

The Relationship of Dominance and Evenness with Productivity and Species Richness in Plant Communities with Different Organization Models

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Abstract—The relationship between dominance and evenness in plant communities organized according to different models—competitive (alpine, subalpine, and low-mountain grasslands), stress-tolerant (alpine heaths and scrubs, subalpine fens, steppes, the forest herbaceous layer), and ruderal—has been analyzed in the Western Caucasus and Ciscaucasia. No correlation between evenness (dominance) and productivity has been revealed in communities of any type. The correlation between dominance and species richness is negative and, in most cases, linear, being stronger in competitive and ruderal than in stress-tolerant cenoses. The correlation between evenness and species richness in grassland communities (the competitive model) is strong, positive, and linear, while this correlation in ruderal and stress-tolerant communities is weak or absent.

Keywords: productivity, species richness, dominance, evenness, plant communities, life history strategies, competition, organization models

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Parameters of evenness (dominance) characterize the degree of uniformity (nonuniformity) in the distribution of species with respect to their role (abundance, biomass) in biological communities [1]. A correct idea of the character and causes of relationship between these factors and productivity and species richness is important for understanding the functioning of ecosystem and for the development of many practical aspects of environmental protection: bioindication, biodiversity conservation, invasive ecology, etc. [1–6]. However, knowledge in this field is still limited and controversial [6–8].

Thus, studies performed in the 1970 to 1990 provided a basis for the opinion that competition in communities of stable and productive habitats leads to a decrease in both evenness and species richness, up to monopolization of area by the most successful competitor. On the other hand, deterioration of environmental conditions and frequent disturbances may result in the disappearance of vulnerable species from the communities and monopolization of resources by the most tolerant of the remaining species [1, 9–11]. Therefore, the species richness and evenness (dominance) of cenoses may be positively (negatively) correlated with each other. However, subsequent studies have shown that correlation between these parameters is often weak or absent in the communities of organ-

isms of certain taxonomic groups, including plants [2, 8, 12–16].

A hypothesis has been proposed that this situation may be due to differences in the type of cenosis organization [8]. In cenoses where competition is weak or absent (non-interactive communities), both species richness and evenness depend mainly on the rate of species immigration. According to predictions based on neutral diversity models, the correlation between these parameters in such cenoses may be positive and significant [8, 17, 18]. On the contrary, species richness and evenness in communities with high-intensity competition (interactive communities) are determined by different processes: species richness is more sensitive to the rate of species immigration, and evenness, to the intensity of biological interactions. Therefore, variation in the abundance of species is often not accompanied by changes in their number and, consequently, the correlation between these parameters proves to be weak [8, 12–14].

According to a number of authors [19–22], interactive plant communities are formed in favorable (stable and productive) habitats; non-interactive communities, in habitats subject to frequent disturbances or exposed to stress factors: a deficit of illumination, moisture, or mineral nutrients, too high or low tem-

peratures, etc. As follows from the concept of the life history strategies of species [19, 23], favorable habitats are dominated by highly competitive perennial species capable of occupying and holding available space but negatively responding to disturbance (*C*-strategists); stable low-productive habitats, by stress-tolerant but competitively weak species (*S*-strategists); and frequently disturbed habitats, mainly by annual species that can rapidly utilize vacant space and resources (*R*-strategists) [19, 23]. According to the multimodel concept advanced by Mirkin [22, 24], herbaceous communities of the first type correspond to the *C-R-S* organization model; communities of the second type, to the abiotic or biotic *S* model; and communities of the third type, to the *R* model.

Theoretically, the type of relationship between evenness (dominance) and productivity can also be determined by the model of cenosis organization. Since stable habitats at the ends of productivity gradient may be almost completely occupied by the most successful *S*- or *C*-strategists, the growth of productivity in extreme habitats will enhance the role of subdominant species, and in favorable habitats, the role of dominant species [7]. It is also possible that the most successful *R*-strategists, which are the first to occupy the space vacated after disturbance, more rapidly reach a high abundance in more productive habitats. Therefore, the correlation between productivity and evenness will be positive in *S*-model communities and negative in *C-R-S* and *R* cenoses.

