

The Effect of Density Compensation in Species-Poor Plant Communities of Mainland Areas (on the Example of the Western Caucasus)

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Abstract—There is much evidence of the effect of density compensation in the island biota, while the data on its distribution pattern and reasons of appearance in the inland communities are still insufficient and contradictory. We have evaluated the intensity of the effect of density compensation in species-poor plant communities of the natural (seminatural), anthropogenic, and fragmented habitats of the Western Caucasus as one of the inland regions. For this purpose, we have compared the species diversity, relative density (biomass) of predominating species, and mean occurrence of accompanying species in closed communities, as well as the species diversity and mean occurrence of species for open communities. The data show that the domination level and mean occurrence of species in the species-poor phytocenoses may differ and may be related to species organization and the regime of local disturbances. Among the studied communities, the rise in the mean species occurrence, contrary to the species diversity, was only revealed for segetal cenoses and plant groups of meander bars, which are mainly formed by species with R-strategy. We suppose that the effect of density compensation in closed communities mainly results from a drop in the density of predominating species as a result of local disturbances or other reasons, in combination with the limited size of their species pool.

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INTRODUCTION

When several species use the same resources, their populations are smaller in comparison than in the situation in which each one uses the resources itself. That is why a decreased abundance or disappearance of some species in communities may be compensated for by the increased abundance of other species. This phenomenon is known as the effect of density compensation (EDC) (Crowell, 1962; MacArthur et al., 1972; Gonzalez and Loreau, 2009). It may be accompanied by the niche expansion of the preserved species (the spectrum of occupied habitats) and may be a part of a larger phenomenon known as the effect of ecological release (Crowell, 1962; Gonzalez and Loreau, 2009).

Initially, the phenomenon was most often related to the biota of islands (Crowell, 1962; MacArthur et al., 1972; Case, 1975; Emlen, 1979; Wright, 1980; Tonn, 1985; Carrascal et al., 1992; Sara and Morand, 2002; Bolotov, 2014). It was then used for inland communities that were at early evolution stages, underwent disturbance, developed under extreme environmental conditions, or underwent anthropogenic transformation (Hawkins et al., 2000; Kaspari et al., 2003; Chernov, 2005; Akatov et al., 2005; Morozov, 2009; Gon-

zalez and Loreau, 2009; Kuznetsova, 2009; Longino and Colwell, 2011). There is an opinion that EDC may favor the stabilization of the functional parameters of ecosystems upon a decrease in their species diversity and that is one of the indicators of the role of the inter-species competition in the community organization (Tonn, 1985; Adler and Bradford, 2002; Bai et al., 2004; Gonzalez and Loreau, 2009). Meanwhile, the information on its distribution and reasons for its appearance in the inland communities is scant and contradictory.

For example, in the opinion of Chernov (2005), the compensation may appear in any low-species cenosis, in particular, those formed in extreme habitats. This is proved by examples of the great density of species populations and the high domination rate (the Berger-Parker index) in various taxocenoses of tundra and Arctic deserts. This point of view was then confirmed by Kuznetsova (2009) by the example of collembolans communities. The scientist points out that the great total number of these invertebrates under extreme conditions is usually related to a high population density of only one species. The part of such species may be as high as 0.7–0.9 of the total number of animals.

There are other numerous data confirming the fact that species-poor cenoses are mainly characterized by a higher relative abundance of predominating species than species-rich cenoses (Able and Noon, 1976; Bigon et al., 1989; Vasilevich, 1991; Panchal and Pandey, 2004; Akatov and Perevozov, 2011; Akatov, 2014). Nevertheless, this correlation cannot be used as the evidence of the EDC, because it may be caused by other processes. The relative abundance of predominating species may be determined by many factors, including biological features of species, the rate of competitive asymmetry among the species under different conditions of the environment, the amount of available resources, or occasional factors (Bakanov, 1987; Vasilevich, 1991; Koike, 2001; Brown et al., 2001; Burnham, 2002; Sugihara et al., 2003; Macia and Svenning, 2005; Raybaud et al., 2009; Kuznetsova, 2009; Anbarashan and Parthasarathy, 2013; Akatov, 2014). The smaller the participation of a dominant is, the more resources remain for other species, the lower is the probability of their death, and the higher is the cenose species diversity (Whitaker 1980; Bigon et al., 1989; McKane et al., 2002; Kunte, 2008). We have already analyzed this problem by the example of tree communities in the Western Caucasus and have not revealed reliable evidence of the concept that species diversity exerts a significant effect on the relative abundance of dominants (Akatov and Perevozov, 2011; Akatov and Chefranov, 2014; Akatov, 2014).

The high mean density of species population in the communities under extreme conditions may be related to other reasons. Many of these cenoses are young from the point of view of evolution, those of the extreme north in particular (Latham and Ricklefs, 1993; Qian and Ricklefs, 2004). Their area may be small and they may be strongly isolated because of specific species composition, for example, the communities of patients with specific ecotops (Rabotnov, 1983). There are data showing that the mean density of ant species in the tropic deserts and rain forests of the New World is lower than in the biomes located to the north of them (Kaspari et al., 2003). The scientists suppose that this is related to some specific features of these communities and to the smaller rate and frequency of their disturbance within the Pleistocene glaciations cycles. The relatively great mean density of species of the same insect group in the top belts of the mountains is explained by historical events (Longino and Colwell, 2011). Nevertheless, their effect on the formation of the EDC is not obvious. For example, the structure of species abundance of night bats in the temperate regions of the New World is similar to that in the tropical regions contrary to ant communities (Stevens and Willig, 2002). In some cases, the low species diversity of communities, which was caused by the effect of historical factors, resulted in a lower population density. By the opinion of Eizenberg (1983), the lower population density of herbivores in the savanna ecosystems in the southeastern Asia in comparison

with that in the similar habitats of Africa is mainly related to the historically formed poorer species composition of the Asian communities and not to the differing ecological capacities of these habitats.

