

Is There a Density Compensation Effect in Plant Communities in Extreme Habitats?

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Abstract—The occurrence of a density compensation effect (DCE) has been estimated in north Caucasian areas of extreme habitats occupied by communities of vascular plants, mosses, and lichens. The species densities have been estimated according to their frequency. The correlation between species number and frequency in the studied areas has failed to confirm the assumption that extreme environmental conditions alone is responsible for the DCE, at least locally.

Keywords: density compensation, species frequency, species richness, vascular plants, mosses, lichens, extreme habitats, north Caucasus

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INTRODUCTION

The density compensation effect (DCE) is known as an increase in the abundance of particular species as a result of their improved resource supply and alleviation of interspecific competition with the loss of other species (MacArthur et al., 1972). It was initially considered a characteristic of mainly insular communities (Crowell, 1962; MacArthur et al., 1972; Case, 1975; Wright, 1980; Tonn, 1985; Carrascal et al., 1992; Sara and Morand, 2002). Then, Yu.I. Chernov (2005) found that this effect is linked to almost all species-poor cenotic systems, including those that develop under extreme environmental conditions. In favor of his assumption, Chernov used as arguments the increased population density of many species and the high dominance level demonstrated by some of them in the taxocenoses of tundras and polar deserts. Then, N.I. Kuznetsova (2009) supported this view by focusing on the high dominance level in species-poor communities of collembolans under extreme conditions.

Nevertheless, Chernov's compensatory processes be regarded as a result of environmental extremeness or did they emerge for other reasons? According to Chernov (2005), all his explanations on the discussed phenomena are controversial and difficult to verify. Actually, the relatively low species richness and high population density of northern biomes, once affected by Pleistocene glaciation, may not be as associated with severe environmental conditions as with their evolutionary youth (Latham and Ricklefs, 1993; Qian and Ricklefs, 2004; Puzachenko, 2006). In turn, the high dominance level in species-poor cenoses may be a consequence of both the DCE and other processes,

such as intensification of competitive advantages of one species over another under conditions of limited resource supply and stress (Akatov et al., 2012).

Unfortunately, the occurrence of and reasons for the DCE are insufficiently covered in the literature. Thus, the question of possible DCE manifestations under extreme environmental conditions remains open. The aim of this work is to consider this problem using a case study of plant communities in the high-mountain zone of the north Caucasus.

MATERIALS AND METHODS

Objects of Study

The objects of our study were herbaceous and shrub communities, as well as groups of epigeic mosses and lichens in the subalpine and alpine belts of the north Caucasus. The material was collected on mountain ridges and massifs in the Belaya, Malaya Laba, and Bol'shaya Laba, Urup, Cherek Bezengiskii, and Alagir river basins. Most of the data were sampled within the Caucasian State Nature Biosphere Reserve and the Kabardino-Balkar Nature Reserve. In the alpine belt, unstable alpine screes were described (associations: *Veronico minutae-Chaerophylletum humilis* Onipchenko 2002; *Campanulo ciliatae-Chamaesciadium acaulis* Onipchenko et Minaeva 2002; *Helianthemum cani* Ermolaeva 2007), areas with a long snow period—mats (*Saxifragetum sibiricae* Onipchenko et Lubeznova 1992), short-grass meadows and heaths (*Pediculari comosae-Eritrichietum caucasici* Minaeva et Onipchenko (2002) (Onipchenko, 2002; Ermolaeva, 2007). In the

Table 1. Description of herbaceous and shrub communities reaching more than 15 cm in height