On the other hand, the intensity of interspecific competition for light is known to depend on the amplitude of variation in the size (biomass) of plants [2, 11, 25], and it is higher than the intensity of competition for mineral resources [2, 14, 26–29]. Therefore, the probability of competitive exclusion of species should be higher and differences in abundance (biomass) between the remaining species should be more distinct in more productive communities (with a taller grass stand) than in less productive communities [2, 25, 30]. Correspondingly, the relationship between productivity and evenness may be negative irrespective of the model of community organization [30]. However, the validity of these hypotheses is still open to doubt, because the number of relevant field studies is limited and their results are ambiguous [6, 7, 25, 30–34].

The purpose of this study was to determine the type of relationship of dominance (evenness) with productivity and species richness in herbaceous communities with different organization models.

MATERIAL AND METHODS

Herbaceous phytocenoses of favorable and extreme habitats were studied in different regions and altitudinal belts of the Western Caucasus and Ciscaucasia. They included alpine heaths, snowbeds, and grasslands; subalpine grasslands and fens; low-mountain

grasslands; the herbaceous layer of oak, beech, and alder forests; low-productive steppes (including dry steppes on solonchic soils); and communities of mostly annual plants in ruderal habitats (areas with construction waste, bare soil or clay ground).

According to current concepts, grassland communities correspond to the competitive (*C-S-R*) model [20, 22, 24, 35]. In particular, dominant species of alpine and subalpine grasslands (*Geranium gymnocaulon*, *Hedysarum caucasicum*, *Festuca woronowii*, etc.) have relatively large biomass, large seeds, and low growth rate, which are characteristic of *C*-strategists; other species of these communities have features of *C*-, *S*-, and *R*-strategists [35]. In turn, most dominants of low-mountain grasslands included in the study (*Botriochloa ischaemum*, *Brachypodium pinnatum*, *Calamagrostis epigejos*) belong to the group of species that can have an effect on species richness [16, 23, 36–39].

Communities of ruderal habitats correspond to the *R* model [19, 20, 22, 24, 40], but many authors have noted that many plants in these habitats have features of *C*-strategists [41, 42]. Communities of other types have been formed under continuous exposure to stress factors. Thus, alpine snowbed cenoses grow in habitats with long-lying snow and, hence, have a short period of vegetative development; cenoses of alpine heath grow in habitats with little snow (at the tops of mountains and ridges), where winter soil temperatures are low; communities of subalpine fens and dry steppes have been formed under conditions of overmoistening and moisture deficit, respectively; and the herbaceous layer in forests receives little light. All these communities correspond to the stress-tolerant (*S*) model [19, 20, 22, 35].

This study was based on 408 aboveground phytomass samples collected from 0.25-m² plots during the field seasons of 2014 to 2017. Information on the location of sampling sites is given in Table 1. The factual material on communities of ruderal habitats was collected in the city of Maykop and its vicinities; on high-mountain communities (alpine grasslands, heaths and snowbeds, subalpine grasslands and fens), in the Caucasian State Nature Biosphere Reserve; on other community types, in habitats without signs of anthropogenic disturbance located beyond specially protected areas. Samples were taken in typical areas of a given community at the peak of grass stand development. More than half of all samples (250) were collected in a regular pattern, along transects including ten 0.25-m² plots each; others were collected in series of three to six samples per site. In the latter case, we selected variants of communities with the maximum, medium, and minimum coverages of dominant species (according to visual estimation).

The samples were sorted out into species and weighed. Sorting of simple samples (with readily identifiable species) was performed in the field or in the laboratory; complex samples were sorted only in the

