

Relationship between Degree of Dominance and Species Richness in Grass Communities with Different Productivities

V. V. Akatov^{a,*}, T. V. Akatova^b, and S. G. Chefranov^a

^aMaykop State Technological University, Maykop, 385000 Russia

^bCaucasian State Natural Biosphere Reserve, Maykop, 385000 Russia

*e-mail: akatovmgti@mail.ru

Received December 12, 2017; in final form, January 19, 2018

Abstract—The aim of this study is to test the assumption that the relationship between the degree of dominance and local species richness may be different in grass communities with different productivities. Alpine, subalpine, and low-mountain grasslands, as well as subalpine mires, alpine communities of low-snow habitats and those with long-term snow cover, steppe communities, and the grass layer of low-mountain forest communities of the Western Caucasus and Ciscaucasia, are used as objects of research. The data on the phytomass of 419 plots with an area of 0.25 m² are studied. The results show that, the higher the mean productivity of communities is, the closer the relationship between the degree of dominance and species richness is, and the closest relationship is observed in meadow communities. Possible causes of these relationships are considered. It is reasonably suggested that this may be due to the features of the organization of plant communities with high and low productivity (in particular, high or low intensity of interspecific competition).

Keywords: grass communities, dominance, species richness, phytomass, competition, life strategies, organizational models

DOI: 10.1134/S1995425518040029

It is predicted that global environmental changes (including climate warming, changes in biogeochemical cycles, an increase in carbon dioxide availability, and habitat eutrophication) may be favorable for many dominants, allowing them to reach a higher level of participation (the degree of dominance) in plant communities in the future than at the present time. The replacement of native by alien dominants may have the same consequences for cenoses (Parker et al., 1999; Reinhart et al., 2005; Chase, 2005; Hillebrand et al., 2008; Hejda et al., 2009; Akatov et al., 2012). However, the higher the involvement of dominant species in the formation of phytocenoses is, the lower the space and the less the resources for other (subordinate) species and, correspondingly, the lower the number of their individuals in plots and the higher the probability of their fallout from communities as a result of environmental fluctuations and disturbances (“the more individuals hypothesis”) (Wright, 1983; Wright et al., 1993; Palmer and van der Maarel, 1995; van der Maarel et al., 1995; Ernest and Brown, 2001; McKane et al., 2002; Kunte, 2008). This mechanism, in combination with the environment-forming activity of dominants on the basis of the selective use of mineral resources, litter layer accumulation, light-regime changes, physicochemical soil properties, allelopathy, etc. (Grime, 2001; Callaway and Ridenour, 2004; Reinhart et al., 2005; Hulme and Bremner, 2006;

Somodi et al., 2008; Csergő et al., 2013; Bartha et al., 2014), should determine the close relationship between their participation in forming cenoses and species richness. Accordingly, the growth in the degree of dominance in plant communities may pose a real threat to them (Hillebrand et al., 2008). However, the results of field studies show that this relationship proves to be really close in some cases, while in others it is weak or absent (Stirling and Wilsey, 2001; Akse-nova et al., 2004; Cherednichenko, 2004; Houlahan and Findlay, 2004; Ma, 2005; Wilsey and Stirling, 2007; Lamb and Cahill, 2008; Sasaki and Lauenroth, 2011; Csergő et al., 2013; Bartha et al., 2014, etc.).

Theoretically, the relationship between the degree of dominance (D) and species richness (S) should depend on the extent to which the number of subordinate species in communities (\hat{S}) is determined by their total biomass (\hat{W}), as well as on the degree to which the total biomass is determined by the relative participation of the dominant species (D). It can be assumed that the pattern of relationships between $\hat{S}(\hat{W})$ and $\hat{W}(D)$ and, hence, $S(D)$ may depend on the productivity of plant communities for a number of reasons.

For instance, according to the idea of species life strategies (Grime, 1977), communities with the dominance of those species which are low competitive but

more tolerant to the effect of abiotic (stress) factors (S-strategists) than others are formed in stable low-productive habitats, while stable high-productive habitats are characterized by the dominance of competitively strong species, which can capture and hold the space (C-strategists). According to the multimodel concept of Mirkin (Mirkin, 1994; Mirkin and Naumova, 2012), the grass communities of the first type belong to the abiotic S-model (communities of stable extreme habitats), while the grass communities of the second type belong to the C-R-S-model (meadow communities).

It is believed that the low-productive communities of the S-model are characterized by a low intensity of interspecific competition (Grime, 1977; Cornell and Lawton, 1992; Rabotnov, 1983; Mirkin and Naumova, 2012, etc.). This assumes that the population productivity in these species is significantly regulated by abiotic environmental conditions; the population dynamics of each species does not depend on other species, and the colonization of these communities by new species is a stochastic process (Cornell and Lawton, 1992; Cornell, 1993; Mirkin and Naumova, 2012). The crucial role in the formation of such communities is played by the size of the pool of tolerant species, which determines the probability of the entry of a certain amount of them into a certain place and their further survival, regardless of nearest neighbors (Yodzis, 1978; Gilyarov, 2011; Onipchenko, 2013). According to this scenario, S-cenoses with certain species richness can be characterized by significantly different ratios of participation (biomass and coverage) of species and vice versa. Therefore, the relationship between $\hat{S}(\hat{W})$ and $S(D)$ may be weak in low-productive cenoses of the S-model. However, the higher the productivity of communities (W) and, accordingly, the density and height of herbage, the higher the intensity of interspecific competition, the differentiation of species with respect to their participation in the herbage, and the probability of competitive exclusion of some of them (Grime, 1977; Huston, 1979; Peet and Christensen, 1988; Bengtsson et al., 1994; Piper, 1995; Drobner et al., 1998; Mulder et al., 2004; Poggio and Ghersa, 2011; Mirkin and Naumova, 2012). Therefore, in high-productive communities of the C-R-S-model, the $\hat{S}(\hat{W})$ relationship and, accordingly, $S(D)$ relationship should be closer.

In addition, communities with low productivity are also usually characterized by low species richness. This may be due not only to the limited amount of available resources, but also to the necessity of the formation of mechanisms of resistance to extreme conditions in the process of evolution, as well as to the generally small size and isolation of low-productive cenoses (Begon, 1996; Qian and Ricklefs, 2004; Longino and Colwell, 2011). Therefore, even a significant decrease in the participation (biomass and coverage) of dominants in such communities and, accordingly, the provision of

extra space and resources will not necessarily lead to a sensible growth in the number of species. As a result, the $\hat{S}(\hat{W})$ relationship may become weak. In contrast, there is a potential for the growth of many species (a significant species pool) in communities that are formed in stable and productive (i.e., favorable) habitats. Therefore, dominant species that limit the amount of resources available for subordinate species may be the most significant, if not the only, factor determining their number (Mirkin and Naumova, 2012; Bartha et al., 2014).

At the same time, since the competitive advantages of the most successful S- and C-strategists should be manifested more significantly in the marginal sites of the productivity gradient, it can be expected that the growth in productivity of extreme habitats should contribute to the diminution of the role of dominant species, while the growth in the productivity of favorable habitats should contribute to an increase in their role (Chalcraft et al., 2009; Šimová et al., 2013). As a result, in the first case (i.e., in S-cenoses), a decrease in the volume of available resources for subordinate species (\hat{W}) due to a growth in the relative participation of dominant species (D) may be enhanced by a decrease in the total productivity of habitats (W), while in the second case (C-S-R-cenoses), it may, in contrast, be compensated by its growth. This may cause the weakening of the $\hat{W}(D)$ relationship and, accordingly, the $S(D)$ relationship in productive C-S-R-cenoses and, on the contrary, an increase in this relationship in the communities of the S-model.