In the opinions of some scientists, the EDC may be formed in communities of anthropogenic habitats (Tomiałojć, 2000; Gonzalez and Loreau, 2009; Kuznetsova, 2009; Morozov, 2009). In his review, N.S. Morozov (2009) analyzes the works that contain evidence that the building-up of suburb biotops usually results in a drop in the number of nesting bird species and a rise in the absolute population density of a small number of bird species that adapt well to urban conditions. The works summarized by Kuznetsova (2009) contain evidence that the low species diversity of collembolan taxocenoses in extreme anthropogenic habitats, which have natural analogs (pastures, dumps of household rubbish, eutrophic areas), is compensated for by the high density of some species (their domination rate may be as high as 90–95%). If there are no natural analogs of the anthropogenic habitats (for example, those contaminated by heavy metals), the low species diversity is not compensated for. By the opinion of the author, this may be related to the absence of specialized species in these communities and the slight interaction between them. The data on species diversity and the pattern of species significance in the human-transformed communities of plants, soil invertebrates, beetles, and birds are summarized in a work by Vainert (1988). It is shown that anthropogenic disturbance results in the species diversity of cenoses and differently directed changes in the pattern of species significance. An increase in the population density of predominating species and a decrease in the density of accompanying species is seen more often than the opposite situation.

A considerable decrease in species diversity and the EDC was not revealed in most human-fragmented cenoses (Klein, 1989; Connor et al., 2000; Brotons et al., 2003; Anjos, 2004; Bender et al., 1998; Ricketts, 2004; Watling and Donnelly, 2006; Morozov, 2009). This may be related to slight isolating properties of the environment (the fragments in an agricultural or technogenic landscape are not the real islands) or to a low rate of species death in combination with the periods of isolation of the communities (Brotons et al., 2003; Anjos, 2004; Watling and Donnelly, 2006). Nevertheless, there are examples of opposite regularities. The strongly fragmented forests of Europe are characterized by a smaller species diversity of nesting birds and a greater share of species with high population density when compared to larger forest massifs (Morozov, 2009).

There are also the examples (the experimental data in particular) of different reactions of species upon the disappearance or a sharp drop in the number of the competitive species as a result of a disturbance or fluctuations of the environment. For example, a decrease

in the number of big species of primates as a result of hunting caused a rise in the density (biomass) of smaller species (Peres and Dolman, 2000; Zambrano et al., 2008). The disappearance of *Castanea dentata* (Marsh.) Borkh. in the broad-leaved forests of the southern part of Appalachian Mountains, which was due to disease caused by an invasive pathogenic species (*Endothia parasitica*), resulted in a considerable rise in the population density of some other tree species: oaks (mainly *Quercus prinus* L. and *Q. rubra* L.), different species of hickory, and *Liriodendron tulipifera* L. in places. A sharp drop in the population density of *American elms* in the plain forest of the United States of America related to Dutch elm disease and phloem necrosis caused a rise in the occurrence of some other species with respect to regional conditions, *Acer saccharum* Marsh. and *Fraxinus americana* L., in particular (Spurr and Barnes, 1984). The data of numerous field experiments provide evidence of the different reactions of plant communities on the disappearance of dominants in them (Souza et al., 2011). For example, this resulted in a decrease in the density of subdominants and in different reactions of other species in the alpine phytocenoses of the western Caucasus (Aksenova et al., 2004; Cherednichenko, 2004; Bidzhieva, 2005). The correlation between the species density of various groups of organisms (plants, mollusks, insects, fishes, reptilians, birds, small mammals, parasitic organisms, and others), using the similar resources is usually positive (synchronous) and not negative (compensational) (Houlahan et al., 2007; Tello et al., 2008; Morozov, 2009; Bloch and Willig, 2012). Some scientists conclude that the variation in the number of competitive species exerts a smaller effect on species participation in the inland communities in comparison with the island cenoses (Buckley and Jetz, 2007).

There is an opinion that, when phytocenoses are formed by species with similar ecological requirements and their structure is determined by the competition between the species, the disappearance of some of them as a result of destruction or isolation should be accompanied by a stronger position of the remaining species. This is not the case for communities composed of ecologically different and slightly competing species, which are unable to increase their productivity even when free resources appear (Wright, 1980; Tonn, 1985; Adler and Bradford, 2002). It may be assumed that the rate of the EDC in communities is determined by their type of organization (model).

Several nonalternative approaches to the specification of such models have been proposed. According to one of them, communities are specified into two groups with intensive (interactive cenoses) and un-intensive (noninteractive cenoses) species interaction (Cornell and Lawton, 1992; Cornell, 1993). The former are mainly determined by biotic interactions, while their role is restricted in the latter. Their niche is opened, and their colonization by new species is occa-

sional. Communities of extreme or often disturbed habitats are assigned to the second group.

Grime recognized three types of habitats with different models of plant communities: (1) stable high-productive, (2) stable low-productive, and (3) often disturbed high-productive ones (Grime, 1977). The communities of the first type are predominated by competitively strong perennials, which can invade the area but suffer from habitat disturbance (*C-strategists*). The habitats of the second type are occupied by competitively weak species that are resistant to the effect of abiotic (stress) factors (*S-strategists*). The third habitat type is mainly represented by highly reproductive annuals, which may quickly use the free areas and resources (*R-strategists*). There is an approximate correspondence of *C* plants to violents, *S* plants to patients, and *R* plants to explorers according to the classification by L.G. Ramenskii (Onipchenko et al., 1998).

Communities that are characterized by very intensive interspecies interaction (for example, forest or meadow associations) are assigned to the *C–S* or *C–R–S* models according to the polymodel concept by B.M. Mirkin. Communities with little interaction between the species are classified as the *S* abiotic (communities under extreme conditions, where competition is almost absent and each species complies with its own population laws) or *R* (often disturbed communities of mainly high-productive habitats) models (Mirkin, 1994; Mirkin and Naumova, 2012). It is assumed that there are numerous transitional types of communities between the main ones. Nevertheless, we have not revealed published works devoted to specificity of the EDC in the communities of different organization types.

Therefore, the question concerning the cases and rates of the EDC manifestation in the communities of mainland areas is open to discussion. Summarizing the published data (Akotov et al., 2013a, 2013b; Akotov et al., 2014; Akotov, 2014; Akotov and Chefranov, 2014) and new materials, we try to answer this question by the example of the Western Caucasus, one of the mainland regions. This area is characterized by considerable landscape, cenotic, and species diversity and is representative for the solution of this kind of problem.