Table 1. Locations of sampling plots

Plot no.	Location	Coordinates	Elevation a.s.l., m	Communities (number of samples)
1	City of Maykop and its vicinities	44°34.036'–44°34.335' N, 40°00.708'–40°08.014' E	240–280	RUD (35)
2	Lesisty Ridge, Belaya River basin	44°35.152'–44°36.122' N, 40°01.041'–40°06.399' E	220–300	HF (85)
3	Skalisty Ridge, Belaya River basin	44°15.464'–44°21.393' N, 40°09.587'–40°12.587' E	498–744	LMG (50), HF (53)
4	Mt. Akhmedov Post, Bol'shaya Laba River basin	44°13.346' N, 41°02.718' E	662	LMG (23)
5	Mt. Oshten, Belaya River basin	43°58.498'–44°01.074' N, 38°57.555'–39°58.900' E	1855–2794	AG (20), AHS (16), SAG (13), SF (18)
6	Mt. Abago, Belaya River basin	43°54.428'–43°55.217' N, 40°08.654'–40°09.120' E	2164–2667	AHS (8)
7	Mt. Yukha, Malaya Laba River basin	43°42.189'–43°43.711' N, 40°40.841'–40°42.651' E	2308–2680	AG (8), SF (4)
8	Mt. Chugush, Mzymta River basin	43°46.443'–43°46.776' N, 40°12.389'–40°12.844' E	2382–2648	AG (4), AHS (5), SAG (4)
9	Atsetuka Ridge, Mzymta River basin	43°32.845'–43°34.278' N, 40°35.247'–40°37.924' E	1858–1897	SAG (10), SF (10)
10	Stavropol Upland	44°51.153' N, 41°56.285' E	585	ST (27)
11	Vicinity of Lake Manych	45°59.833' N, 43°14.405' E	30–75	ST (15)

Here and in Tables 2, 3 and Figs. 1, 2: AG, alpine grasslands; SAG, subalpine grasslands; LMD, low-mountain grasslands; AHS, alpine heaths and snowbeds; SF, subalpine fens; ST, steppes; HF, forest herbaceous layer; RUD, ruderal communities.

laboratory. One to three typical samples from each series were dried and weighed; for the remaining samples, dry weight was determined based on the values of desiccation shrinkage coefficient. Thus, the total productivity of communities was estimated based on the dry weight of living biomass, and relative significance of individual species, based on its wet weight. It is considered that biomass gives a more accurate idea of the degree of differentiation in the proportions of species in communities, compared to other characteristics [1, 20]. The small size of sampling plots (0.5×0.5 m) implies that the results of this study are relevant only on a small spatial scale. However, the majority of similar studies [6, 7, 17, 25, 43–45] have also been performed on a similar scale, with the size of the plots ranging from 0.25×0.25 to 1×1 m.

The collected material was used to determine the values of the following parameters: W and W_d , total wet and dry phytomass weights per 0.25 m²; W_i , wet phytomass weight of each species; S , species richness (number of plant species per 0.25 m²); $d = W_1 / W$, relative significance of the most abundant species, or the degree of dominance (Berger–Parker index [1, 46]); J' , Pielou's index of evenness calculated on the basis of Shannon–Wiener's index ($J' = H/H_{\max}$; $H = -\sum p_i \ln p_i$, where p_i is the proportion of the i th species in the total phytomass, and $H_{\max} = \ln S$ are H values in the situa-

tion where all species have equal relative significance) [1, 47]. Despite criticism [48, 49], this index has been used most frequently over many years [1, 5, 6, 8, 12, 39, 49, 50]. Moreover, indices d and J' well complement each other, since the former depends on the relative significance (abundance and biomass) of the dominant species alone, while the latter is sensitive to the significance ratio of not only high-rank but also low-rank species [1].

According to the hypotheses described above, the relationship of dominance (d) and evenness (J') with productivity (W_d) and species richness (S) in communities with different organization models could be positive, negative, or absent. Its type for each community type was determined by plotting linear and polynomial (quadratic) regression models, assuming that statistical significance confirmed for only linear regression coefficients was indicative of a linear relationship, while that confirmed for both linear and quadratic or only quadratic coefficients, of a curvilinear relationship. For the same purpose, we additionally compared adjusted coefficients of determination (R_{adj}^2) for linear and polynomial models. The strength of correlation between variables was evaluated by estimating statistical significance of regression coefficients (Student's t -test) and nonadjusted coefficients of determination