It should be also taken into account that statements on more intensive competition in more active cenoses, as well as the role of this competition in the formation of close relationship between D and S , are often disputed (Tilman, 1980; Stirling and Wilsey, 2001; Wilsey and Stirling, 2007; Bennett and Cahill, 2012; reviews: Goldberg and Novoplansky, 1997; Mirkin and Naumova, 2012; Onipchenko, 2013). In particular, according to Wilsey and Stirling (2007), in communities with low or zero competition, both species richness and evenness (dominance) are mainly determined by the rate of species immigration and, according to the predictions of neutral diversity models, the relationship between these characteristics may be positive and significant (Caswell, 1976; Bell, 2000; Stirling and Wilsey, 2001; Wilsey and Stirling, 2007). In contrast, in competitive communities, these characteristics are determined by different processes. The species richness is more sensitive to the rate of species immigration and evenness (dominance) is more dependent on the intensity of biotic interactions. Therefore, changes in the abundance of species in such communities should not necessarily involve changes in their number and, thus, the relationship between these characteristics may be weak (Wilsey and Stirling, 2007).

Table 1. Location of sampling plots

| No. | Area | Coordinates | Elevation above sea level, m | PC (number of samples) |
|-----|---|---|------------------------------|---|
| 1 | Lesisty Ridge, Belaya River Basin | 44°35.152'–44°36.122' N, 40°01.041'–40°06.399' E | 220–300 | HF (74) |
| 2 | Skalisty Ridge, Belaya River Basin | 44°15.464'–44°21.393' N, 40°09.587'–40°12.587' E | 498–744 | LMG (64), HF (48) |
| 3 | Akhmedov Post Mountain, Bolshaya Laba River Basin | 44°13.346' N, 41°02.718' E | 662 | LMG (14) |
| 4 | Oshten Mountain, Belaya River Basin | 43°58.498'–44°01.074' N, 38°57.555'–39°58.900' E | 1855–2794 | AG (50), AH (11), AS (16), SAG (29), SF (16) |
| 5 | Abago Mountain, Belaya River Basin | 43°54.428'–43°55.217' N, 40°08.654'–40°09.120' E | 2164–2667 | AH (7) |
| 6 | Yukha Mountain, Malaya Laba River Basin | 43°42.189'–43°43.711' N, 40°40.841'–40°42.651' E | 2308–2680 | AG (3), SF (3) |
| 7 | Chugush, Mzymta River Basin | 43°46.443'–43°46.776' N, 40°12.389'–40°12.844' E | 2382–2648 | AG (4), AS (4) |
| 8 | Atsetuka Ridge, Mzymta River Basin | 43°32.845'–43°34.278' N, 40°35.247'–40°37.924' E | 1858–1897 | SAG (7), SF (4) |
| 9 | Shize Mountain, Abin River Basin | 44°44.508' N, 38°09.283' E | 540 | ST (16) |
| 10 | Stavropol upland | 44°51.153' N, 41°56.285' E | 585 | ST (16) |
| 11 | environs of Lake Manych | 45°59.833' N, 43°14.405' E | 30–75 | ST (33) |

In Tables 1–3: PC, type of plant community; AG, alpine grasslands; SAG, subalpine grasslands; LMG, low-mountain grasslands; AH, alpine heaths; AS, alpine mats; SF, subalpine mires; ST, steppes; HF, herbaceous layer of forests.

Therefore, the current knowledge of the organization of plant communities admits different variants of correlation between the productivity of $S(D)$ and the strength of $S(D)$ relationship. However, it remains unclear which of them is largely implemented in nature. This study attempted to answer this question based on the example of grass communities of a wide range of stable habitats.

MATERIALS AND METHODS

The objects of the research included grass phytocenoses of relatively stable habitats in different areas and altitudinal belts of the Western Caucasus and Ciscaucasia: alpine mats; heaths and grasslands; subalpine grasslands and mires; low-mountain grasslands; the grass layer of alder, beech, and oak forests; and different steppe variants. According to the current knowledge, the meadow communities can be referred to the C-S-R organizational model (Onipchenko et al., 1998; Mirkin and Naumova, 2012). Communities of other types have been formed under stress conditions. For instance, the cenoses of alpine mats are confined to habitats with long-term snow cover; therefore, they have a short vegetation period; the cenoses of alpine heaths are confined to low-snow habitats (ridge tops and crests), which are characterized by low soil temperatures in winter; the communities of subalpine

mires have been formed under surplus water conditions; the steppe communities have been formed under water stress conditions; and the communities of the grass layer of forests have been formed under insufficient light conditions. All of them can be referred to the S-model (Grime, 1977, 2001; Rabotnov, 1983; Onipchenko et al., 1998; Mirkin and Naumova, 2012). At the same time, it should be emphasized that this distribution is fully relevant only for cenoses in the marginal sites of the productivity gradient. Other communities are most likely at a transient stage (Grime, 1977, 2001; Mirkin and Naumova, 2012).

This study is based on 419 aboveground biomass samples that were collected in plots with an area of 0.25 m² during field seasons from 2014 to 2017 (the data on the location of sites of their sampling are given in Table 1). Samples were taken in typical sites of communities during the period of maximum herbage development. Some of them were taken on a regular basis in the form of transects from ten plots with an area of 0.25 m²; other samples were collected in series, three to six samples per plot. In the second case, we selected variants of communities with the highest, lowest, and medium projective cover of dominant species according to visual evaluation. Samples were sorted out by species and weighted. One to three most typical samples from each series were then dried and

individually weighted. The dry weight of the other samples of each series was determined by the values of the drying coefficient.

Based on the collected actual material, we determined the values of the following parameters: W , Wd , and \hat{W} (the dry weight of the total herbage biomass (productivity) and the biomass of the dominant species and subordinate species per 0.25 m² (we proceeded from the assumption that the values of the drying coefficient are approximately the same for the biomass of different sample components); W_m , the mean productivity of samples in cenoses dominated by a certain species; D , the ratio of the biomass of the dominant species to the total biomass (the degree of dominance and the Berger–Parker index) (Berger and Parker, 1970; Magurran, 1988); S and \hat{S} , the total number of species and number of subordinate species (except for the dominant species) per 0.25 m²; and S_{\max} , the maximum value of S that was revealed in the samples of communities dominated by a certain species. This parameter is considered an indicator of the size of the species pool.

The data were analyzed in two stages. At the first stage, we estimated the relationship between $S(D)$, $\hat{S}(\hat{W})$, $\hat{W}(D)$, and $D(W)$ for communities with a certain dominant species (the independent variable is in brackets). For this purpose, we used the Spearman rank correlation coefficient (R). It is low sensitive to significantly different values of characteristics and makes it possible to measure the degree of association between the characteristics, irrespective of the distribution law and form of relationship. At the second stage, we determined the pattern and strength of the relationship between R_{SD} , $R_{S\hat{W}}$, $R_{\hat{W}D}$, R_{DW} , S_{\max} , and W_m . The type of relationship was determined by constructing linear and quadratic regression models. It was assumed that the statistical significance only of linear regression coefficients indicates the linear nature of relationship, while the statistical significance of linear and quadratic coefficients or only of quadratic coefficients indicates the nonlinear pattern (the relationship was tested using the Student's t -test). The strength of the relationship between the characteristics was determined by calculating the unadjusted coefficient of determination (Fisher's F -test was used to estimate its statistical significance), the paired Pearson coefficient of correlation, and the partial correlation coefficient. Regression models with different numbers of factors were compared using the adjusted coefficient of determination (R_{adj}^2). Before the analysis, we made sure that the series of the values of the study parameters were close to the normal distribution. The calculations were made in Microsoft Excel 2007 and Statistica 6.0.