MATERIALS AND METHODS

Investigation Region and Objects

In this work, we have used the data obtained in the period of 1986–2014. The studied region covers the area from the Taman' Peninsula to the high ridges of Karachaevo-Cherkessiya. The investigation object is represented by plant communities of natural (seminatural) and anthropogenic habitats. They are characterized by relatively favorable or extreme conditions, various isolation rates, and different formation histories.

The natural (seminatural) habitats are occupied by various forest types (subalpine birch, high-mountain and middle-mountain beech and beech-fir forests, and low-mountain forests predominated by oriental beech, common and durmast oak, black pine, and common yew); low- and middle-mountain meadow and steppe communities (including those of isolated mountains and ridges), subalpine and alpine meadows (including isolated ones); and communities of low-snow habitats and those with long-term snow cover, mires, movable and immobile talus deposits, meander bars, and solonchaks (succulent halophytes). The anthropogenic habitats are represented by synanthropic communities of cities and suburbs (sandlots, old loans, and road sides), fallows with the participation of invasive species, fields with annual crops, low- and high-mountain pastures, stock pens, and others. The description of these cenoses is given in the published issues (Orlov, 1951, 1953; Grudzinskaya, 1953; Grebenshchikov et al., 1990; Onipchenko, 2002; Grechushkina et al., 2010; Akatov et al., 2013a, 2013b; Akatov et al., 2014; Akatov and Chefranov, 2014).

The actual data on the synanthropic communities were collected in Maikop (200–250 m above sea level), Ust'-Labinsk (60 m), and Krasnodar (40 m) cities and their suburbs; near the settlements in the basin of the Belaya River (190–720 m); and in the high-mountain part of the Lagonaki Upland (the basin of the Belaya River, 1640–2000 m above sea level) and on the Abishira-Akhuba Ridge (the basin of the Bol'shoi Zelenchuk River, 2400–2600 m above sea level). The data on natural and slightly disturbed grass communities were obtained in the mountains in the basins of the Belaya, Malaya Laba and Bol'shaya Laba, Mzymta, Pshada, Ubin, and Aderba Rivers, in addition to other rivers (300–2800 m above sea level) and on the Taman' Peninsula.

We also described the communities of the meander bars along the Belaya, Mzymta, Zapadniy Dagomys, Psezuapse, and Shepsi Rivers (50–200 m) and forests in the basins of the Malaya Laba and Bol'shaya Laba, Belaya, Pshada, Vulcan, Nebug, Agoi, Shakhe, Sochi, Khosta, and Mzymta Rivers, as well as some other rivers. Many of the described forests were located in the specially preserved natural areas (the Caucasus Biosphere Reserve, the Bol'shoi Utrish Reserve, the Sochi National Park, the Bol'shoi Tkhach Nature Park, and the Maikop Botanical Preserve).

The studied groups of vascular plants of mobile talus deposits, meander bars, and fields with annual crops are open, i.e. are mainly characterized by low projective cover. The rest communities are closed. A relatively small species diversity is typical for the communities of extreme and some anthropogenic and fragmented habitats. For tree communities, these are the areas at the top limit of forest vegetation and on dry southern slopes. For grass and bush cenoses, small species diversity is seen in high-mountain habitats

(2600–2900 m above sea level); in the areas with very thin (characterized by low soil temperature in winter) or very thick (with short growing period) snow cover in winter; on mobile, excessively moistened, or saline deposits; and on the plots under considerable impact of livestock, recreation, and transport.

The low species diversity of some communities is related to their isolation or formation history. For example, the tree layer in the high-mountain and subalpine forests consists of a few number of the boreal and caucasian species, the majority of which appeared in the Caucasus early in Pleistocene or late in Pliocene (Maleev, 1941; Ratiani, 1979; Kleopov, 1990): *Betula litwinowii* similar to *B. pubescens*, *Acer trautvetteri*, *Sorbus aucuparia*, and *Salix caprea* (the names of vascular plants in the article are given according to (Zernov, 2006)). That is to say, these communities are young. The cenoses of high-mountain mires and halophytic succulents were considerably more widespread in the past (Tumadzhyanov, 1962; Golub et al., 2001), but their area is small at the present time because of the particular species composition (they are formed by specific patients) and high isolation.

We have studied three groups of the fragmented phytocenoses of the Western Caucasus in order to evaluate the rate of the EDC in them.

(1) Subalpine middle-grass meadows (28 plots) located on eight isolated (12 plots) and six unisolated (16 plots) high-mountain massifs in the basins of the Belaya, Bol'shaya Laba and Malaya Laba, Shakhe, and Mzymta Rivers. The isolated massifs are mainly separated one from another by beech and beech-fir forests. The area of forestless plant cover varies from 0.01 to 36.5 km², and the distance to the nearest larger massif is from 0.68 to 12 km. The spore-pollen analysis of the Holocene deposits has shown that the area of high-mountain communities here was considerably greater 4000–3000 years ago (Kvavadze and Rukhadze, 1989). The long-term upward migration of vegetation altitudinal zones began then (it is seen up to now) and was regularly interrupted by their downward migration. As a result, the described high-mountain massifs were isolated from larger ones and ridges over the last one-thousand-year-long period (Akatov and Akatova, 1999).

(2) The plots of mountain steppes located along the Greater Caucasus Mountain Ridge (GCR) from Novorossiisk to the Mikhailovskii Pereval settlement (seven plots) and on the forestless summits of the isolated Shize, Sober-Bash, Obrez, and Oblego mountains (11 plots) in the Northwestern Caucasus at the altitude 500–700 m above sea level. The length of the steppe zone of the GCR is about 36 km and the width is from 0.2 to 1.5 km. The area of the forestless plots on the mountain summits is 0.15–1.5 km². The distance between them and the larger plots is 4.5–20 km. At the beginning and in the middle of the 19th century, the forested area of the mountains in this part of the West-

ern Caucasus was insignificant, and most forestless areas were occupied by pastures, fields, and hays (Vereshchagin et al., 1971). It may be assumed that the area of steppe communities was greater in that period and that their isolation was lower. Late in the 19th—early in the 20th century, the forests were almost completely regenerated, which was obviously related to a decrease in the population density in the region and favorable climatic conditions (Vereshchagin et al., 1971).