Table 2. Characteristics of plant communities

Community, elevation a.s.l. (dominant species)	<i>n</i>	W_d	<i>S</i>
<i>C-S-R</i> model			
AG, 2000–2650 m (<i>Onobrychis biebercheitnii</i> , <i>Kobresia caprifolia</i> , <i>Alchemilla vulgaris</i> , <i>Geranium gymnocaulon</i> , <i>Hedysarum caucasicum</i>)	32	78.3 ± 6.7	9.8 ± 1.1
SAG, 1850–2450 m (<i>Calamagrostis arundinacea</i> , <i>Festuca woronowii</i> , <i>Brachypodium rupestre</i> , <i>Inula grandiflora</i> , <i>Senecio platyphylloides</i>)	27	112.8 ± 4.4	18.8 ± 1.5
LMG, 490–750 m (<i>Botriochloa ischaemum</i> , <i>Brachypodium pinnatum</i> , <i>Calamagrostis epigejos</i> , <i>Chrysopogon gryllus</i> , <i>Inula salicina</i> subsp. <i>aspera</i> , <i>Salvia verticillata</i>)	73	103.0 ± 2.9	12.7 ± 0.6
<i>S</i> model			
AHS, 2100–2800 m (<i>Campanula tridentata</i> , <i>Carex tristis</i> , <i>Festuca ovina</i> , <i>Kobresia persica</i> , <i>Carum caucasicum</i> , <i>Leontodon hispidus</i> , <i>Pedicularis nordmanniana</i> , <i>Plantago atrata</i> , <i>Ranunculus crassifolius</i> , <i>Sibbaldia parviflora</i> , <i>Silene dianthoides</i> , <i>Trifolium badium</i> , <i>Veronica gentianoides</i>)	29	39.0 ± 3.5	14.0 ± 0.9
SF, 1850–2150 m (<i>Allium schoenoprasum</i> , <i>Carex rostrata</i> , <i>C. transcaucasica</i> , <i>Cirsium simplex</i> , <i>Eriophorum vaginatum</i> , <i>Menyanthes trifoliata</i> , <i>Primula auriculata</i>)	35	50.0 ± 3.5	8.5 ± 0.7
ST, 75–600 m (<i>Stipa lessingiana</i> , <i>S. pulcherrima</i> , <i>Salvia verticillata</i> , <i>Teucrium chamaedrys</i> , <i>Allium albidum</i> , <i>Artemisia lercheana</i> , <i>Poa bulbosa</i>)	42	55.4 ± 4.6	15.4 ± 1.3
HF, 220–500 m (<i>Aegopodium podagraria</i> , <i>Allium ursinum</i> , <i>Carex divulsa</i> , <i>C. pallescens</i> , <i>C. sylvatica</i> , <i>Dryopteris filix-mas</i> , <i>Festuca drymeja</i> , <i>Galeobdolon luteum</i> , <i>Salvia glutinosa</i> , <i>Symphytum grandiflorum</i> , <i>Trifolium medium</i>)	138	22.8 ± 1.1	5.9 ± 0.3
<i>R</i> model			
RUD, 200–240 m (<i>Acalypha australis</i> , <i>Amaranthus blitoides</i> , <i>Ambrosia artemisifolia</i> , <i>Bidens frondosa</i> , <i>Chenopodium album</i> , <i>Conyza canadensis</i> , <i>Digitaria sanguinalis</i> , <i>Ranunculus repens</i> , <i>Setaria verticillata</i> , <i>Solidago canadensis</i> , <i>Sonchus oleraceus</i>)	35	138.4 ± 8.4	8.6 ± 0.6

Designations: *n*, number of samples; W_d , average sample dry weight (g/0.25 m²); *S*, average number of species per 0.25 m². Species names are given according to [73].

(Fisher's *F*-test). Calculations were made using Microsoft Excel 2007 and Statistica 6.0.

RESULTS

The results of the study are presented in Tables 2, 3 and Figs. 1, 2. Table 2 shows general characteristics of plant communities included in analysis. It follows from these data that ruderal communities (the *R* model) are most productive. Among competitive communities (the *C-S-R* model), alpine grasslands have, on average, lower productivity than subalpine and low-mountain grasslands. The herbaceous layer in shady forests is the least productive among *S*-cenoses. Species richness is the highest in phytocenoses of subalpine grasslands (the *C-S-R* model), exceeding its average level in low-mountain grasslands (the *C-S-R* model), steppes, alpine heaths and snowbeds (the *S* model). The minimum number of species per plot is characteristic of the forest herbaceous layer (the *S* model).