An analysis of the above-presented correlations makes it possible to estimate the pattern of dependence of the strength of $S(D)$ relationship on the pro-

ductivity of grass communities (W_m), as well as the role of the above-described mechanisms in its formation. For instance, the negative correlation between W_m and R_{SD} may testify against the Wilsey and Stirling's hypothesis (2007). This negative correlation may be associated with the features of organization of low- and high-productive communities or with the number of species that can potentially grow in these communities or with the combined effect of these factors. If the second mechanism is determinant, it should be expected that R_{SD} and $R_{S\hat{W}}$ should be correlated less significantly with productivity (W_m) than with S_{\max} . The reverse situation may favor the importance of the first mechanism. A certain effect on the $S(D)$ relationship can also be made by different patterns of change in the relative participation of dominants on the gradient of growth in cenosis productivity. The negative pattern of the $D(W)$ relationship can contribute to enhancing the $\hat{W}(D)$ relationship and, accordingly, the $S(D)$ relationship, while the positive pattern can contribute to their weakening.

RESULTS

The results of the research are given in Tables 2–4 and Figs. 1–4. Table 2 shows that subalpine and low-mountain grasslands and steppes with the dominance of *Stipa pulcherrima* are the most productive among the studied communities. They are also characterized by the highest species richness. The lower productivity and species richness are characteristic of communities of dry steppes, subalpine mires, alpine heaths, and mats; the communities of the grass layer of forests have the lowest values of these characteristics. The dominant species in the communities of almost all types under consideration can reach a high level (somewhat less or more than 90%). Among them, the higher degree of dominance is generally characteristic of productive meadow cenoses and low-productive communities of the grass layer of forests, while low-productive nonforest cenoses have a lower productivity. On the whole, the relationship between these characteristics is statistically insignificant (the Pearson correlation coefficient $r = -0.039$, $n = 22$).

Figure 1a and Table 4 show that the relationship between the degree of dominance (D) and species richness (S) differs in communities with the dominance of different species and is significantly correlated with productivity (W_m). The relationship between them is negative linear; the W_m variation explains 42% of the R_{SD} variation. Figure 1a also shows that more productive communities are characterized by moderate and high R_{SD} values, while low-productive communities are characterized by a significant variation of this parameter. To test the presence of the linear component in the correlation between W_m and R_{SD} , we added the quadratic component in the linear regres-

Table 2. Characteristic of studied plant communities

| PC | Dominant species | <i>n</i> | $W_m(W_{\min}-W_{\max})$ | $S_m(S_{\min}-S_{\max})$ | $D_m(D_{\min}-D_{\max})$ |
|-----|---|----------|--------------------------|--------------------------|--------------------------|
| AG | <i>Alchemilla retinervis</i> Buser | 14 | 101.5 (63.7–39.4) | 7.4 (4–11) | 0.83 (0.59–0.97) |
| AG | <i>Geranium gymnocaulon</i> DC | 22 | 76.2 (39.7–171.4) | 14.7 (9–24) | 0.57 (0.25–0.86) |
| AG | <i>Kobresia macrolepis</i> Meinsh. | 21 | 39.7 (22.4–73.4) | 7.5 (4–12) | 0.79 (0.61–0.95) |
| SAG | <i>Brachypodium rupestre</i> (Host) Roem. et Schult | 20 | 100.4 (69.7–160.9) | 20.5 (6–35) | 0.50 (0.26–0.92) |
| SAG | <i>Calamagrostis arundinacea</i> (L.) Roth | 16 | 107.8 (46.4–163.6) | 14.4 (6–27) | 0.61 (0.31–0.90) |
| LMG | <i>Botriochloa ischaemum</i> (L.) Keng | 23 | 88.7 (38.3–149.4) | 12.8 (6–19) | 0.60 (0.26–0.93) |
| LMG | <i>Brachypodium pinnatum</i> (L.) P.Beauv. | 20 | 100.7 (56.8–142.7) | 13.2 (8–21) | 0.69 (0.24–0.88) |
| LMG | <i>Calamagrostis epigeios</i> (L.) Roth | 22 | 120.3 (54.9–186.8) | 7.5 (3–15) | 0.71 (0.34–0.94) |
| LMG | <i>Geranium sanguineum</i> L. | 13 | 130.6 (95.4–163.6) | 22.9 (18–29) | 0.60 (0.50–0.67) |
| AH | <i>Carex tristis</i> M.Bieb. et al. | 18 | 47.3 (20.8–96.8) | 14.8 (9–23) | 0.38 (0.22–0.63) |
| AS | <i>Taraxacum stevenii</i> DC. et al. | 20 | 31.1 (8.2–69.6) | 12.9 (6–22) | 0.47 (0.24–0.88) |
| SF | <i>Carex rostrata</i> Stokes | 23 | 34.4 (18.2–62.1) | 6.5 (2–16) | 0.49 (0.24–0.89) |
| ST | <i>Stipa pulcherrima</i> C.Koch | 16 | 103.0 (70.4–168.8) | 20.5 (14–32) | 0.41 (0.16–0.72) |
| ST | <i>Agropyron pinifolium</i> Nevski | 16 | 77.1 (54.9–105.3) | 11.2 (8–14) | 0.44 (0.20–0.71) |
| ST | <i>Stipa lessingiana</i> Trin. et Rupr. | 10 | 37.1 (16.0–68.9) | 9.1 (7–11) | 0.48 (0.26–0.81) |
| ST | <i>Artemisia lercheana</i> Weber ex Stechm. | 23 | 50.2 (14.3–75.3) | 8.0 (6–9) | 0.66 (0.28–0.98) |
| HF | <i>Aegopodium podagraria</i> L. | 18 | 26.5 (7.9–40.1) | 5.2 (3–7) | 0.66 (0.44–0.88) |
| HF | <i>Allium ursinum</i> L. | 19 | 29.0 (11.8–42.6) | 6.1 (4–8) | 0.68 (0.34–0.89) |
| HF | <i>Dryopteris filix-mas</i> (L.) Schott | 22 | 26.8 (8.2–54.3) | 4.2 (3–6) | 0.73 (0.43–0.98) |
| HF | <i>Festuca montana</i> M.Bieb. | 28 | 13.8 (3.8–53.5) | 4.6 (3–8) | 0.77 (0.49–0.98) |
| HF | <i>Symphytum grandiflorum</i> DC. | 20 | 18.8 (8.1–28.7) | 3.6 (2–6) | 0.74 (0.42–0.99) |
| HF | <i>Trifolium medium</i> L. | 15 | 26.3 (15.5–34.6) | 13.1 (10–18) | 0.46 (0.31–0.67) |

n, Number of samples; W , dry weight of sample ($\text{g}/0.25 \text{ m}^2$); S , number of plant species per 0.25 m^2 ; D , degree of dominance (Berger–Parker index); the numbers in the table field designate the average, minimum and maximum values of parameters.

sion equation; however, it was found to be statistically insignificant. Table 3 shows that the closest relationship between the degree of dominance and species richness is observed in meadow communities. It is lower in relatively productive steppe cenoses and communities of alpine heaths, mats, and some types of grass layer of forests (with the dominance of *Symphytum grandiflorum* and *Allium ursinum*) and statistically insignificant in the low-productive communities of steppes with the dominance of *Stipa lessingiana* and *Artemisia lercheana* in most cenoses of the grass layer of forests.

