

# The Correlation Between Dominance Level and Local Species Richness: An Analysis of the Underlying Causes by the Example of the West Caucasian Arboreal and Avian Communities

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**Abstract**—It is known that the local species richness of biological communities with a high dominance level is usually lower than in communities with a low dominance. Taking into account the complex nature of the dominance phenomenon, the causes underlying this correlation can be diverse, yet they commonly remain beyond the scope of performed analyses. The goal of this work was to consider this issue by the example of West Caucasian tree and insectivorous bird communities. The results demonstrate that the correlation between the dominance level and local species richness to a considerable degree (50–60%) is a consequence of preemption of a larger or smaller amount of resources by the dominant species. However, the ecological processes determining the general pattern of resource distribution among species also play a certain role in these relationships, as well as the size of the species pool, which concurrently influences both the local species richness of communities and the number of potential dominants. The relative contributions of various mechanisms to the establishment of the considered correlation depend on the degree to which the rank structure of species abundance in communities matches the geometric series model.

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The dominance level is the ratio of the individuals of the most abundant species to the total number of individuals in a biological community (Berger–Parker index: Bakanov, 1987; Lebedeva and Krivolutskii, 2002). The correlation of this parameter with the species richness of cenoses is among the generally accepted ecological patterns. It is known that, the higher the dominance level, the lower the species richness (Able and Noon, 1976; Bigon et al., 1989; Vasilevich, 1991, 2009; Panchal and Pandey, 2004; Devlal and Sharma, 2008). However, note that the authors in the majority of papers fail to proceed further than the mere statement of this correlation. The underlying causes, taking into account the complex nature of the dominance phenomenon, can be diverse.

In particular, the dominance level can be determined by the specific bioecological features of the dominant species (including its life strategy, degree of eurybionicity, and specific features of the response to altered environmental conditions and productivity of habitats), the competitive abilities of concomitant species, and the random circumstances that arise in each individual part of a community (Bakanov, 1987; Vasilevich, 1991, 2009; Mirkin and Naumova, 1998; Il'yash et al., 2003). In all of these cases, the main mechanism of the influence of dominants on the species richness in communities is the reduction in the

resources accessible for other species. A high correlation between the amount of resources (productivity of habitats), total number of individuals, and species richness in cenoses has been reported in many papers (Wright et al., 1993; Brown et al., 2001; McKane et al., 2002; Kaspari et al., 2003; Puzachenko, 2006; Mönkkönen et al., 2006; Yee and Juliano, 2007). Therefore, it is reasonable to assume that, the higher the abundance of a dominant species in a community (independently of the underlying reasons), the fewer resources remain available for the concomitant species and the lower their potential population size, and, correspondingly, the higher the probability of their extinction due to environmental fluctuations, and the lower the species richness (Whittaker, 1980; Bigon et al., 1989; Mirkin and Naumova, 1998; McKane et al., 2002; Kunte, 2008; Mirkin et al., 2009). The examples of increase in the diversity in communities of various types caused by the removal of dominants or decrease in their population, as well as the examples of a decrease in diversity with an increase in the abundance of the dominant or introduction of new highly competitive species in a community (Bobbink and Willems, 1987; Human and Gordon, 1997; Silliman and Bertness, 2004; Vasilevich, 2009), demonstrate the significance of this mechanism as the cause underlying the correlation between the dominance level and the

species richness of cenoses (Paine, 1980; Bakanov, 1987; Bigon et al., 1989; Kunte, 2008; Vasilevich, 2009).