The results of analyzing the relationship of dominance and evenness with productivity and species richness (Table 3, Figs. 1, 2) show that:

(1) There is no linear correlation between evenness (the degree of dominance) and productivity in com-

munities of any type, regardless of organization model: linear regression coefficients and determination coefficients in all cases lack statistical significance (Table 3). To test for nonlinearity in the relationship between these parameters, we added a quadratic component to the linear regression equations, but it also proved to be statistically nonsignificant in all cases.

(2) The correlation between species richness and the degree of dominance in the majority of communities is linear, negative, and statistically significant (Table 3, Fig. 1), being stronger in competitive and ruderal communities (of grasslands and disturbed habitats) than in stress-tolerant communities (heaths and snowbeds, fens, forest herbaceous layer). Indications for the presence of a nonlinear component in the relationship between these parameters exist only in subalpine grassland communities: (a) both linear and quadratic components are statistically significant ($d = 0.001 * S^2 - 0.070 ** S + 1.289$; $*p < 0.05$, $**p < 0.01$), and (b) the adjusted coefficient of determination is higher in the polynomial than in the linear model ($R_{adj}^2 = 0.53$ vs. 0.41). Communities of this type are characterized by the highest species richness, up to 35 species per 0.25 m² (Table 2, Fig. 1), with *d* values decreasing only in the interval of 7 to 25 species

Table 3. Results of linear regression analysis of dominance (d) and evenness (J') versus productivity (W_d) and species richness (S) in plant communities of different types

Community (model)	n	Ratios							
		d/W_d		J'/W_d		d/S		J'/S	
		b	R^2	b	R^2	b	R^2	b	R^2
AG ($C-S-R$)	32	0.000	0.00	-0.000	0.00	-0.033***	0.80	0.027***	0.72
SAG ($C-S-R$)	27	-0.002	0.04	0.003	0.10	-0.019***	0.43	0.017***	0.48
LMG ($C-S-R$)	73	-0.001	0.01	0.001	0.03	-0.034***	0.58	0.024***	0.53
AHS (S)	29	-0.002	0.03	0.000	0.01	-0.020***	0.35	0.006	0.08
SF (S)	32	-0.000	0.02	-0.001	0.00	-0.024***	0.32	-0.009	0.07
ST (S)	42	-0.002	0.06	-0.001	0.02	-0.014***	0.22	0.010**	0.19
HF (S)	138	-0.000	0.00	-0.000	0.00	-0.031***	0.35	0.009*	0.03
RUD (R)	32	0.001	0.05	-0.000	0.01	-0.039***	0.56	0.026**	0.24

Designations: n , number of samples; b , linear regression coefficient (significance level: * $p < 0.05$, ** $p < 0.01$, *** $P < 0.001$); R^2 , coefficient of determination (values statistically significant at $p < 0.05$ are boldfaced).

($d = -0.032S + 1.040$; $R^2 = 0.52$, $p < 0.001$) and remaining generally unchanged at higher S values.

(3) The correlation of species richness with evenness is positive, linear, and strong in grassland communities (the $C-S-R$ model), positive, linear, and moderate in ruderal and steppe cenoses (the R and S models, respectively); and very weak or absent in other S -communities (heaths and snowbeds, fens, forest herbaceous layer) (Fig. 2, Table 3). In general, species richness in the majority of communities is less strongly correlated with evenness than with dominance, and this difference in competitive communities is less distinct than in communities with other organization models (Fig. 2, Table 3).

DISCUSSION

Thus, we have revealed no relationship between evenness (dominance) and productivity in herbaceous communities of the Western Caucasus and Ciscaucasia, irrespective of the model of their organization. This result is not unexpected, since similar data have been obtained by other authors [7, 32, 50]. Therefore, preference cannot be given to any of the hypotheses described above. This situation may be due to the simultaneous effect of several factors on the evenness–productivity relationship. Thus, as productivity decreases, the degree of between-species differentiation in tolerance to abiotic environmental factors may increase simultaneously with a decrease in the degree of differentiation based on competitiveness for light. Moreover, an extreme environment cannot provide for the sustainability of populations of locally rare species, which results in increasing evenness of low-productive cenoses [7, 30, 51]. On the other hand, intense competition in highly productive communities will not lead to a significant decrease in evenness if these communities are formed by ecologically equivalent (com-

petitively symmetrical) species, as in the tree layer of tropical forests [6, 18, 31] and probably in some types of grasslands [39]. Finally, the frequency of disturbances in low-productive communities may exceed that in highly productive communities, which can also have an effect on the structure of species abundance [31]. In general, we share the opinion that the conditions in which productivity actually has an influence on the distribution pattern of species abundance within a community and the mechanisms of this influence are still poorly understood and require more attention from ecologists [7].