Figures 1b and 1c show the pattern of $R_{S\hat{W}}$ and $R_{\hat{W}D}$ relationship with the productivity of communities (W_m). In both cases it is linear and significant: positive between W_m and $R_{S\hat{W}}$ and negative between W_m and $R_{\hat{W}D}$ (Table 4). The low-productive communities are characterized by a significant variation in the values of $R_{S\hat{W}}$ and $R_{\hat{W}D}$ here. The correlation between $R_{S\hat{W}}$ and R_{SD} is statistically significant (the Pearson correlation coefficient $r = -0.659$, $n = 22$, $P < 0.001$); the same thing concerns the correlation between $R_{\hat{W}D}$ and R_{SD} (the Pearson correlation coefficient $r = 0.452$, $n = 22$, $P < 0.05$).

According to Fig. 2 and Table 4, there is a linear, positive, statistically significant relationship between the mean productivity (W_m) and maximum species richness of plant communities (S_{\max}). At the same time, Fig. 3a and Table 4 show the absence of a linear relationship between S_{\max} and $R_{S\hat{W}}$. No essential features of the presence of the nonlinear component in the correlation between these characteristics were revealed either. However, a linear negative relationship was revealed between S_{\max} and R_{SD} (Fig. 3b, Table 4). It is statistically significant, but weaker than that between W_m and R_{SD} . At the same time, the partial coefficient of correlation between W_m and R_{SD} (i.e., at constant S_{\max} values) is statistically significant (the partial correlation coefficient $r = -0.617$, $n = 22$, $P < 0.01$) and insignificant between S_{\max} and R_{SD} (at constant W_m values) (the partial correlation coefficient $r = -0.192$, $n = 22$). In addition, we calculated the values of the adjusted coefficient of determination for equations of regression of R_{SD} on W_m , as well as for equations of regression of R_{SD} on W_m and S_{\max} . They were found to be almost identical: $R_{\text{adj}}^2 = 0.393$ in the first case and 0.397 in the second. That is, the addition of the new

Table 3. Spearman correlation coefficient for $S(D)$, $\hat{S}(\hat{W})$, $\hat{W}(D)$, and $D(W)$ relationships

| PC | Dominant species | n | R_{SD} | $R_{\hat{S}\hat{W}}$ | $R_{\hat{W}D}$ | R_{DW} |
|-----|---|-----|---------------|----------------------|----------------|---------------|
| AG | <i>Alchemilla retinervis</i> Buser | 14 | -0.677 | 0.818 | -0.947 | -0.05 |
| AG | <i>Geranium gymnocaulon</i> DC | 22 | -0.766 | 0.334 | -0.827 | 0.52 |
| AG | <i>Kobresia macrolepis</i> Meinsh. | 21 | -0.695 | 0.536 | -0.729 | 0.313 |
| SAG | <i>Brachypodium rupestre</i> (Host) Roem. et Schult | 20 | -0.687 | 0.57 | -0.892 | 0.243 |
| SAG | <i>Calamagrostis arundinacea</i> (L.) Roth | 16 | -0.831 | 0.654 | -0.851 | 0.353 |
| LMG | <i>Botriochloa ischaemum</i> (L.) Keng | 23 | -0.705 | 0.549 | -0.895 | 0.05 |
| LMG | <i>Brachypodium pinnatum</i> (L.) P.Beauv. | 20 | -0.729 | 0.648 | -0.929 | -0.298 |
| LMG | <i>Calamagrostis epigeios</i> (L.) Roth | 22 | -0.661 | 0.863 | -0.94 | -0.644 |
| LMG | <i>Geranium sanguineum</i> L. | 13 | -0.694 | 0.405 | -0.632 | -0.33 |
| AH | <i>Carex tristis</i> M.Bieb. et al. | 18 | -0.454 | 0.538 | -0.239 | 0.003 |
| AS | <i>Taraxacum stevenii</i> DC. et al. | 20 | -0.568 | 0.374 | -0.426 | -0.084 |
| SF | <i>Carex rostrata</i> Stokes | 23 | -0.482 | 0.67 | -0.686 | 0.03 |
| ST | <i>Stipa pulcherrima</i> C.Koch | 16 | -0.491 | 0.622 | -0.759 | 0.106 |
| ST | <i>Agropyron pinifolium</i> Nevski | 16 | -0.474 | 0.61 | -0.574 | 0.179 |
| ST | <i>Stipa lessingiana</i> Trin. et Rupr. | 10 | -0.3 | 0.77 | -0.345 | 0.297 |
| ST | <i>Artemisia lercheana</i> Weber ex Stechm. | 23 | 0 | 0.063 | -0.69 | -0.154 |
| HF | <i>Aegopodium podagraria</i> L. | 18 | 0.289 | 0.178 | -0.436 | 0.698 |
| HF | <i>Allium ursinum</i> L. | 19 | -0.444 | 0.623 | -0.83 | 0.186 |
| HF | <i>Dryopteris filix-mas</i> (L.) Schott | 22 | 0.123 | 0.185 | -0.763 | 0.434 |
| HF | <i>Festuca montana</i> M.Bieb. | 28 | -0.347 | 0.357 | -0.691 | 0.307 |
| HF | <i>Symphytum grandiflorum</i> DC. | 20 | -0.423 | 0.295 | -0.844 | 0.603 |
| HF | <i>Trifolium medium</i> L. | 15 | -0.042 | 0.133 | -0.575 | 0.321 |

Values that are statistically significant at $P < 0.05$ are in semibold.

explanatory variable (S_{\max}) in the equation of regression of R_{SD} on W_m did not lead to a decrease in the explained variation in R_{SD} .

Tables 3 and 4 and Fig. 4 show that the relationship between the productivity (W) and degree of domi-

Table 4. Results of an analysis of the relationship between characteristics on the basis of construction of linear regression models

| Variables | | n | Model | R^2 | P |
|----------------------|------------|-----|-----------------------|-------|--------|
| y | x | | | | |
| R_{SD} | W_m | 22 | $y = -0.005x - 0.125$ | 0.42 | <0.01 |
| $R_{\hat{S}\hat{W}}$ | W_m | 22 | $y = 0.003x + 0.301$ | 0.25 | <0.05 |
| $R_{\hat{W}D}$ | W_m | 22 | $y = -0.003x - 0.539$ | 0.24 | <0.05 |
| S_{\max} | W_m | 22 | $y = 0.151x + 7.369$ | 0.43 | <0.001 |
| R_{SD} | S_{\max} | 22 | $y = -0.020x - 0.122$ | 0.32 | <0.01 |
| $R_{\hat{S}\hat{W}}$ | S_{\max} | 22 | $y = 0.006x + 0.393$ | 0.05 | NS |
| R_{DW} | W_m | 22 | $y = -0.005x + 0.450$ | 0.33 | <0.01 |

n , Number of communities under study; R^2 , unadjusted coefficient of determination (P , level of statistical significance; NS, the value is nonsignificant); the values of the linear regression coefficient that are significant at $P < 0.05$ are semibold.

nance (D) in the studied communities can be both negative and positive. On the whole, the negative relationship between these characteristics occurs somewhat more frequently in more productive cenoses (C-R-S-model), while the positive relationship is most often observed in less productive cenoses (S-model) (Table 3, Fig. 4) and statistically significant only in three types of communities: positive in the communities of the grass layer of forests dominated by *Aegopodium podagraria* and *Symphytum grandiflorum* (S-model) and negative in low-mountain grasslands dominated by *Calamagrostis epigeios* (C-R-S-model) (Table 3). The latter type of community is characterized by a high degree of relationship between D and \hat{W} (Table 3); however, on the whole, the correlation between R_{DW} and $R_{\hat{W}D}$ is statistically insignificant (the Pearson correlation coefficient $r = 0.169$, $n = 22$).