Communities; altitude a.s.l. (number of descriptions)	Dominant and constant species	<i>N</i>	<i>F</i>	<i>Cd</i>
Meadows; 1700–2450 m (24)	<i>Calamagrostis arundinacea</i> , <i>Festuca woronowii</i> , <i>Bromopsis variegata</i> , <i>Poa longifolia</i> , <i>Brachypodium rupestre</i> , <i>Geranium sylvaticum</i> , <i>Anemone fasciculata</i>	36.20 (12–51)	0.46 (0.33–0.56)	1.81 (1–3)
Snowbed communities with <i>Geranium gymnocaulon</i> and <i>Alchemilla retinervis</i> ; 1920–2100 m (20)	<i>Geranium gymnocaulon</i> , <i>Alchemilla retinervis</i> , <i>Inula grandiflora</i> , <i>Phleum alpinum</i> , <i>Chaerophyllum rubellum</i> , <i>Rumex alpestris</i> , <i>Anthoxanthum odoratum</i>	17.35 (5–32)	0.36 (0.20–0.56)	3.50 (2–4)
Snowbed communities with <i>Rhododendron caucasicum</i> ; 1940–2340 m (12)	<i>Rhododendron caucasicum</i> , <i>Vaccinium myrtillus</i> , <i>Oxalis acetosella</i> , <i>Lerchenfeldia flexuosa</i> , <i>Polygonum carneum</i> , <i>Alchemilla retinervis</i> , <i>Solidago virgaurea</i>	7.92 (3–16)	0.27 (0.16–0.48)	4.00 (4–4)
Subalpine bogs; 1800–2150 m (10)	<i>Carex rostrata</i> , <i>Carex transcaucasica</i> , <i>Carum caucasicum</i> , <i>Taraxacum stevenii</i> , <i>Trifolium badium</i> , <i>Primula auriculata</i> , <i>Cardamine seidlitziana</i> , <i>Swertia iberica</i>	8.80 (3–15)	0.51 (0.13–0.75)	3.30 (2–4)

Mean and limiting (in brackets) values: *N* is species richness of communities; *F* is mean frequency of accompanying species; *Cd* is projective coverage of dominants, grades. Names of species are given by Zernov, 2006.

subalpine belt, phytocenoses of mesophytic and wet meadows were described (associations *Betonici macranthae*–*Calamagrostietum arundinaceae* Onipchenko 2002, according to Onipchenko, 2002); *Cirsio-Nardetum strictae* Akatov 1989, according to Akatov, 1989), areas with a long snow period (including associations of *Hedysaro caucasicae*–*Geranietum gymnocauli* Rabotnova 1987, according to Onipchenko, 2002); *Lerchenfeldio*–*Rhododendretum caucasici* Onipchenko et Sennov 2002, according to Onipchenko, 2002), bogs (*Primulo auriculatae*–*Caricetum rostratae* Akatov 1989, *Primulo auriculatae*–*Caricetum dacicae* Akatov 1989, according to Akatov, 1989). Groups of mosses and lichens were described in communities dominated by *Rhododendron caucasicum* Pallas and *Juniperus depressa* Steven, alpine meadows and heaths, subalpine meadows, and areas with a long snow period. Among the described communities, groups of vascular plants growing on unstable alpine screes, as well as those of mosses and lichens, are open, i.e., characterized by a predominantly low total projective coverage (to 15%), while other groups are closed.

Habitats where the species richness of communities was relatively low were treated as extreme. For herbaceous and shrub cenoses, these are habitats located at a significant altitude (2600–2900 m asl) with either a small or high depth of snow cover in winter (the former are characterized by negative soil temperatures in winter, while the latter are marked by a short vegetation period) and a mobile or waterlogged substrate. For groups of mosses and lichens, these are areas with a long snow period, tangles of high-mountain shrubs, and plant communities with high and dense grasses.

Collection Methods

Data used to calculate the number of species (*N*) and their frequency (*F*) in communities (the frequency was regarded as the index of species density) were collected in the field. The species richness of plant communities growing on unstable alpine screes was estimated in 25-m² areas. The species frequency within their limits was determined by laying down ten plots (0.5 m²) in a regular pattern. The species richness of closed herbaceous and shrub communities was estimated in 15 (16)-m² areas; the species frequency, in 20 plots (0.5 m² each). In addition, the projective coverage of individual species was estimated in communities of vascular plants, which was expressed as grades: (1) 1–25%, (2) 26–50%, (3) 51–75%, (4) 76–100%. Groups of mosses and lichens were described in 25-m² areas, in which ten plots (0.1 m² each) were laid down in a random pattern. The samples were taken from these plots. Species of the above taxonomic groups were identified under laboratory conditions.