The results of our research show that the relationship between species richness and evenness (dominance) is more distinct in communities corresponding to the competitive and ruderal models (i.e., dominated by species with features of C - and R -strategists) than to the stress-tolerant model (dominated by S -strategists). Areas with a small number of species in competitive communities are characterized by a high degree of dominance (low evenness); in ruderal communities, by a high degree of dominance but significant variation in J' values; and in stress-tolerant communities, by significant variation in both J' and d values. To explain these results, let us consider different mechanisms (features) of the formation of species richness and species abundance pattern in communities with different organization models.

Thus, competitive communities formed in stable and productive habitats can potentially include a relative large number of species (i.e., have a large species pool). Therefore, dominants are the most significant, if not the only, factor of decrease in their species richness. They reduce the resources and space available to other species and impede their penetration into communities by producing a thick litter layer [16, 23, 37, 38]: the more abundant the dominant and the thicker

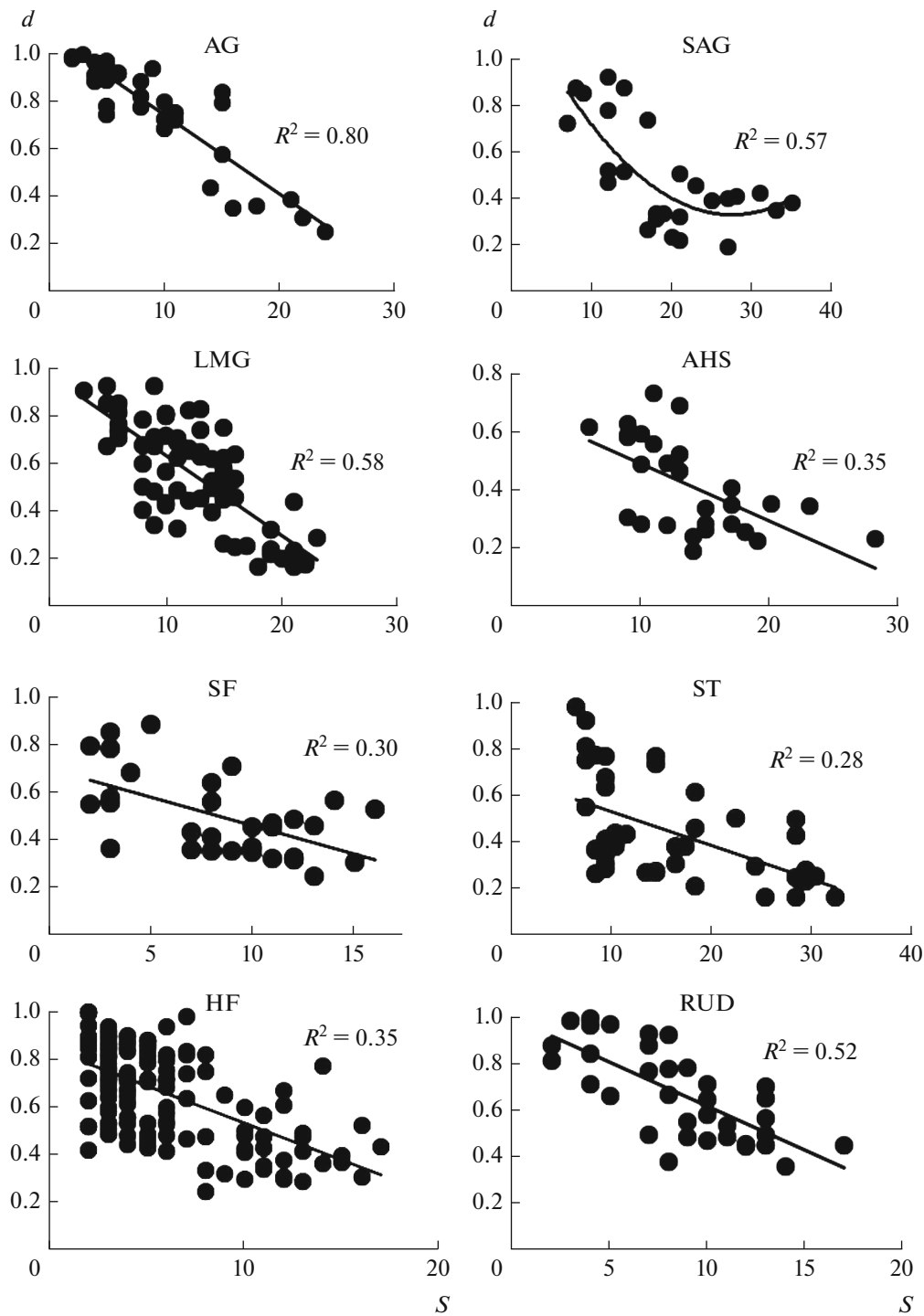


Fig. 1. Relationship between dominance (d) and species richness (S) in different plant communities.

the litter, the less the amounts of space and resources available to other species; the smaller the number of nondominant plants in the plot, the lower the probability that they will represent many different species [52–56]. Such a mechanism provides for a close relationship between evenness and species richness, and, as follows from [16], the more distinct the features of

C -strategists in dominant species, the closer is this relationship.

Plant species growing in frequently disturbed productive habitats (in communities at the initial stages of secondary succession) have a high, but probably variable, capacity for dispersal but not for displacing other species from the plots, and it is therefore considered

