOI: 10.1007/698\_2021\_734
- Lebedev S.A., Kostianoy A.G., Kravchenko P.N., Shevyakova O.P. 2021. Seasonal and interannual variability of NDVI in the Republic of Adygea. In: M.K. Bedanokov, S.A. Lebedev, A.G. Kostianoy (Eds.): *The Republic of Adygea Environment*. Vol. 106. Cham: Springer. P. 443–461. DOI: 10.1007/698\_2021\_742
- Levine J.M., Vilà M., D’Antonio C.M., Dukes J.S., Grigulis K., Lavorel S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences* 270(1517): 775–781. DOI: 10.1098/rspb.2003.2327
- Ma W., He J.S., Yang Y., Wang X., Liang C., Anwar M., Zeng H., Fang J., Schmid B. 2010. Environmental factors covary with plant diversity–productivity relationships among Chinese grassland sites. *Global Ecology and Biogeography* 19(2): 233–243. DOI: 10.1111/i.1466-238.2009.00508.x
- Magurran A. 1988. *Ecological diversity and its measurement*. Princeton: Princeton University Press. 181 p.
- Onipchenko V.G. 2002. *Alpine vegetation of the Teberda Reserve, the Northwest Caucasus*. Zürich: Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel. 168 p.
- Onipchenko V., Mark A.F., Wells G. 2005. Floristic richness of three perhumid New Zealand alpine plant communities in comparison with other regions. *Austral Ecology* 30(5): 518–525. DOI: 10.1111/j.1442-9993.2005.01466.x
- Onipchenko V.G., Dudova K.V., Akhmetzhanova A.A., Khomutovskiy M.I., Dzhatdoeva T.M., Tekeev D.K., Elumeeva T.G. 2020. Which plant strategies are related to dominance in alpine communities? *Zhurnal Obshchei Biologii* 81(1): 37–46. DOI: 10.31857/S0044459620010054 [In Russian]
- Onipchenko V.G., Semenova G.V. 1995. Comparative analysis of the floristic richness of alpine communities in the Caucasus and the Central Alps. *Journal of Vegetation Science* 6(2): 299–304. DOI: 10.2307/3236225
- Onipchenko V.G., Semenova G.V., van der Maarel E. 1998. Population strategies in severe environments: alpine

- plants in the northwestern Caucasus. *Journal of Vegetation Science* 9(1): 27–40. DOI: 10.2307/3237220
- Panov V.D. 2000. *Climatic conditions and ecological status of the highland areas of the Republic of Karachaevo-Cherkessia. Evaluation of ecological condition in highland and foothill ecosystems of Caucasus*. Stavropol: Kavkazskiy Krai. P. 53–62. [In Russian]
- Powell K.I., Chase J.M., Knight T.M. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany* 98(3): 539–548. DOI: 10.3732/ajb.1000402
- Powell K.I., Chase J.M., Knight T.M. 2013. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. *Science* 339(6117): 316–318. DOI: 10.1126/science.1226817
- Rabotnov T.A. 1983. *Phytocoenology*. Moscow: Moscow State University. 296 p. [In Russian]
- Rejmánek M., Richardson D.M., Pyšek P. 2013. Plant invasions and invasibility of plant communities. In: E. van der Maarel, J. Franklin (Eds.): *Vegetation Ecology*. Chichester: Wiley-Blackwell. P. 387–424.
- Shiffers E.V. 1953. *The vegetation of the North Caucasus and its natural feeding grounds*. Moscow: AS USSR. 400 p. [In Russian]
- Srivastava D.S., Lawton J.H. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* 152(4): 510–529. DOI: 10.1086/286187
- Stohlgren T.J., Rejmánek M. 2014. No universal scale-dependent impacts of invasive species on native plant species richness. *Biology Letters* 10(1): 20130939. DOI: 10.1098/rsbl.2013.0939
- Varshanina T.P., Mitusov D.V. 2005. *Climatic resources of landscapes of the Republic of Adygea*. Maykop: Adygea State University. 237 p. [In Russian]
- Wright D.H. 1983. Species-Energy Theory: An Extension of Species-Area Theory. *Oikos* 41(3): 496–506. DOI: 10.2307/3544109

## ВОЗДЕЙСТВИЕ ДОМИНАНТОВ НА ВИДОВОЕ БОГАТСТВО И СТЕПЕНЬ РАЗЛИЧИЯ ВИДОВОГО СОСТАВА ВЫСОКОГОРНЫХ РАСТИТЕЛЬНЫХ СООБЩЕСТВ ЗАПАДНОГО КАВКАЗА (КАВКАЗСКИЙ ГОСУДАРСТВЕННЫЙ ПРИРОДНЫЙ ЗАПОВЕДНИК, РОССИЯ)

В. В. Акатов<sup>1,2,\*</sup>, Т. В. Акатова<sup>1</sup>, С. Г. Чефранов<sup>2</sup>, Т. Г. Ескина<sup>1</sup>

<sup>1</sup>Кавказский государственный природный заповедник, Россия

<sup>2</sup>Майкопский государственный технологический университет, Россия

\*e-mail: akatovmgti@mail.ru

Потепление климата может вызвать не только сокращение площади высокогорной растительности, но и изменение численности многих видов, в том числе доминирующих, что может иметь дополнительные негативные последствия для растительных сообществ. Поэтому знание того, как доминанты влияют на сообщества высокогорных растений в различных пространственных масштабах, важно для прогнозирования изменений в их видовом богатстве в будущем. В данном исследовании мы хотим ответить на следующие вопросы: 1) Как зависит видовое богатство высокогорных растительных сообществ Западного Кавказа от участия в них доминирующих видов? 2) Можно ли объяснить эту взаимосвязь на основе энергетической гипотезы? 3) Влияют ли доминанты на степень сходства (или различия) видового состава растительных сообществ, расположенных в разных местообитаниях? Исследования проводились на территории Кавказского государственного природного заповедника. Объектами исследования служили семь однородных участков растительных сообществ с преобладанием *Alchemilla retinervis*, *A. oxyspala.*, *Geranium gymnocaulon*, *Carex capillifolia*, *Inula grandiflora*, *Calamagrostis arundinacea*, *Epilobium angustifolium*. На каждом из них были отобраны пробы биомассы с 25–30 площадок площадью 0.25 м<sup>2</sup>, которые затем разбирали по видам и взвешивали. Участие доминантов (степень доминирования) оценивалось по соотношению их биомассы и биомассы проб в целом. Результаты показывают, что, во-первых, для большинства изученных высокогорных растительных сообществ характерна тесная связь между относительным участием доминанта и видовым богатством на небольших участках. Во-вторых, ее можно объяснить на основе энергетической гипотезы. В-третьих, растительные сообщества с относительно высоким участием доминантов характеризуются несколько более низким сходством видового состава, чем сообщества с низким их участием. Мы пришли к выводу, что доминанты оказывают преимущественно локальное влияние на видовое богатство высокогорных растительных сообществ Западного Кавказа. Однако рост их участия ведет к снижению встречаемости многих сопутствующих видов и, соответственно, может сделать эти виды более уязвимыми к воздействию других факторов.

**Ключевые слова:** биомасса, видовое богатство, видовое сходство, видовой пул, доминанты, сопутствующие виды, травяное сообщество