In all, 68 areas were described in communities of unstable alpine screes and 127 areas in closed phytocenoses. The total number of areas from which mosses and lichens were sampled was 68 and 72, respectively. The general description of studied communities, as well as values of the estimated parameters, are given in Tables 1–3.

Analysis Methods

Since the high level of dominance in species-poor cenoses may be a consequence of both the DCE and other processes, when testing this effect in the high-altitude communities, we confined ourselves to comparing their species richness (*N*) and mean frequency of

Table 2. Description of herbaceous communities with plants lower than 15 cm

Communities, altitude a.s.l. (number of descriptions)	Dominant and constant species	<i>N</i>	<i>F</i>	<i>Cd</i>
Short-grass meadows 1850–2900 m (36)	<i>Festuca ovina</i> , <i>Carex huetiana</i> , <i>Carex tristis</i> , <i>Alchemilla caucasica</i> , <i>Campanula tridentata</i> , <i>Anthemis marschalliana</i> , <i>Pedicularis sibthorpii</i> , <i>Gentiana pyrenaica</i>	27.63 (16–46)	0.62 (0.31–0.76)	1.64 (1–3)
Heaths (with significant participation of lichens) 2200–2900 m (9)	<i>Festuca ovina</i> , <i>Carex huetiana</i> , <i>Carex tristis</i> , <i>Alchemilla caucasica</i> , <i>Campanula tridentata</i> , <i>Anthemis marschalliana</i> , <i>Pedicularis sibthorpii</i> , <i>Gentiana pyrenaica</i>	19.28 (17–23)	0.67 (0.61–0.80)	2.22 (2–3)
Mats (snowbed communities) 2200–2500 m (16)	<i>Taraxacum stevenii</i> , <i>Sibbaldia semiglabra</i> , <i>Pedicularis nordmanniana</i> , <i>Nardus stricta</i> , <i>Corydalis conorhiza</i> , <i>Carum caucasicum</i>	19.81 (15–26)	0.57 (0.29–0.77)	1.58 (1–3)
Alpine unstable screes 2300–2900 m (42)	<i>Dentaria bipinnata</i> , <i>Corydalis alpestris</i> , <i>Saxifraga sibirica</i> , <i>Oxyria digyna</i> , <i>Chaerophyllum humile</i> , <i>Lamium tomentosum</i>	5.5 (1–9)	0.36 (0.10–0.95)	1 (1–1)

Mean and limiting (in brackets) values: *N* is species richness of communities; *F* is mean frequency of accompanying species; *Cd* is projective coverage of dominants, grades. Names of species are given by Zernov, 2006.

Table 3. Description of groups of epigeic mosses and lichens

Communities; altitude a.s.l. (number of descriptions)	Dominant and constant species	<i>N</i>	<i>F</i>	<i>Fd</i>
Groups of epigeic mosses				
Meadows with short grasses and heaths; 2000–2500 m (36)	<i>Rhytidium rugosum</i> , <i>Polytrichum commune</i> , <i>Hupnum cupressiforme</i> , <i>Dicranum spadicum</i> , <i>Pleurozium schreberi</i> , <i>Entodon concinnus</i>	11.47 (3–20)	0.37 (0.10–0.57)	0.91 (0.3–1.0)
Meadows with medium grasses; 1950–2300 m (6)	<i>Abietinella abietina</i> , <i>Pleurozium schreberi</i> , <i>Hylocomium splendens</i> , <i>Rhytidiadelphus triquetrus</i> , <i>Rhodobryum roseum</i>	10.83 (4–20)	0.49 (0.20–0.49)	0.85 (0.7–1.0)
With <i>Rhododendron caucasicum</i> and <i>Juniperus depressa</i> ; 1850–2200 m (12)	<i>Rhytidiadelphus triquetrus</i> , <i>Dicranum scoparium</i> , <i>Hylocomium splendens</i> , <i>Pleurozium schreberi</i>	10.08 (4–20)	0.27 (0.19–0.40)	0.78 (0.6–1.0)
Snowbed communities; 2000–2400 m (14)	<i>Sanionia uncinata</i> , <i>Brachythecium salebrosusm</i> , <i>Polyrtichastrum sexangulare</i> , <i>Syntrichia norvegica</i> , <i>Distichium inclinatum</i>	8.79 (2–20)	0.28 (0.10–0.50)	0.77 (0.2–1.0)
Groups of epigeic lichens				
Meadows with short grasses and heaths; 2000–2500 m (49)	<i>Cetraria islandica</i> , <i>C. ericetorum</i> , <i>Cladonia arbuskula</i> , <i>Cl. subrangiformis</i> , <i>Cl. pyxidata</i> , <i>Flavocetraria cucullata</i> , <i>Thamnolia vermicularis</i>	11.41 (5–22)	0.46 (0.18–0.78)	0.99 (0.9–1)
Meadows with medium grasses; 1950–2300 (4)	<i>Cetraria islandica</i> , <i>Cladonia cariosa</i> , <i>Cl. pyxidata</i> , <i>Peltigera rufescens</i>	3.50 (1–6)	0.15 (0–0.28)	0.35 (0.1–0.8)
Meadows with short grasses and heaths; 2000–2500 m (18)	<i>Cetraria islandica</i> , <i>Cladonia cariosa</i> , <i>Cl. pyxidata</i> , <i>Peltigera rufescens</i> , <i>Lecanora epybrion</i>	4.00 (1–8)	0.21 (0–0.47)	0.45 (0.1–1)