DISCUSSION

The results indicate that, the higher the productivity of communities is, the higher the extent to which their species richness is determined by the biomass of subordinate species and, the higher the extent to which the dominants determine this biomass and the closer

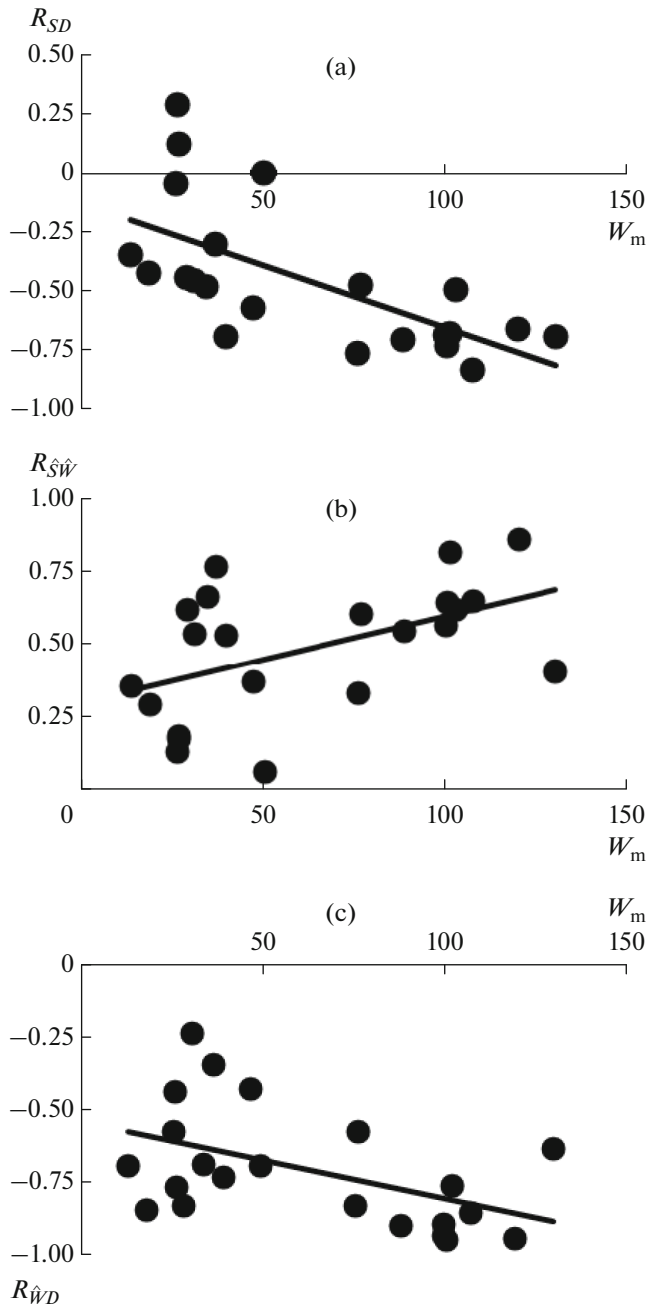


Fig. 1. Correlations between mean the productivity of communities dominated by certain species (W_m) and the relationship in these communities: (a) between degree of dominance (D) and species richness (S); (b) between number (\hat{S}) and total phytomass (\hat{W}) of subordinate plant species; and (c) between degree of dominance (D) and total phytomass of subordinate species (\hat{W}). Here and in the other figures, the strength of the relationship was estimated using the Spearman rank correlation coefficient (R).

the relationship between their relative participation in the formation of cenoses and species richness. Accordingly, it can be expected that the growth in the degree of dominance due to the change in environmental conditions, the replacement of native by alien

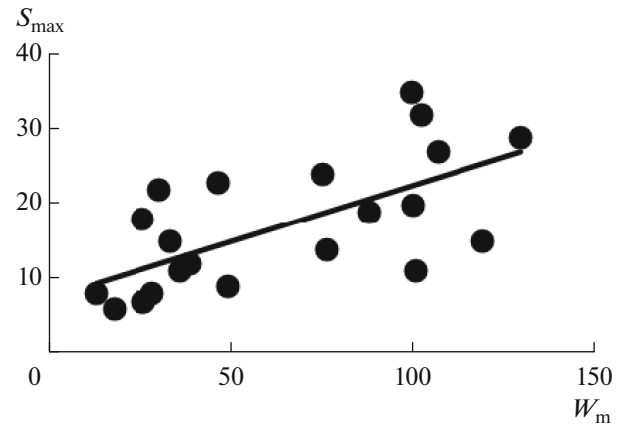


Fig. 2. Correlation between mean productivity (W_m) and maximum species richness (S_{max}) in communities dominated by a certain species.

dominants, or other causes will have more serious consequences for the species richness of more productive plant communities.

The correlation between the $R_{\hat{S}\hat{W}}$ and R_{SD} relationships and the mean productivity of communities (W_m) may be determined by the features of the organization of low- and high-productive cenoses (high or low intensity of interspecific competition) or by different numbers of species that can grow in these cenoses. Our results argue for the first consumption. First, we did not reveal a significant contribution of S_{max} to the explanation of $R_{\hat{S}\hat{W}}$ and R_{SD} variation, irrespective of W_m . Second, low-productive communities are characterized by a significant variation in the degree of relationship between all the study parameters, which can be predicted for cenoses with a significant role of stochastic processes in their formation. Third, the high degree of correlation between D and S is mainly observed in meadow communities, i.e., in those with the C-R-S-organization model. In particular, steppe communities dominated by *Stipa pulcherrima* and *Agropyron pinifolium* are characterized by a lower degree of correlation between these characteristics than meadow cenoses with the same productivity that are dominated by *Alchemilla retinervis*, *Geranium gymnocaulon*, *Brachypodium pinnatum*, etc. (Table 3). Therefore, our data are consistent with the assumption of Wilsey and Stirling (2007), according to which differently organized plant communities can differ in the pattern and strength of relationship between evenness (dominance) and species richness. However, they do not confirm the opinion of these authors that the closer relationship between these characteristics should be observed in cenoses with a low intensity of interspecific competition. Therefore, let us also pay attention to the fact that most dominants in the studied grasslands of the low-mountain belt (*Botriochloa ischaemum*, *Brachypodium pinnatum*, and *Calamagrostis*