(3) Piedmont and low-mountain broadleaved forests (58 plots) with the predominance or considerable participation of *Quercus robur*. 27 plots are located in 27 isolated forest fragments, and 31 plots represent the continuous forest massif in the basins of the Belaya and Laba Rivers. The area of the investigated areas varies from 9.5–616 ha, the distance to the boundary with continuous forest massifs is 0.2–37.8 km, and the mean distance to the three nearest plots of the same type is 0.1–19.2 km. The period of isolation of the plots is about 50–150 years (Zagurnaya, 2011).

Methods of Investigation

A simple indirect method is usually used to reveal the EDC. It consists in the analysis of the ratio between the mean species density and the species diversity of communities. It is assumed in the case of the EDC manifestation that low-species communities are characterized by a higher ratio when compared to high-species communities (Taylor, 1996; Oberdorff et al., 1998; Longino and Colwell, 2011). Nevertheless, the high mean density of species in the low-species communities may be only related to the high density of the predominating species, which is caused by different processes. That is why we individually analyzed the density of predominating and accompanying species in closed communities. The participation of predominating species was evaluated by their fresh phytomass for grass communities and by the number of trees with trunk diameter more than 6 cm at breast height for tree stands. The density of accompanying species in closed communities and of all species in the open groups was evaluated by their occurrence.

The material for the analysis was collected by a similar approach. The descriptions of the tree layer in forest phytocenoses were made on uniform forest plots of about 1 ha in the area located at different altitudes on the slopes of various aspects and steepness. Each plot was characterized by ten test plots of 300 m² in the area. Tree species with a trunk diameter of more than 6 cm at breast height were listed, and their number was quantified on some test plots. The species diversity of alpine communities on talus deposits was evaluated for plots of 25 m² in the area. To determine the mean occurrence of species, ten sampling areas (0.5 m²) were regularly laid within each plot of 25 m². The data for the other communities were obtained on the plots

of 15 (16) m² (species diversity) and on 20 (25) test plots of 0.5 m² (species occurrence). The fresh mass of each species of vascular plants was determined for closed grass communities on the plots of 0.25 m².

The analytical material includes 65 plots with tree stands (the area is 3000 m²), for which the number of tree species was quantified; 140 plots on which the species occurrence on the plots of 300 m² was determined; 95 plots of grass phytocenoses of 0.25 m² in the area with the data on the green mass of species of vascular plants; 481 plots of grass and bush phytocenoses (the area is 15, 16, or 25 m²) with the data on the occurrence of the vascular plant species on the plots of 0.5 m². Based on the descriptions, we determined the following parameters: S —the number of plant species on the plots of 15, 16, or 25 m² for grass and bush communities or the number of tree species with trunk diameter more than 6 cm in the area of 3000 m² for tree stands; N and N_d —the total number of plants and the total number of plants of predominating tree species in the area of 3000 m²; W and W_d —the total green phytomass and green phytomass of predominating grass species in the area of 0.25 m²; N_d/N and W_d/W —the relative density (phytomass) of predominating species (the domination rate); F —the mean occurrence of tree species in the area of 300 m² or the mean occurrence of grass and bush species (of accompanying ones in closed communities and of all species in the open groups) in the areas of 0.5 m².

Organization Models of Plant Communities

The EDC was evaluated with consideration of the organization model of plant communities. This parameter was determined on the basis of the habitat type and community structure and of published descriptions of particular types of plant communities (Grime, 1977; Rabotnov, 1983; Mirkin, 1994; Onipchenko et al., 1998; Onipchenko and Semenova, 2004; Evstigneev, 2010; Lebedeva et al., 2011; Mirkin and Naumova, 2012). According to these data, the meadow communities of all altitudinal zones (except for the alpine one) and the communities of low bushes of habitats with long-term snow cover of the subalpine belt may be assigned to the C – S – R model. They are predominated by *Botriochloa ischaemum*, *Brachypodium rupestre*, *Festuca woronowii* (= *F. varia*), *Geranium gymnocaulon*, *Hedysarum caucasicum*, *Alchemilla retinervis*, *Rhododendron caucasicum*, and other species. These plants are characterized by considerable biomass, large seeds, and a relatively low growth rate, which corresponds to the C -strategy. The accompanying species bear features of C -, S -, and R -strategy (Rabotnov, 1983; Onipchenko et al., 1998; Onipchenko and Semenova, 2004; Lebedeva et al., 2011; Mirkin and Naumova, 2012). Most of the described tree stands may be surely assigned to this model,

Ratio between species diversity and participation (phytomass, occurrence) of predominating and accompanying species

Communities	Parameters		<i>n</i>	<i>R</i> ²	<i>r</i>	<i>P</i>
	independent	dependent				
Tree stands (<i>C–S–R</i> model)	<i>S</i>	N_d/N	65	0.501	–0.708	<0.001
	<i>S</i>	F_s	140	0.024	–0.155	<0.1
Natural closed grass stands and bushes (<i>C–S–R</i> model)	<i>S</i>	W_d/W	27	0.657	–0.811	<0.001
	ln <i>S</i>	ln <i>F</i> _s	69	0.494	0.702	<0.001
Natural closed grass stands (<i>S–R</i> model)	<i>S</i>	W_d/W	32	0.631	–0.794	<0.001
	<i>S</i>	F_s	81	0.012	0.109	
Synanthropic closed grass stands (<i>C</i> , <i>S</i> , and <i>C–S–R</i> models)	<i>S</i>	W_d/W	36	0.478	–0.691	<0.001
	<i>S</i>	F_s	137	0.032	0.178	<0.1
Open grass stands:				0.010		
of alpine talus deposits (<i>S–R</i> model)	<i>S</i>	F_s	97		–0.100	
of meander bars (<i>R–S</i> model)	<i>S</i>	F_s	72	0.132	–0.363	<0.01
of fields with annual crops (<i>R</i> model)	<i>S</i>	F_s	25	0.317	–0.563	<0.01

n is the number of plots; *R*² is determination coefficient; *r* is the Pearson correlation coefficient; *P* is significance level.