Mean and limiting (in brackets) values: *N* is species richness of groups; *F* is mean frequency of accompanying species; *Fd* is frequency of dominants. Names of mosses are given by Ignatov et al., 2006; names of lichens are given by Urbanavichyus, 2010.

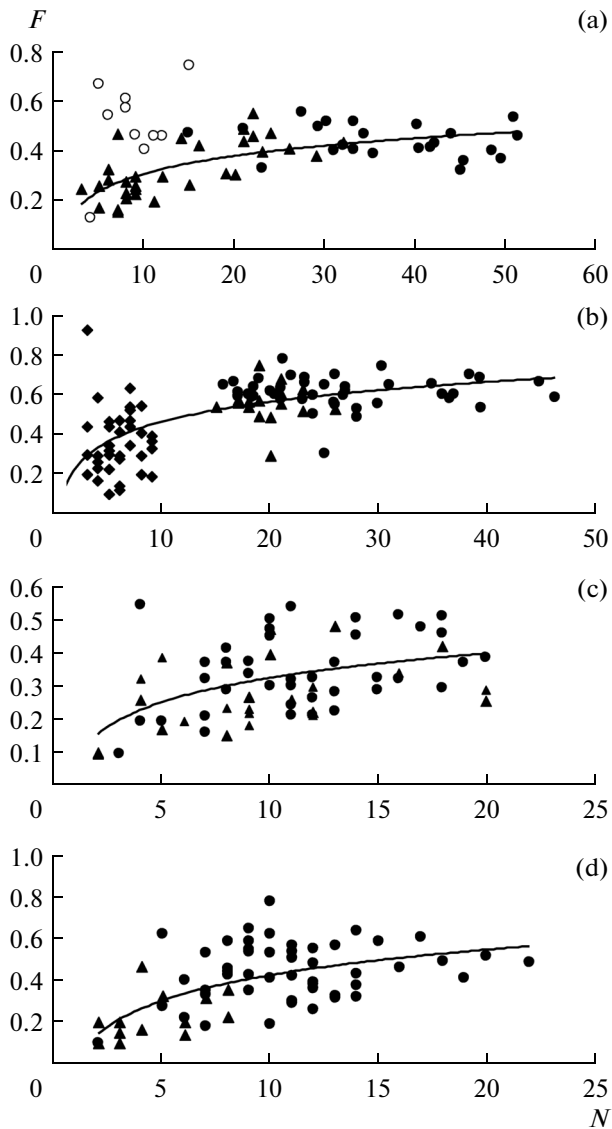


Fig. 1. Ratio between mean frequency of accompanying species of vascular plants, epigeic mosses, and lichens (F) and species richness of their communities (N). (a) Communities of vascular plants higher than 15 cm; (b) communities of vascular plants shorter than 15 cm; (c) communities of epigeic mosses; (d) communities of epigeic lichens. Black circles are communities of meadows and heaths; black triangles are communities of areas with a long snow period; black rhombs are communities of unstable alpine screens; white circles are subalpine bogs.

accompanying species of vascular plants, mosses, and lichens (F) within the studied areas. Interpretation of the ratio between values of these parameters was based on the results of earlier numerical experiments (Akotov et al., 2013; Akotov and Chefranov, 2014).