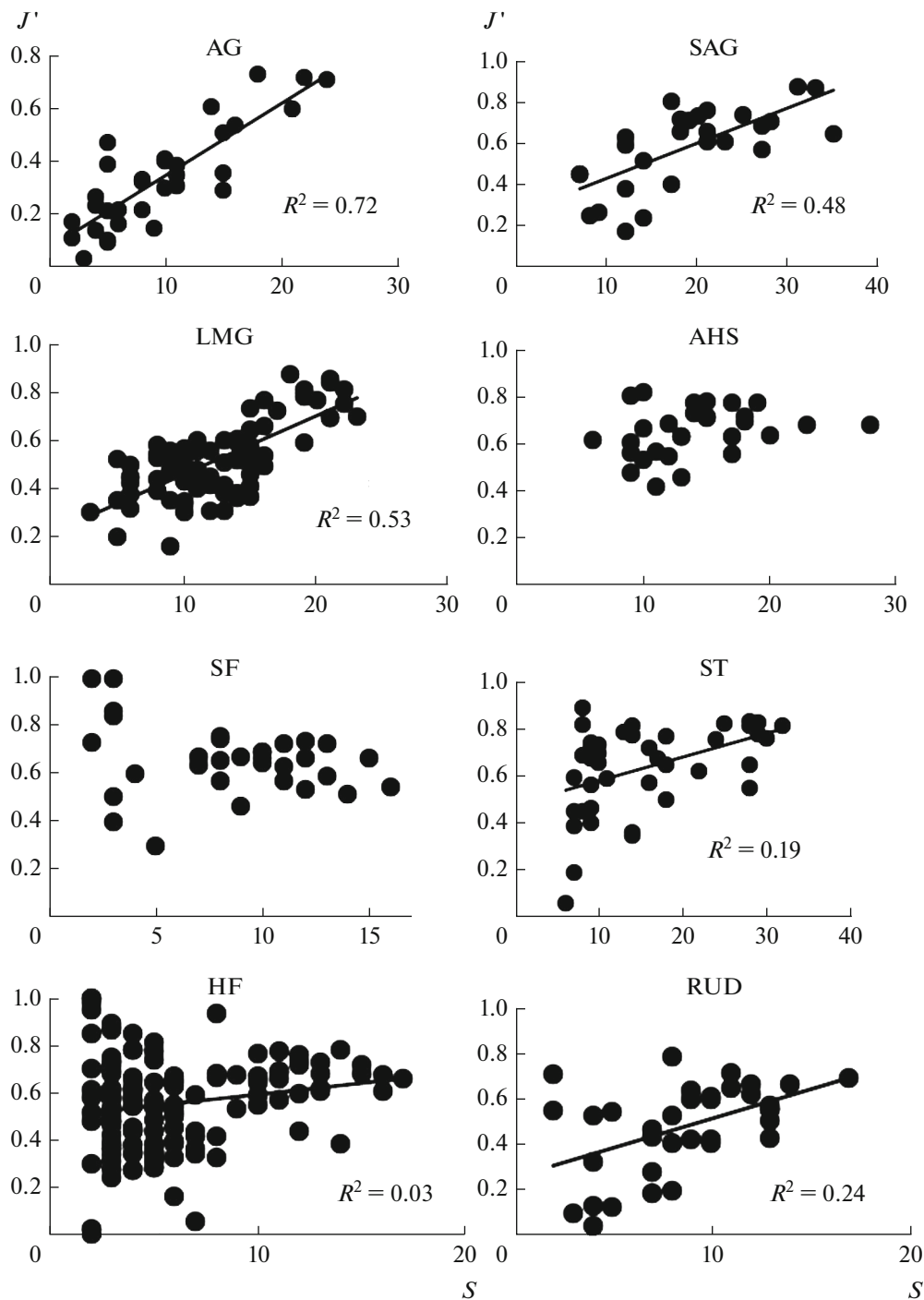


Fig. 2. Relationship between evenness (J') and species richness (S) in different plant communities.

that competition in R -cenoses is either absent or very weak [19, 20, 22, 57]. The most successful R - or CR -strategists pioneering in vacant areas can rapidly produce dense colonies, thereby physically interfering with the establishment of other species, but cannot retain their dominant position for a long time [23, 58]. The number of such species in a particular plot depends on chance. However, our results show that this mechanism

may account for a significant relationship between dominance (evenness) and species richness, although less closely than in the C - S - R -cenoses.

Communities with the S model are characterized by a low level of interspecific competition [19–22], and local species die-off in them occurs under impact of abiotic factors. Of crucial significance for their formation are the size of the pool of tolerant species (the

more extreme environmental conditions, the smaller its size) and the probability for these species to occur in a certain location and survive there independently their nearest neighbors [21, 59, 60]. This scenario implies the possibility of formation of *S*-cenoses containing a small number of species with different ratios of their abundance (biomass): from distinct dominance of one of the most successful stress tolerators to approximately equal abundance of several such species. On the other hand, the species pool in communities of extreme habitats is small, and even a significant decrease in the relative abundance of dominants is unlikely to result in an appreciable growth of species richness. As a consequence, evenness in *S*-cenoses with a small number of species is highly variable and poorly correlated with species richness (Fig. 2).

CONCLUSIONS