because they are predominated by species with *C*- (oaks), *C–S*- (hornbeam and beech), or *C–R*-strategy (pine), and the most accompanying species are represented by species with *S*-strategy (linden, elm, maples) (Evstigneev, 2010). The organization model of tree stands with *Betula litwinowii* (birch crooked forest) is not so obvious. Birch is assigned to the typical exponents, which participate in the formation of phytocenoses at the first stage of forest regeneration after fires or other impact (Rabotnov, 1983; Evstigneev, 2010). Nevertheless, the birch forests in the Western Caucasus are mainly represented by climax communities formed at the top boundary of forest vegetation. Their composition and structure is similar to that of beech crooked forests (with the predomination of the species with *C–S*-strategy), which formed at the same altitudes but in areas with thicker snow cover in winter. The species behavior may differ under various growing conditions (Rabotnov, 1983). For example, representatives of the violent group only play this role under particular conditions. Based on this consideration, we did not specify the birch forests into a separate group.

The described natural communities of vascular plants of the *S* and the *S–R* models are represented by cenoses of alpine heaths of low-snow habitats, closed grass communities of the areas with long-term snow cover and talus deposits, subalpine mires, and succulent halophytes on solonchaks on the banks and dried bottoms of salt water reservoirs of the Taman' Peninsula (Rabotnov, 1983; Onipchenko et al., 1998; Onipchenko and Semenova, 2004; Mirkin and Naumova, 2012).

The segetal plant groups located on productive but often disturbed plots are assigned to the *R* model, and the other types of synanthropic communities represent

the *C–R–S* models (Mirkin et al., 2007; Mirkin and Naumova, 2012). The latter may differ in the participation of species with *R*- and *S*-strategies. The share of exponents is higher in the series of communities of regenerative successions, while the participation of patients is greater in the communities of allogenic successions developed under the effect of grazing and other external factors (Mirkin et al., 2007; Mirkin and Naumova, 2012). The meander bars may be assigned to the low-productive and often disturbed habitats. Their open plant groups are mainly formed by species transported from the other slightly disturbed (forest and meadow) or synanthropic communities. They may obviously be assigned to the *R–S* model.

RESULTS

We have evaluated the rate of the EDC manifestation in the plant cover of the Western Caucasus by a comparison of the species diversity, relative density (phytomass) of predominating species, and mean occurrence of the accompanying species for closed plant communities and the species diversity and mean species occurrence for open cenoses. We investigated the plant communities of different organization models. The studied factors of a decrease in the species diversity of the communities included extreme environmental conditions, anthropogenic and historical factors, and habitat fragmentation.

Natural (Seminatural) Habitats

All of the low-species closed cenoses that formed under extreme environmental conditions are in general characterized by a higher relative density (phyto-

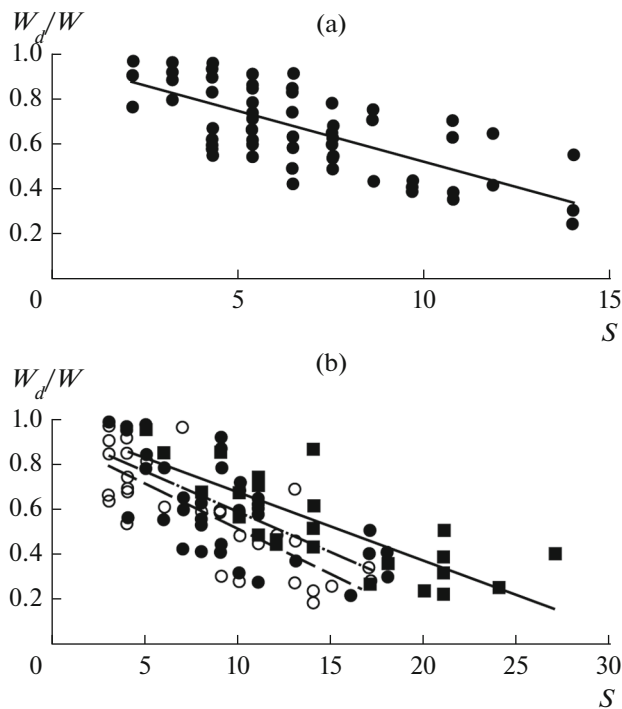


Fig. 1. Correlation between species diversity and domination level in closed plant communities. (a) Tree stands, (b) grass and bush communities (black squares and solid regression line designate the $C-S-R$ model of organization, white circles and dashed line signify the $S-R$ model, and black circles and dashed line with dots show synanthropic communities).

mass) of the predominating species when compared to the communities of more favorable habitats (table, Fig. 1). The domination level in the grass communities of the $C-S-R$ model is higher than in the cenoses of the $S-R$ model, the species diversity being equal. The low-species cenoses of the $S-R$ model are in addition characterized by great variation of this parameter (Fig. 1b).

The ratio between the number and mean occurrence of the accompanying species in various types of closed communities is different. In grass communities of the $C-S-R$ model, low-species cenoses are characterized by a smaller mean occurrence of accompanying species than communities with a greater species number (table, Fig. 2b). In the tree stands and closed grass communities of the $S-R$ model, the correlation between the species diversity and mean occurrence of the accompanying species is practically absent (table, Figs. 2a and 2c). The variations in this parameter are better pronounced in the low-species communities of these types when compared to the cenoses with greater species number.