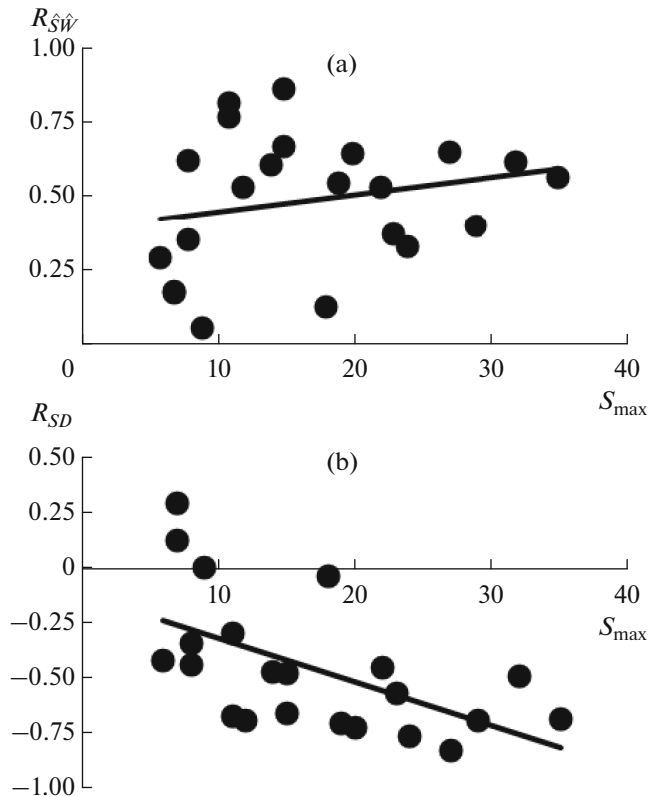


Fig. 3. Correlation between maximum species richness in communities dominated by a certain species (S_{\max}) and relationship (a) between number (\hat{S}) and total phyto-mass (\hat{W}) of subordinate plant species and (b) between degree of dominance (D) and species richness (S) in these communities.

epigeios) are species that are known for their ability to influence species richness (Bobbink and Willemis 1987; Grime, 2001; Sedláková and Fiala, 2001; Somodi et al., 2008; Csergő et al., 2013; Bartha et al., 2014; Vasilevich, 2014). In addition, according to the research of Csergő et al. (2013), the more pronounced the features of the C-strategy of dominant species are, the more significant these abilities are.

The results also showed that, despite the previous assumptions (Chalcraft et al., 2009), the negative relationship between the productivity and degree of dominance is somewhat more often observed in more productive cenoses (C-R-S-model), while the positive relationship is more often observed in less productive cenoses (S-model). However, it proved to be statistically significant only in 3 of the 22 studied types of communities: negative in communities with a relatively high productivity and positive in the other two types of communities with a relatively low productivity. In most of the communities, the relationship between these characteristics is weak and, therefore, the effect of this factor on the $S(D)$ relationship was found to be insignificant.

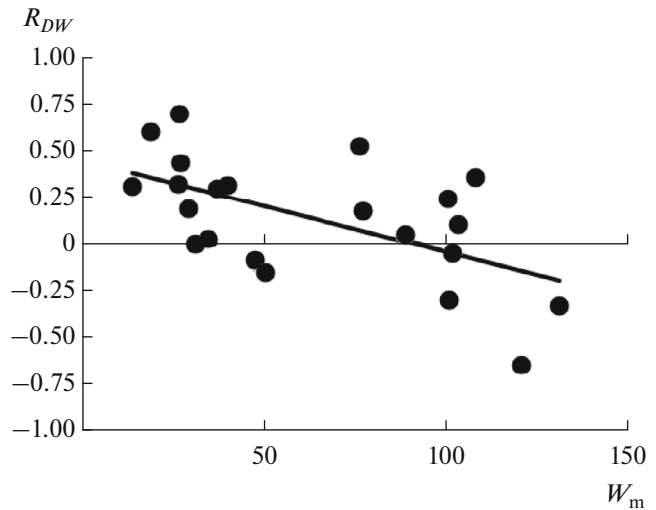


Fig. 4. Correlations between mean productivity of communities dominated by a certain species (W_m) and $D(W)$ relationship.

The finding of the absence of a close relationship between the degree of dominance and productivity in plant communities was also made by other authors (Vermeer and Verhoeven, 1987; Chalcraft et al., 2009; Poggio and Ghersa, 2011; Vasilevich, 2015, etc.). Supposedly, this may be due to the simultaneous effect of several competing factors on this correlation. Thus, the decrease in habitat productivity may lead to a simultaneous increase in the degree of species differentiation with respect to the level of tolerance to abiotic environmental conditions and the decrease in the degree of their differentiation with respect to the ability to compete with each other. At the same time, intensive competition in high-productive communities will not lead to a significant growth in the degree of dominance if they are formed by ecologically equivalent (competitively symmetrical) species, as in the tree layer of tropical forests (Hubbell, 1979; Bell, 2000; Zhang et al., 2015) and, possibly, in communities of some types of meadows (Vasilevich, 2014).

In conclusion, let us focus on three conditions that limit the value of our results.

(1) This article considers the phytocenoses only of stable habitats. The communities of frequently disturbed habitats that are structured mainly by processes of species expansion (R-model) were not included in our analysis (Mirkin, 1994; Mirkin and Naumova, 2012). They generally consist of annual plant species that can quickly use extra space and resources (R-strategists) (Grime, 1977, 2001). According to the opinion of Grime, dominant species with the ruderal strategy have a greater effect on species richness than stress-tolerant dominants. Previously we compared the relationship between D and S in forest-stand sites (structured mainly by competition) and open communities of river shoals (mainly structured by species expan-

sion) (Akátov et al., 2017). We used sample plots with different areas but with equal amplitude of variation in the number of individuals (shoots): 300 and 3000 m² for forest stands and 0.5 and 5 m² for river shoal communities. The results showed that this relationship was closer in forest stands than in river shoal communities. However, while in large plots, this difference was significant (the Pearson correlation coefficient $r = -0.51$ and -0.10 , respectively); in small plots it was statistically insignificant ($r = -0.69$ and -0.58). Most of the invasive plant species are currently ruderal. They grow mainly in R-cenoses and often become dominant (Rejmánek, 1989; Lonsdale, 1999; Richardson and Pyšek, 2006). At the same time, publications provide both examples of their significant effect on the species richness of communities and examples of absence of this effect (Meiners et al., 2001; Houlahan and Findlay, 2004; Sagoff, 2005; Hulme and Bremner, 2006; Eskinina et al., 2012). It is believed that the participation of invasive species is correlated with the productivity of communities (Rejmánek, 1989); however, the pattern of the $S(D)$ relationship with the productivity of communities remains unclear.

(2) The results of field studies more often support the idea of a unimodal form of relationship between productivity and species richness (reviews: Begon, 1996; Adler et al., 2011; Šimová et al., 2013; Vasilevich, 2015, etc.). It assumes that the high species richness is characteristic of communities with mean productivity, while the low species richness is characteristic of communities with both low and high productivity. In the latter case, this may be determined by an intensive competition for light or by some other factors, as well as by a small number of plant individuals in the plots due to their large area (Begon, 1996; Oksanen, 1996; Adler et al., 2011; Šimová et al., 2013; Vasilevich, 2015, etc.). Therefore, some authors consider the low species richness in high-productive cenoses as artefacts (Oksanen, 1996). In this regard, this research covered only the part of the gradient of productivity within which a growth in the species richness of communities was observed (up to 200 g/0.25 m²) (Akátov and Akátova, 2016).

(3) The small area of the sampling plots (0.25 m²) means that our findings pertain only to a small spatial scale. Most studies aimed at solving similar problems used approximately the same scale (0.1–1 m²) (Chalcraft et al., 2009; Adler et al., 2011; Lebedeva et al., 2011; Poggio and Ghersa, 2011; Csergő et al., 2013, etc.). However, as was shown above, the pattern of relationship between the degree of dominance and species richness can significantly vary with a change in the area of sample plots (Akátov et al., 2017).