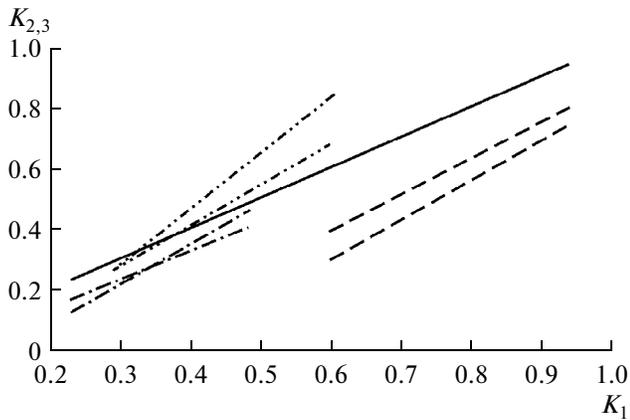
The opinion that the dominance level, as well as species richness, is a manifestation of emergence is also currently widely held (Able and Noon, 1976; Brown et al., 2001; Sugihara et al., 2003; Raybaud et al., 2009; etc.). Arguing in favor of this are the results of long-term observations of communities of different systematic groups demonstrating a relative stability in the species abundance distribution pattern and species richness of cenoses with time, while their species composition and ranks of individual species can considerably change (Brown et al., 2001; Nally, 2007). Here, the species rank is its number in the total list of species forming a community ranked in descending or ascending order of significance. In particular, it is believed that the sequence of estimates of species abundances (rank structure) in small patches of cenoses or their individual components (for example, layers) frequently approaches a geometric series (Motomura's model), despite random variations:  $N_i = N_1(1 - K)^{i-1}$ , where  $i$  is the species rank (the lower the abundance, the higher the rank);  $N_i$  is the number of individuals of the  $i$ th rank;  $N_1$  is the number of species of the first, most abundant, species;  $N_i$  is the total number of species in a patch of community; and  $K = N_1/N_i$  is the dominance level. The geometric series model (GSM) for species abundance distribution corresponds to the niche preemption hypothesis by R. Whittaker (1980). This model implies that each species in patches of a community in the order of decrease in abundance (increase in rank) utilizes a constant ( $K$ th) part of the remaining community resources. For example, if the strongest competitor (dominant) occupies 70% of the niche area utilizing the corresponding fraction of community resources, the second species in the rank is able to occupy the corresponding fraction of the niche space remaining after the first one; the third species, the corresponding fraction of the niche space remaining after the first and second species; and so on.

According to this model, the fraction of the community resources utilized by the most abundant species (dominant) is not a particular case (the result of their specific bioecological features or random circumstances) but rather reflects the general pattern of niche space distribution among the species under particular conditions. Correspondingly, it should be characteristic of the communities with a higher dominance level of the most competitive species to have not only a lower amount of resources available for the concomitant species but also a more "rigid" distribution of these resources among them (i.e., higher  $K$  values), which can influence the species richness, other conditions being equal.

Other types (models) of species abundance structure are also known (for a review, see Whittaker, 1980; Levich, 1980; Magurran, 1992; Lebedeva and Krivo-

lutskaa, 2002; Smurov et al., 2002; Ferreira and Petere, 2008; etc.). They imply both more and less uniform distributions of resources as compared with the geometric series model and, correspondingly, more or less pronounced dominance of one of the species. The former include, for example, the lognormal model and MacArthur's "broken stick" model, and the latter include a hyperbolic model. In particular, the hyperbolic model proposed by Levich (1980) is close to the geometric series model, but the  $K$  value in it decreases with an increase in the species ranks. Therefore, the abundance of several first species decreases more drastically, whereas the abundance of rare species declines more smoothly than with the GSM (Smurov et al., 2002). In this case, the hyperbolic model when considering the overall set of species in a community suggests a more inhomogeneous distribution of their abundances than with the GSM; the situation is reversed for concomitant species only. According to the lognormal model, which was first used to analyze biological communities by Preston (1948, 1962), the  $K$  values for the first-rank species are higher than those for the species of several subsequent ranks; however, according to the MacArthur random niche boundary hypothesis, the contrary is true. Note that both the lognormal and MacArthur models are characteristic of the communities with a relatively low dominance level. Correspondingly, the patterns of resource distribution among the concomitant species according to these three models (hyperbolic, lognormal, and MacArthur's) are less dependent on the dominance level of the first-rank species, as compared with GSM. However, simple calculations demonstrate that a positive correlation between the  $K$  values for the first-rank species and several species of subsequent ranks (for example, second and third), which utilize a considerable part of the community resources, is characteristic of all the listed models (Fig. 1).

Finally, several biologists in the 1980s–1990s substantiated the concept of a considerable influence exerted on local richness by the community species pool: a group of species inhabiting a certain region and potentially able to exist in these communities (species pool hypothesis: Cornell, 1985; Ricklefs, 1987; Eriksson, 1993; Zobel et al., 1998; etc.). It is known that a considerable number of factors can determine the regional species pool size, including regional environmental conditions, speciation rate and duration, and unique historical events (Ricklefs, 1987; Qian and Ricklefs, 2004). In particular, Ricklefs believes that a relatively low diversity of tree species on territories with a cold climate can be associated with colonization difficulties, due to the need in evolutionary development for mechanisms providing tolerance to low temperatures and frost (Latham and Ricklefs, 1993; Ricklefs et al., 1999; Qian et al., 2003; Qian and Ricklefs, 2004). Physiological stress and extreme climatic phenomena, including frosts, can have a direct impact on spreading of other groups of organisms, both plant



**Fig. 1.** The expected (calculated) ratios between the  $K$  values of the first-rank species and the two species with subsequent ranks (second and third) in the communities with the species abundance rank structure corresponding to several models. Solid line denotes the geometric series model ( $K$  values are equal for all ranks); dashed lines, hyperbolic model; dot–dash, lognormal model; and dot–two dashes, MacArthur’s model. The equations used for computations were taken from Preston, 1962; Whittaker, 1980; and Smurov et al., 2002. The parameter values were specified arbitrarily.