According to this approach, we modeled scenarios of probable changes in N and F in case of either the presence or absence of compensatory processes. The

results of computer analysis allowed the following assumptions:

(1) In the case of a high DCE, the mean frequency of accompanying species can be expected to increase along the gradient of decreasing species richness of communities.

(2) If there is no DCE, the mean frequency of species in species-poor communities may be lower than that in cenoses with average and high species richness.

(3) The absence of a relationship between the species richness and average frequency of species may be a consequence of either moderate compensatory or random processes. In the latter case, there should be stable values of the mean frequency combined with growing variations in this parameter as the species richness decreases (the high species richness decreases variations in the cenotic parameters via statistical averaging) (Tilman, 1998; Stevens et al., 2003).

Since the size of individuals may have a significant influence on their frequency within small areas, herbaceous and shrub communities with plants growing as high or less than 15 cm were considered separately. The statistical parameters were calculated using Microsoft Excel 2003.

RESULTS

The results are given in Fig. 1 and Tables 1–4. Figure 1a and Tables 1 and 4 show the ratio between the mean frequency of accompanying species, projective coverage of dominant species, and species richness of herbaceous and shrub communities with plants reaching more than 15 cm in height. As can be seen from Table 1, the species richness was lower in communities of subalpine bogs and areas with a long snow period, including those dominated by *Rhododendron caucasicum*; in contrast, it was higher in the subalpine meadows with midgrasses. Species-poor communities are characterized by a higher, on average, coverage of dominant species than those consisting of more species.

As shown in Table 4, the correlation between the species richness of these communities (N) and average frequency of accompanying species (F) is positive, statistically significant, and, at the same time, relatively low (N determines about 10% of variations in F). Nevertheless, it becomes much higher the analysis is performed without consideration of bog communities, which are characterized by a higher average frequency of species compared to the species-poor cenoses of other types (Fig. 1a, Table 4).

Fig. 1b, as well as Tables 2 and 4, show the ratio between mean frequency of accompanying species, coverage of dominant species, and species richness of herbaceous phytocenoses with short grasses (with the grass stand of less than 15 cm in height). As shown in Table 2, the lowest species richness is typical for the open communities of unstable alpine screens, the average one is in the areas with either little or plenty of

Table 4. Dependence of mean frequency of accompanying plant species (F) on species richness of communities (N)

Communities	Factor	n	R^2	r	P
Shrub and herbaceous, grasses higher than 15 cm: in general, without bogs	N	66	0.1026	0.320	<0.05
	$\ln N$	56	0.480	0.693	<0.001
Herbaceous, grasses shorter than 15 cm; in general, without unstable alpine screes	$\ln N$	109	0.428	0.654	<0.001
	N	61	0.008	0.091	–
Mosses	$\ln N$	68	0.237	0.487	<0.001
Lichens	$\ln N$	72	0.405	0.636	<0.001

n is number of sample plots; R^2 is determination coefficient, r is Pearson's correlation coefficient; P is significance level.

snow (heaths and mats), and the highest one is in the alpine meadows. It also follows from the same table that the dominant species of unstable alpine screes are characterized by the lowest projective coverage, those of heaths are marked by the highest coverage, and the communities of meadows and mats different significantly in their species richness have the average one. As it comes from Fig. 1b and Table 4, if to combine all data on these communities, the relationship between species richness ($\ln N$) and average frequency of accompanying species (F) will be positive; if to take into account only closed communities, no relationship will be found.

In Table 3, the ratio is given between the frequency of most abundant species, average frequency of accompanying species, and species richness of groups of epigeic mosses. As it can be seen, the groups of mosses, which developed on different types of habitats, are characterized by similar average and limiting values of these parameters. Thus, each of them has groups with both relatively low and high species richness. In addition, as it follows from Fig. 1c and Table 4, there is a positive dependence between the species richness ($\ln N$) and mean frequency of accompanying species in the groups of epigeic mosses. Therefore, species-poor groups are characterized by a lower, on average, frequency of species than multispecies ones.