Therefore, our results lead to the conclusion that the closer relationship between the degree of dominance and species richness was observed in more productive (dense and/or high) herbage, which is most likely due to more intensive interspecific competition.

However, further research is required to determine the extent to which the revealed regularities could be universal, given changes in the spatial scope of research, an increase in the range of variation in the productivity of communities, and an increase in the spectrum of models of their organization.

ACKNOWLEDGMENTS

This article provides results of the research that was financially supported by the Russian Foundation for Basic Research (grant no. 16-04-00228).

REFERENCES

- Adler, P.B., Seabloom, E.W., Borer, E.T., et al., Productivity is a poor predictor of plant species richness, *Science*, 2011, vol. 333, pp. 1750–1753.
- Akátov, V.V. and Akátova, T.V., Dominance level in grass communities with different models of the organization, in *Raznoobrazie i klassifikatsiya rastitel'nosti* (Diversity and Classification of Vegetation), Korzhenevskii, V.V. and Ermakov, N.B., Eds., Yalta: Gos. Nikitskii Bot. Sad, 2016, vol. 143, pp. 16–24.
- Akátov, V.V., Akátova, T.V., and Shadzhe, A.E., Species richness of tree and shrub layers in riparian forests of the Western Caucasus dominated by alien species, *Russ. J. Ecol.*, 2012, vol. 43, no. 4, pp. 294–301.
- Akátov, V.V., Akátova, T.V., and Chefranov, S.G., Degree of dominance and species diversity in the plant communities with high and low intensity of interspecies competitiveness, *Zh. Obshch. Biol.*, 2017, vol. 78, no. 4, pp. 52–64.
- Aksenova, A.A., Onipchenko, V.G., and Blinnikov, M.S., Experimental study of plant relationships. Dominant removals. Alpine lichen heaths, in *Alpine Ecosystems in the Northwest Caucasus*, Onipchenko, V.G., Ed., Dordrecht: Kluwer, 2004, pp. 236–244.
- Bartha, S., Szentés, 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., et al., Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands, *Appl. Veg. Sci.*, 2014, vol. 17, no. 2, pp. 201–213.
- Begon, M., Harper, J.L., and Townsend, C.R., *Ecology: Individuals, Populations and Communities*, New York: Wiley, 1996.
- Bell, G., The distribution of abundance in neutral communities, *Am. Nat.*, 2000, vol. 155, no. 5, pp. 606–617.
- Bengtsson, J., Fagerström, T., and Rydin, H., Competition and coexistence in plant communities, *Tree*, 1994, vol. 9, no. 7, pp. 246–250.
- Bennett, J.A. and Cahill, J.F., Jr., Evaluating the relationship between competition and productivity within a native grassland, *PLoS One*, 2012, vol. 7, no. 8, p. e43703.
- Berger, W.H. and Parker, F.L., Diversity of planktonic foraminifera in deep-sea sediments, *Science*, 1970, vol. 168, pp. 1345–1347.
- Bobbink, R. and Willems, J.H., Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in Chalk Grass-

- lands: a threat to a species-rich ecosystem, *Biol. Conserv.*, 1987, vol. 40, no. 4, pp. 301–314.
- Callaway, R.M. and Ridenour, W.M., Novel weapons: a biochemically-based hypothesis for invasive success and the evolution of increased competitive ability, *Front. Ecol. Environ.*, 2004, no. 2, pp. 433–436.
- Caswell, H. Community structure: a neutral model analysis, *Ecol. Mon.*, 1976, vol. 46, pp. 327–354.
- Chalcraft, D.R., Wilsey, B.J., Bowles, C., and Willig, M.R., The relationship between productivity and multiple aspects of biodiversity in six grassland communities, *Biodiversity Conserv.*, 2009, vol. 18, pp. 91–104.
- Chase, J.M., Towards a really unified theory for metacommunities, *Funct. Ecol.*, 2005, vol. 19, pp. 182–186.
- Cherednichenko, O.V., Experimental study of plant relationships. Dominant removals. Removals in the *Geranium gymnocaulon*–*Hedysarum caucasicum* meadow, in *Alpine Ecosystems in the Northwest Caucasus*, Onipchenko, V.G., Ed., Dordrecht: Kluwer, 2004, pp. 244–250.
- Goldberg, D. and Novoplansky, A., On the relative importance of competition in unproductive environments, *J. Ecol.*, 1997, vol. 85, pp. 409–418.
- Cornell, H.V., Unsaturated patterns in species assemblage: the role of regional processes in setting local species richness, in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D., Eds., Chicago: Chicago Univ. Press, 1993, pp. 243–253.
- Cornell, H.V. and Lawton, J.H., Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective, *J. Anim. Ecol.*, 1992, vol. 61, pp. 1–12.
- Csergő, A.M., Demeter, L., and Turkington, R., Declining diversity in abandoned grasslands of the Carpathian Mountains: do dominant species matter? *PLoS One*, 2013, vol. 8, no. 8, p. e73533. doi 10.1371/journal.pone.0073533
- Drobner, U., Bibby, J., Smith, B., and Wilson, J.B., The relation between community biomass and evenness: what does community theory predict, and can these predictions be tested? *Oikos*, 1998, vol. 82, pp. 295–302.
- Ernest, S.K.M. and Brown, J.H., Homeostasis and compensation: the role of species and resources in ecosystem stability, *Ecology*, 2001, vol. 82, no. 8, pp. 2118–2132.
- Eskina, T.G., Akatov, V.V., and Akatova, T.V., Composition and species richness of fallow plant communities with predominance of adventive species (Belaya River basin, Western Caucasus), *Russ. J. Biol. Invasions*, 2012, vol. 3, no. 3, pp. 55–66.
- Gilyarov, A.M., In search for universal patterns in the organization of communities: The concept of neutrality has paved the way to a new approach, *Biol. Bull. Rev.*, 2011, vol. 1, no. 1, pp. 13–25.
- Grime, J.P., Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory, *Am. Nat.*, 1977, vol. 111, no. 982, pp. 1169–1194.
- Grime, J.P., *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, Chichester: Wiley, 2001, 2nd ed.
- Hejda, M., Pyšek, P., and Jarošík, V., Impact of invasive plants on the species richness, diversity and composition of invaded communities, *J. Ecol.*, 2009, vol. 97, pp. 393–403.
- Hillebrand, H., Bennett, D.M., and Cadotte, M.W., Consequences of dominance: a review of evenness effects on local and regional ecosystem processes, *Ecology*, 2008, vol. 89, no. 6, pp. 1510–1520.
- Houlahan, J.E. and Findlay, C.S., Effect of invasive plant species on temperate wetland plant diversity, *Conserv. Biol.*, 2004, vol. 18, no. 4, pp. 1132–1138.
- Hubbell, S.P., Tree dispersion, abundance, and diversity in a tropical dry forest, *Science*, 1979, vol. 203, pp. 1299–1309.
- Hulme, P.E. and Bremner, E.T., Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal, *J. Appl. Ecol.*, 2006, vol. 43, pp. 43–50.
- Huston, M.A., General hypothesis of species diversity, *Am. Nat.*, 1979, vol. 113, no. 1, pp. 81–101.
- Kunte, K., Competition and species diversity: removal of dominant species: increases diversity in Costa Rican butterfly communities, *Oikos*, 2008, vol. 117, pp. 69–76.
- Lamb, E.G. and Cahill, J.F., When competition does not matter: grassland diversity and community composition, *Am. Nat.*, 2008, vol. 171, pp. 777–787.
- Lebedeva, V.Kh., Tikhodeeva, M.Yu., and Ipatov, V.S., The structure of the meadow plant community, *Bot. Zh.*, 2011, vol. 96, no. 1, pp. 3–21.
- Longino, J.T. and Colwell, R.K., Density compensation, species composition, and richness of ants on a neotropical elevational gradient, *Ecosphere*, 2011, vol. 2, no. 3, pp. 1–20.
- Lonsdale, W.M., Global patterns of plant invasions and the concept of invisibility, *Ecology*, 1999, vol. 80, pp. 1522–1536.
- Ma, M., Species richness vs. evenness: independent relationship and different responses to edaphic factors, *Oikos*, 2005, vol. 111, pp. 192–198.
- Magguran, A., *Ecological Diversity and Its Measurement*, Princeton, NJ: Princeton Univ. Press, 1988.
- Maarel van der, E., Noest, V., and Palmer, M.W., Variation in species richness on small grassland quadrates: niche structure or small-scale plant mobility? *J. Veg. Sci.*, 1995, vol. 6, pp. 741–752.
- McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., and Murray, G., Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra, *Nature*, 2002, vol. 415, pp. 68–71.
- Meiners, S.J., Pickett, S.T.A., and Cadenasso, M.L., Effects of plant invasions on the species richness of abandoned agricultural land, *Ecography*, 2001, vol. 24, pp. 633–644.
- Mirkin, B.M., Which plant communities do exist? *J. Veg. Sci.*, 1994, vol. 5, no. 2, pp. 283–284.
- Mirkin, B.M. and Naumova, L.G., *Sovremennoe sostoyanie osnovnykh kontseptsii nauki o rastitel'nosti* (Modern General Scientific Concepts on Vegetation), Ufa: Gilem, 2012.