Theoretically, plant communities can differ in the pattern of the relationship of evenness (dominance) with productivity and species richness, and this may be due to different models of their organization. We have tested this hypothesis in herbaceous communities of the Western Caucasus and Ciscaucasia. The results show that the relationship between species richness and evenness (dominance) is expressed most clearly in communities with the competitive model, less clearly in ruderal cenoses, and weakly in communities with the stress-tolerant model, while the relationship between evenness (dominance) and productivity have not been revealed in any of these community types.

Finally, it appears appropriate to give attention to some practical aspects of ecology related to the results of this study. First, they provide evidence that, unlike the communities of organisms of some other taxonomic groups [3, 61], phytocenoses formed under extreme environmental conditions are not necessarily characterized by low evenness, and therefore this parameter cannot be used as an indicator of such conditions, at least when the influence of natural factors is considered. Second, the replacement of native dominants by alien species may have serious consequences for the species richness of plant communities, since aliens as competitors may prove to be stronger [4, 62–66]. At present, new regions are more frequently invaded by *R*-strategists; therefore, alien species in recipient regions occur mainly in ruderal cenoses [67–70]. However, the situation may change in the future because of invasion by *C*- and *S*-strategist species and evolutionary adaptation to new types of habitats in alien species already present in the region [70–72]. The results of our research indicate that the realization of such a scenario may have more serious consequences for competitive than for stress-tolerant communities, since the former are characterized by a closer relationship between the degree of dominance (evenness) and species diversity.

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