and animal (Able and Noon, 1976; Sanders et al., 2003; Hawkins et al., 2003; Morozova, 2008). On the other hand, it is assumed that a warm climate and intensive solar radiation determine a high rate of the evolutionary process enhancing development of species richness (Rhode, 1992; Kaspari et al., 2003; Brown et al., 2004; Gillooly and Allen, 2007; Wang et al., 2009). In addition, some historical factors that are not directly associated with the current climatic conditions, but which still frequently act in the same direction, can also have a certain effect on the species pool size of communities (Ricklefs, 1987; Qian and Ricklefs, 2004). For example, it is postulated that the biomes of the regions located closer to the poles, which experienced the Pleistocene ice age, are relatively poorer in species than the regions located to the south; this is also due to their young age (Latham and Ricklefs, 1993; Qian and Ricklefs, 2004; Puzachenko, 2006). Numerous examples of the effect of competitive release in the taxocenoses of tundra and polar deserts (Chernov, 2005), which is typical of island communities, can be regarded as an argument in favor of this hypothesis. This is to a certain degree true for mountain biocenoses located at a considerable altitude (Able and Noon, 1976; Akatov et al., 2003, 2005).

According to Vasilevich (1991), the number of potential dominants in plant communities is to a considerable degree determined by the environmental conditions and total number of species growing under particular conditions. For example, only a small set of species grows in the zone of extreme conditions for plants, which automatically limits the number of species able to reach a high abundance and dominate under these con-

ditions. Therefore, the portion of resources utilized by the most abundant species is usually rather large. However, both the total number of species and the number of potential dominants increase in the regions with more favorable conditions. Correspondingly, the dominance level of such a species in individual habitats appears lower than it could be when it is the only one contending for dominance. Moreover, the more favorable the environmental conditions, the larger the number of species able to reach a high abundance and the lower the dominance level of each of them in particular areas. Later, Chernov (2005) expressed a similar opinion. Based on analysis of the community structures in extreme habitats (mainly zoocenoses), he concluded that a small number of species created conditions for a drastic population predominance of the “strongest” among these species. Kuznetsova (2009) paid attention to a narrow range of potential dominants and high values of the Berger–Parker index (0.7–0.9) in small-species collembolan taxocenoses established under extreme conditions.

A synthesis of the species pool hypothesis and the dominance concept of Vasilevich suggests that the presence of a correlation between the dominance level and number of species in patches of cenoses can be determined by dependences of both characteristics on a third variable: the regional species pool size, which in turn reflects both the current environmental conditions and the history of community establishment.

The goal of this work was to determine the reasons underlying the correlation between the relative abundance of the dominant and local species richness in two types of biological communities: West Caucasian communities of trees and insectivorous birds.

## MATERIALS AND METHODS

The objects of this study were the tree layers of West Caucasian plain and mountain forests and insectivorous bird communities. The material of the tree layer in forest phytocenoses was collected in 2000–2009 in the basins of the Malaya Laba, Belaya, Vulcan, Nebug, Agoi, Shepsi, Shakhe, Sochi, Khosta, and Mzymta rivers mainly in the landscape-protected areas of various statuses (Caucasian Biosphere Reserve, Sochi National Park, Bol’shoi Tkhach Nature Park, and Maikop Botanical Reserve). Uniform forest patches with an area of about 1 ha with different aspects and degrees of slope were selected for describing the tree layer. Within each patch, 10 test sites  $20 \times 15$  m in size were selected. The forest phytocenosis was described for each test site. This description included the list of all tree species with a trunk diameter exceeding 6 cm at chest height. The descriptions were made in the forest formations most widespread in the region, namely, subalpine birch and beech crooked forest (dominant species, *Betula litwinowii* Doluch. and *Fagus orientalis* Lipsky); medium- and high-altitude mountain beech–fir forests (dominant species, *Abies nordman-*

*niana* (Steven) Spach and *Fagus orientalis*); low-altitude mountain forests with dominance of *Quercus petraea* L. ex Liebl., *Taxus baccata* L., and *Pinus palasiiana* D. Don. on the southern macroslope and *Quercus robur* L. and *Carpinus betulus* L. on the northern macroslope; and riverine forests with dominance of *Alnus glutinosa* (L.) Gaertner, *A. incana* (L.) Moench, *Carpinus betulus*, and *Fagus orientalis*. The composition and structure of these communities have been described in many papers, for example, Grudzin-skaya, 1953; Koval' et al., 1980; Grebenshchikov et al., 1990; Bebiya, 2002; Frantsuzov, 2006. The total number of chosen and described patches of the tree layer was 58; correspondingly, the total number of test sites with an area of 300 m<sup>2</sup> was 580.