There is no correlation between species diversity and mean species occurrence in the plant groups of talus deposits in the alpine belt. The range of this parameter is greater in the low-species cenoses in comparison with high-species ones (table, Fig. 3a). In

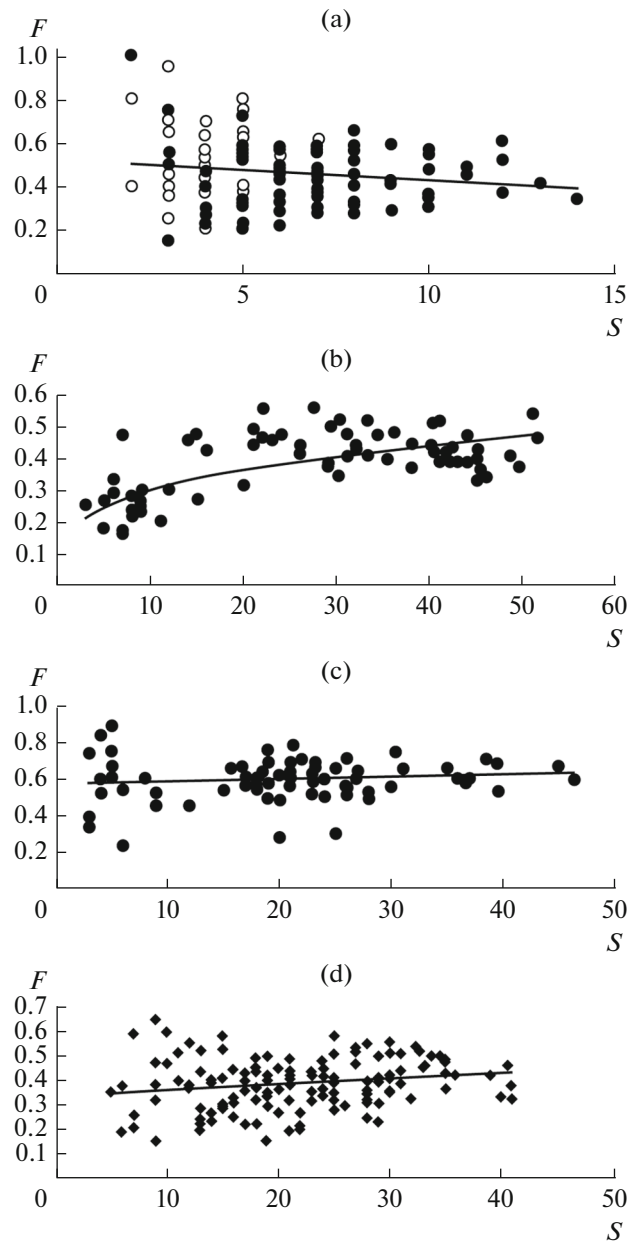


Fig. 2. Correlation between species diversity and mean occurrence of accompanying species in closed plant communities. (a) Tree stands (white circles signify subalpine and high-mountain forests, black circles denote the rest communities); (b) grass and bush communities of the $C-S-R$ model of organization; (c) grass communities of the $S-R$ model; (d) synanthropic communities.

the plant groups of the meander bars, there is a slight negative (but statistically significant) correlation between the species diversity and species occurrence (table, Fig. 3b). The variation in the mean data of this parameter is also greater in the low-species communities when compared to the high-species ones.

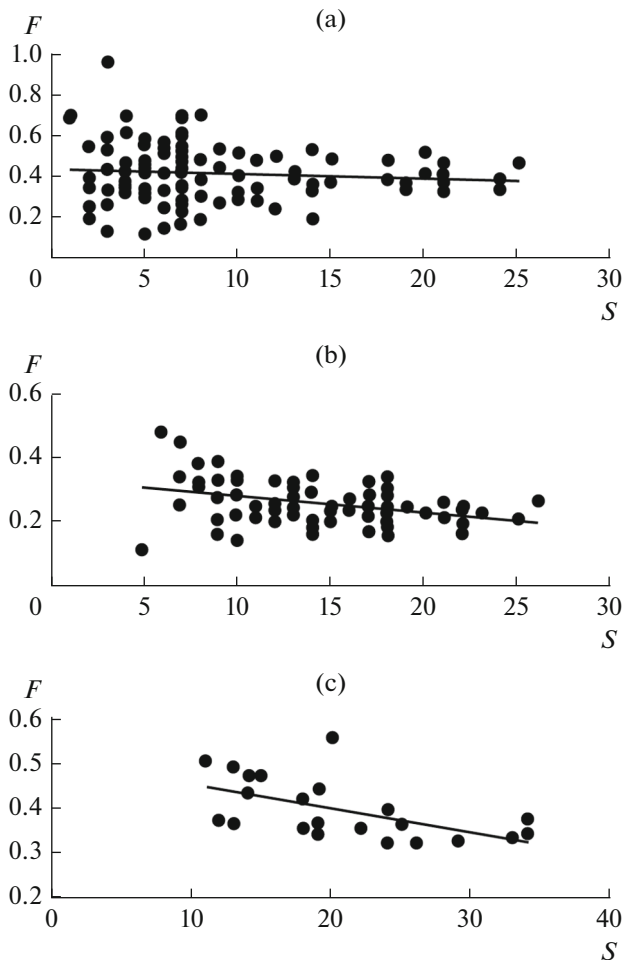


Fig. 3. Correlation between species diversity and mean occurrence of species in open plant communities. (a) Alpine talus deposits; (b) meander bars; (c) field with annual crops.

Anthropogenic Habitats

The analysis of the anthropogenic habitats has revealed the following regularities. (1) The species diversity is lower in the communities of the habitats undergone poaching by man and the effect of transport, as well as in those developed in the areas of cattle camps and migration ways. Wastelands, fallows, and pastures are characterized by higher species diversity. (2) There is a statistically significant negative correlation between the species diversity and relative mass of predominating species in the closed communities (table, Fig. 1b). (3) The domination level is on the average lower in synanthropic communities than in the natural cenoses of the $C-S-R$ model and higher than in the communities of the $S-R$ model, the species diversity being equal (Fig. 1b). (4) The correlation between the species diversity and the mean occurrence of accompanying species in the synanthropic communities is practically absent (table, Fig. 2d). The range of the mean occurrence is somewhat higher in low-spe-

cies cenoses than in high-species ones. (5) The open segetal cenoses are characterized by a negative correlation between the species diversity and the mean species occurrence. The ranges of the latter parameter in these communities are similar (Fig. 3c).