- Mulder, C.P.H., Bazeley-White, E., Dimitrakopoulos, P.G., Hector, A., Scherer-Lorezen, M., and Schmid, B., Species evenness and productivity in experimental plant communities, *Oikos*, 2004, vol. 107, pp. 50–63.
- Oksanen, J., Is the humped relationship between species richness and biomass an artefact due to plot size? *J. Ecol.*, 1996, vol. 84, pp. 293–295.
- Onipchenko, V.G., *Funktsional'naya fitotsenologiya: sinekologiya rastenii* (Functional Phytocenology: Synecology of the Plants), Moscow: Krassand, 2013.
- Onipchenko, V.G., Semenova, G.V., and van der Maarel, E., Population strategies in severe environments: alpine plants in the northwestern Caucasus, *J. Veg. Sci.*, 1998, vol. 9, pp. 27–40.
- Palmer, M.W. and van der Maarel, E., Variance in species richness, species association and niche limitation, *Oikos*, 1995, vol. 73, pp. 203–213.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., and Goldwasser, L., Impact: toward a framework for understanding the ecological effects of invaders, *Biol. Invasions*, 1999, vol. 1, pp. 3–19.
- Peet, R.K. and Christensen, N.L., Changes in species diversity during secondary forest succession on the North Carolina piedmont, in *Diversity and Pattern in Plant Communities*, During, H.I., Werge, M.I.A., and Willems, J.H., Eds., Hague: Academic, 1988, pp. 233–245.
- Piper, J.K., Composition of prairie plant communities on productive versus unproductive sites in wet and dry years, *Can. J. Bot.*, 1995, vol. 73, pp. 1635–1644.
- Poggio, S.L. and Ghersa, C.M., Species richness and evenness as a function of biomass in arable plant communities, *Weed Res.*, 2011, vol. 51, pp. 241–249.
- Qian, H. and Ricklefs, R.E., Taxon richness and climate in Angiosperms: is there a globally consistent relationship that precludes region effects? *Am. Nat.*, 2004, vol. 163, no. 5, pp. 773–779.
- Rabotnov, T.A., *Fitotsenologiya* (Phytocenology), Moscow: Mosk. Gos. Univ., 1983.
- Rejmánek, M., Invasibility of plant communities, in *Biological Invasions: A Global Perspective*, New York: Wiley, 1989, pp. 369–388.
- Reinhart, K.O., Greene, E., and Callaway, R.M., Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the Rocky Mountains, *Ecography*, 2005, vol. 28, pp. 573–582.
- Richardson, D.M. and Pyšek, P., Plant invasions: merging the concepts of species invasiveness and community invasibility, *Progr. Phys. Geogr.*, 2006, vol. 30, no. 3, pp. 409–431.
- Sagoff, M., Do non-native species threaten the natural environment? *J. Agric. Environ. Ethics*, 2005, vol. 18, pp. 215–236.
- Sasaki, T. and Lauenroth, W.K., Dominant species, rather than diversity, regulates temporal stability of plant communities, *Oecologia*, 2011, vol. 166, no. 3, pp. 761–768.
- Sedláková, I. and Fiala, K., Ecological degradation of alluvial meadows due to expanding *Calamagrostis epigejos*, *Ekológia* (Bratislava), 2001, vol. 20, no. 3, pp. 226–333.
- Šimová, I., Li, Y.M., and Storch, D., Relationship between species richness and productivity in plants: the role of sampling effect, heterogeneity and species pool, *J. Ecol.*, 2013, vol. 101, pp. 161–170.
- Somodi, I., Virágh, K., and Podani, J., The effect of the expansion of the clonal grass *Calamagrostis epigejos* on the species turnover of a semi-arid grassland, *Appl. Veg. Sci.*, 2008, vol. 11, pp. 187–194.
- Stirling, G. and Wilsey, B., Empirical relationships between species richness, evenness, and proportional diversity, *Am. Nat.*, 2001, vol. 158, pp. 286–300.
- Tilman, D., Resources: a graphical mechanistic approach to competition and predation, *Am. Nat.*, 1980, vol. 116, pp. 362–393.
- Vasilevich, V.I., Species diversity in upland meadow communities of the north-west of European Russia, *Bot. Zh.*, 2014, vol. 99, no. 2, pp. 226–236.
- Vasilevich, V.I., Species diversity of moist meadows in European Russia, *Bot. Zh.*, 2015, vol. 100, no. 4, pp. 372–381.
- Vermeer, J.G. and Verhoeven, J.T.A., Species composition and biomass production of mesotrophic fens in relation to the nutrient status of the organic soil, *Acta Oecol., Oecol. Plant.*, 1987, vol. 8, pp. 321–330.
- Wilsey, B. and Stirling, G., Species richness and evenness respond in a different manner to propagule density in developing prairie microcosm communities, *Plant. Ecol.*, 2007, vol. 190, pp. 259–273.
- Wright, D.H., Species-energy theory: an extension of species-area theory, *Oikos*, 1983, vol. 41, pp. 496–506.
- Wright, D.H., Currie, D.J., and Maurer, B.A., Energy supply and patterns of species richness on local and regional scales, in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D., Eds., Chicago: Chicago Univ. Press, 1993, pp. 66–75.
- Yodzis, P., Competition for space and the structure of ecological communities, *Lect. Notes Biomath.*, 1978, vol. 25, pp. 1–191.
- Zhang, J., Qiao, X., Liu, Y., Lu, J., Jiang, M., Tang, Z., and Fang, J., Species-abundance distributions of tree species varies along climatic gradients in China's forests, *J. Plant Ecol.*, 2015, vol. 23, no. 9, pp. 1–7.

Translated by D. Zabolotny