Figure 1d and Tables 3 and 4 show the ratio between the mean frequency of accompanying species, the frequency of the most abundant species, and species richness of groups of epigeic mosses. As can be seen from Table 3, the lowest species richness is found in groups from areas with a long snow period and subalpine meadows with midgrasses and heaths. Species-poor groups of lichens are characterized by a lower, on average, frequency of the most abundant species and by the mean frequency of accompanying species than groups consisting of more species. As follows from Fig. 1d and Table 4, there is a positive statistically significant correlation between the species richness ($\ln N$) and average frequency of accompanying species (F).

DISCUSSION AND CONCLUSIONS

The results of our study show that the extreme habitats of the north Caucasian high-mountain zone are occupied mainly by plant communities with a relatively low and not high frequency of accompanying species. It can be assumed that this phenomenon may be caused by two factors.

First, a decrease in the quality of the environment (reduction in resources and vegetation period, increased frequency of disturbances, etc.) may lower the abundance (projective coverage, frequency) of each or all species, as well as result in the development of open interactive communities, such as plant communities of mobile mounds, mosses, and lichens.

Second, as environmental conditions worsen, competition between species may not ease, perhaps becoming even more intensive and asymmetric. Competitive advantages of dominant species intensify, their abundance and projective coverage increase, and the abundance (frequency) of other species gets lower. As a result, closed phytocenoses with a high level of dominance and low frequency of accompanying species develop in extreme habitats, e.g., communities of areas with a long snow period dominated by *Rhododendron caucasicum*, *Geranium gymnocaulon* DC, or *Alchemilla retinervis* Buser.

The second assumption is supported, e.g., by the fact that the occurrence of species in communities of extreme habitats is commonly very consistent with the geometrical model (Whittaker, 1980; Meggaran, 1992; Kuznetsova, 2009). According to this model, as the species richness of cenoses decreases, first-rank species include more and more of their individuals, while other ranks subsequently (from one rank to another) include more and more of the remaining individuals. In addition, the density of first-rank species increase, while that of other species decreases.

Phytocenoses of subalpine bogs are of special interest. They are characterized by a low species richness and relatively high mean frequency of accompanying species, which is a sign of the DCE. Nevertheless, note that these communities develop in specific habitats, they are

represented by small segments in the studied area, and used to be more widespread in the past (Tumadzhyanov, 1962). In the opinion of I.I. Tumadzhyanov, they are an example of relict (extinct) bog formations, which are rare in the Caucasus, once widespread on the periphery of ancient glaciation in the lower belts of the north Caucasus (Tumadzhyanov, 1962). From the viewpoint of flora classification, these communities are depleted variants representing associations of northern eutrophic bogs of the class *Scheuchzerio–Caricetea nigrae* (Nordh. 1936) Tx. 1937 (Akatov, 1989; Onipchenko, 2002). For this reason, it can be assumed that manifestation of the DCE in them is caused not so much by extreme environmental conditions as by the above-listed factors, i.e., by the peculiarities of their history and isolation.

Earlier, we obtained similar results with plant communities of anthropogenic habitats and the tree layer of the west Caucasus (Akatov et al., 2013; Akatov and Chefranov, 2014). In particular, they demonstrated the transformation of natural habitats into anthropogenic ones, resulting in decreased species richness of communities within small areas, but it did not cause the DCE to spread. We also revealed that poor-species communities of trees in the west Caucasus may be characterized by both high and low mean density of accompanying species. Herewith, the highest number of areas, where the population density turned out to be increased, was found in the species-poor high-mountain and subalpine communities that developed in habitats considered as extreme for forest plants, as well as cenoses with more species with dominance or participation of *Quercus robur* L. and *Castanea sativa* Miller, which are distributed under the favorable (warm and humid) conditions of low mountains. In addition, all these communities are considered species-depleted as a result of historical processes (Maleev, 1941; Ratiani, 1979; Galushko, 1976; Dolukhanov, 1980).

Therefore, our results do not prove the assumption that extreme environmental conditions of both natural and anthropogenic origin alone cause the DCE, at least locally.

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