Fragmented Habitats

The species diversity of the subalpine meadows in the isolated mountain regions is lower and the mean species occurrence is only somewhat lower than in the unisolated communities (the mean species number is 29.6 and 35.5 per 16 m², and the mean occurrence is 0.51 and 0.47, respectively). The difference between the mean occurrences of the species in these communities is statistically significant at $P < 0.5$ (Fig. 4a). The species diversity in the mountain steppes of isolated mountain massifs is lower than of those of the GCR, while the mean species occurrence is almost similar (the mean species number per 15 m² is 31 and 45.7, and the mean occurrence is 0.34 and 0.35, respectively (Fig. 4b)). The species diversity and mean occurrence of accompanying tree species of fragmented and unfragmented tree stands are practically similar (the mean species amount is 8 and 9.3 per 3000 m², and the mean occurrence is 0.49 and 0.47, respectively) (Fig. 4c). We have constructed plots of the range/logarithms of the species density mean for the plots of fragmented and unfragmented tree stands in order to compare their species densities. The analysis shows that the mean density of tree species of particular ranges is lower on plots of fragmented forests as compared to unfragmented ones (Akatoev et al., 2013b).

DISCUSSION

We have analyzed the type of the ratio between the species diversity and density (phytomass or occurrence) of species in the communities of the Western Caucasus, a large region with diverse natural landscapes, in order to evaluate the rate and intensity of the EDC in the plant cover of the inland areas. The objects of investigation were represented by ten groups of plant communities. Seven of them were represented by closed cenoses of different types, and three groups included open communities of vascular plants.

The communities of the three groups underwent fragmentation some time ago (subalpine meadows, mountain steppes, and broadleaved forests) and similar unfragmented or less fragmented phytocenoses were compared to them. It was revealed that isolation resulted in an increase in the mean density of accompanying species only in the subalpine meadows that underwent fragmentation one thousand years ago. We have already mentioned that other investigators did not reveal the EDC in most human-fragmented communities, presumably because of the low rate of species death and the short isolation period (Klein, 1989; Anjos, 2004; Ricketts, 2004).

We have also revealed that the low-species closed cenoses (tree stands and natural and synanthropic grass and bush communities) are on average characterized by a greater domination level when compared to high-species cenoses (Fig. 1). It should be mentioned that the grass cenoses of the $S-R$ model and the synanthropic communities in less favorable habitats are characterized by a lower domination rate in comparison with the natural cenoses of the $C-S-R$ model (Fig. 1b). For example, the communities of alpine meadows that developed at a distance of 1 m or closer to the edge of a snow patch (predominated by *Carum caucasicum*, *Taraxacum stevenii*, *Sibbaldia semiglabra*, and other species) are characterized by a low or moderate domination level (0.24–0.62). Similar data (0.19–0.60) were obtained for the cenoses of low-grass meadows and heaths located at significant altitudes (2600–2800 m above sea level). The dominants are represented by *Festuca ovina*, *Carex huetiana* (= *C. umbrosa*), *Campanula tridentata*, *Vaccinium vitis-idaea*, and *Kobresia persica*. In addition, the species-poor cenoses of the $S-R$ model formed by species of specific ecotopes and located in the most extreme habitats (high-mountain mires and solonchaks) are characterized by great variation of the domination level. For example, the relative density of predominating species varies from 0.54 to 0.98 in the species-poor communities of solonchaks predominated by *Bassia hirsuta*, *Salicornia perennans*, and *Atriplex verrucifera* and from 0.45 to 0.97 in the cenoses of the high-mountain mires predominated by *Carex rostrata*, *Carex dacica*, and *Eriophorum vaginatum*.

The mean species occurrence is smaller in the species-poor cenoses than in the species-rich ones for only one group of plants (bush and grass communities of the $C-S-R$ model). For two groups (cenoses of annual crops and meander bars), the species occurrence is higher in the species-poor cenoses, and the parameter varies considerably in the remaining communities (forests, natural grass $S-R$ models, and synanthropic cenoses).

The revealed regularities may be explained by several probable types of variation in the community structure with a decrease in its species diversity. It may be assumed that poorer environmental conditions for the communities of the $C-S-R$ model cause an increase in the competitive asymmetry of their species. The advantages of the dominants become greater, their relative number and biomass increase, and the quantity (occurrence) of other species decreases. As a result, closed species-poor cenoses are characterized by a great domination and a low mean density (occurrence) of accompanying species (Figs. 1b and 2b). This may be seen by the example of cenoses in the habitats with long-term snow cover predominated by *Rhododendron caucasicum*, *Geranium gymnocaulon*, or *Alchemilla retinervis*.

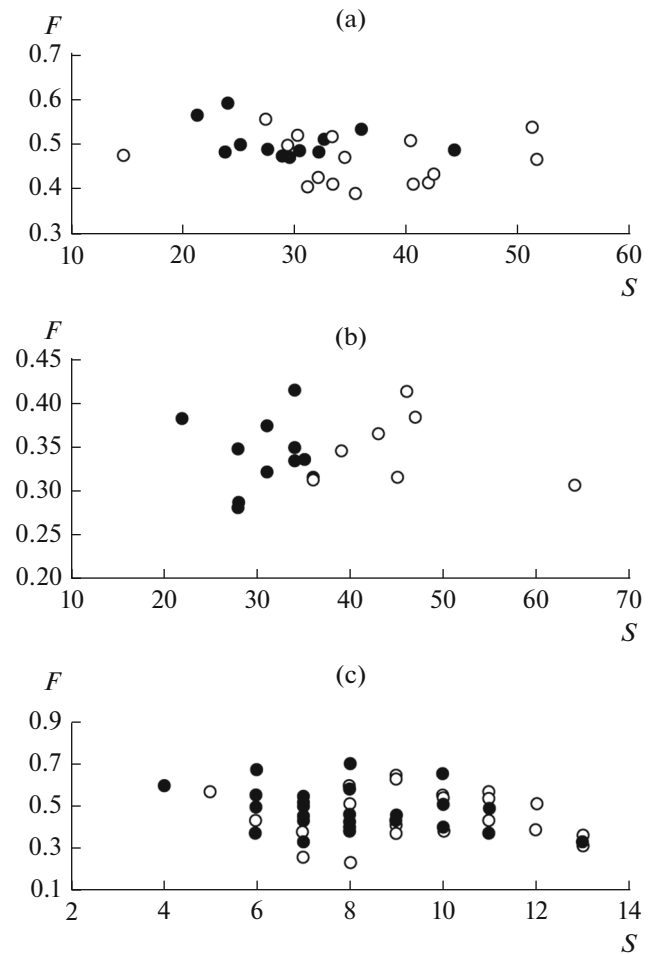


Fig. 4. Correlation between species diversity and mean occurrence of accompanying species in fragmented and unfragmented plant communities. (a) Subalpine meadows, (b) mountain steppes, (c) tree stands of low-mountain and piedmont forests. White circles signify unfragmented communities, and dark circles denote fragmented communities.

Nevertheless, succession of this kind is only possible in the competition-balanced communities of the $C-S-R$ model. At the same time, cenoses, forests in particular, do not always achieve this status because of occasional processes and local impacts (windfalls; selective cutting; damage by insects, rodents, and ungulates; and fungus and bacterial diseases). That is why the density of dominants may differ even within uniform habitats on small plots of forests (Dolukhanov, 1964; Golgofskaya, 1967; Rabotnov, 1983; Spurr and Barnes, 1984; Vasilevich, 1991). The smaller the the participation of dominant is, the more resources remain for the accompanying species. The lower is the number of species that can use these resources (which is related to the sizes of the species pools of the communities), the more resources will be received by each species and the higher will be the mean density of these species. Therefore, the variation rate of the mean

density (occurrence) of the accompanying species will be higher in cenoses with a smaller size of species pool (in the tree stands of subalpine and high-mountain forests) at a similar variation rate of domination level (Figs. 1a and 2a).

The closed grass communities of the $S-R$ model differ from those of the $C-S-R$ model by the predomination of species with S -strategy. Hence, the domination level is lower and the mean participation (occurrence) of other species is higher in the communities of the $S-R$ model than in the cenoses of the $C-S-R$ model (Figs. 1b, 2b, and 2c), the species diversity being equal. Figure 1B also shows that patients (S -strategists) cannot preserve a high domination level in the extreme habitats, in contrast to contrary to violents (C -strategists). In combination with the small size of the species pool of the communities related to isolation or historical factors (subalpine mires or solonchaks), this may be the cause of significant variation in the mean density (occurrence) of the accompanying species and its rise to high levels in places (Fig. 2c).

It has been already mentioned that dense synanthropic communities are assigned to the $C-R-S$ model of organization (Mirkin et al., 2007; Mirkin and Naumova, 2012). Our data are not in contradiction with this assumption. Nevertheless, they are characterized by a lower correlation between the species diversity and the relative participation of dominants when compared to the natural communities of the same model. This may be related to the relatively low competitive ability of the dominants in the synanthropic cenoses (in the natural communities of the $S-R$ model) and (or) their more frequent disturbance (tree stands). The great variation in the number of dominants results in considerable variation in the mean occurrence of the accompanying species and the absence of its correlation with the species diversity of communities (table, Fig. 2d).

The occurrence of plant species in the open communities of the $S-R$ model (alpine talus deposits) is determined by their specific features and occasional processes and depends slightly on the species interaction (Cornell, 1993; Mirkin and Naumova, 2012). So, when the species diversity of these communities decreases, the mean occurrence of the community-forming species is not directionally changed (table, Fig. 3a). In addition, high species diversity causes a decrease in the variability of cenotic parameters (Tilman et al., 1998; Stevens et al., 2003), and the variation range of the mean species occurrence should be higher in species-poor cenoses than in species-rich ones. We have already confirmed this with data from quantitative experiments (Akotov et al., 2013a). Our data show that a decrease in species diversity is accompanied by an increase in the mean species occurrence only in the communities of the R and $R-S$ models (segetal cenoses and communities of the meander bars) (table, Figs. 3b and 3c). This may be explained

by the high reaction rate of explorers (the species with R -strategy) on the increase in the available resources and probably by small differences in the growing conditions of the plots under these types of cenoses with different species numbers. The capability of R -strategists to increase the population density (occurrence) with the appearance of available resources is also confirmed by other data, for example, by variations in the segetal cenoses in Europe that resulted from the application of herbicides beginning from the 1950s (Vainert et al., 1988). This factor stimulated the selection of resistant plant species, which had the opportunity to spread under the conditions of smaller competition. This resulted in the formation of cenoses composed of a small number of species with relatively high and almost equal participation.

CONCLUSIONS

The obtained data show that (i) the natural and anthropogenic fragmentation of plant communities has not resulted in significant EDC; (ii) grass cenoses of the $S-R$ model and synanthropic communities of less favorable habitats are characterized by a lower domination level in comparison with natural communities of the $C-S-R$ model; (iii) the mean density (occurrence) of species in the species-poor cenoses of various types may differ and be related to their organization model and local disturbance.

We have revealed a pronounced EDC (the rise in the mean species occurrence, contrary to species diversity) for segetal cenoses and a less pronounced one for the plant groups of meander bars among all of the studied plant communities of the Western Caucasus. This is obviously related to the uniform habitats of these communities and the considerable number of explorers, which react quickly to a rise in the available resources.

The species-poor bush and grass communities of the $C-S-R$ model are characterized by a high domination level and low mean occurrence of accompanying species, which is probably related to the increase in the competitive asymmetry between the species at the deterioration of the environmental conditions. In the remaining closed communities (tree stands, natural grass cenoses of the $S-R$ models, and synanthropic communities), the low species diversity is accompanied by considerable variations in the mean occurrence of accompanying species. A similar regularity is seen for the cenoses of alpine talus deposits, which may be explained by the absence of species interaction here and the independent dynamics of the numbers of populations. The relatively high mean occurrence of species in some areas of talus deposits is related to occasional processes and not to compensation.

Variation in the mean occurrence of species in closed communities is obviously related to the difference in the number of dominants. It is related to local

disturbances in the forests of the $C-S-R$ model, to the relatively low competitive ability and occasional processes of species regeneration in the grass cenoses of the $S-R$ model (mires and solonchaks), and to all of these reasons in the synanthropic communities. While the variation in the relative abundance of dominants is similar in these cenoses, the variation in the mean occurrence of accompanying species and hence the probability of its high levels is higher in cenoses with smaller species pools. The greater mean density (occurrence) of plant species in some closed communities is related to occasional and compensation processes. It may be assumed that this EDC manifestation is most widely spread in the communities of the inland areas.

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