The material on the insectivorous bird population was collected during the nesting periods of 2007–2009. The route surveys were conducted according to a standard protocol (Ravkin and Chelintsev, 1990) in the basins of the Belaya, Shakha, and Malaya Laba rivers by the same recorder. As a rule, the surveys started 1 h after sunrise and continued for 2–3 h. Over this time, the recorder covered 4 to 7 km with a mean speed of 2–3 km/h. The route went along forest paths or roads without disturbing the natural vegetation canopy. The surveys on steep slopes were directed from the top downwards. To level the phenophases connected with the altitudinal zonality, the surveys were first conducted in the low-altitude belt (late May/early June), then in the medium-altitude belt (early/mid-June), and finally in the high-altitude belt (mid-/late June). In total, nine biotopes were examined, with 4–11 surveys in each. The total number of route surveys was 61 and the total length was about 300 km. The results of these route surveys were published (Perevozov, 2008, 2009a, 2009b).

The values of the following parameters were determined based on the collected material:  $P$ , species pool of communities (total number of tree species recorded in the forest patches of certain formations or of insectivorous birds along the survey routes within certain biotopes, which represents a cenotic approach to determining the species pool size; Zobel et al., 1998);  $N_t$ , the mean density of the overall forest stand, i.e., the mean number of trunks per 300 m<sup>2</sup> and the number of birds per 1 km<sup>2</sup>;  $N_s$ , the mean number of trunks of concomitant species (all species except for the dominant) per 300 m<sup>2</sup> and the population density of concomitant avian species;  $N_i$ , the mean number of tree and bird species of the  $i$ th rank in the forest patches or survey routes;  $K_1 = N_1/N_t$ , the dominance level of the most competitive species, as well as  $K_2 = N_2(N_t - N_1)$ ,  $K_3$ , and  $K_i$ ; and  $S_t$  and  $S_s$ , the mean numbers of species and concomitant species of trees in test sites of 300 m<sup>2</sup> and birds per 1 km<sup>2</sup>.

Multiple correlation regression analysis was used to verify the correctness of the above hypotheses. This method allows the relative effects of each of the factors ( $N_s$ ,  $K_1$ , and  $P$ ) on the dependent variable ( $S_s$ ) to be

estimated, abstracting from the correlation of variation of each factor with the variations of other factors (Eliseeva and Yuzbashev, 1996; Puzachenko, 2004). We assumed that, if the first hypothesis on the mechanisms of correlation between the dominance level and species richness, which was described in the beginning of the paper, was correct, this method would detect a correlation of  $N_s$  with  $S_s$ ; if the second hypothesis was correct, a correlation between  $K_1$ ,  $N_s$ , and  $S_s$ ; and if the third one was correct, a correlation of  $P$  with  $S_s$ .

The relative contributions of  $K_1$ ,  $N_s$ , and  $P$  to the prediction of local species richness ( $S_s$ ) were assessed based on a standard regression coefficient ( $Beta$ ) and coefficient of separate determination ( $d^2$ , the product of the pairwise correlation coefficient of a factor and its  $Beta$  coefficient). The used statistical method is intended for analysis of multifactor linear correlations; therefore, in the case when the correlation between the factors  $K_1$ ,  $N_s$ , or  $P$  was nonlinear, it was linearized by taking the logarithms of  $N_s$  and/or  $S_s$  and  $P$  values (Puzachenko, 2004). The computations were made using the programs Microsoft Excel 2003 and Statistica 6.0.

## RESULTS

### *General Characterization of the Studied Communities*

The characterization of the tree layer in forest phytocenoses is shown in Table 1. It is evident from Table 1 that it is characteristic of the described communities to show a considerable variation in the number of individuals (number of tree trunks with a diameter exceeding 6 cm at chest height) on the test sites of 300 m<sup>2</sup>. The minimal mean value of this parameter for a test site was recorded in dry oak forests near the coast of the Black Sea (eight individuals per 300 m<sup>2</sup>), and the maximal value was found in the subalpine beech crooked forest (67.5 individuals). However, the variation in mean values of this parameter for certain community types is relatively low, mainly falling within the range of 15–20 trunks. The effect of this characteristic on the species richness of communities is insignificant: the pairwise correlation coefficient for  $N_t$  and  $S_t$  is 0.162. When discharging the maximal  $N_t$  value (67.5 individuals), this coefficient increases to a statistically significant value of 0.358 ( $n = 57$ ,  $p < 0.01$ ). However, even in this case,  $N_t$  determines no more than 13% of the variation in  $S_t$ .

The mean dominance level of the most competitive species in the patches ( $K_1$ ) varied from 0.33 to 0.97, and for community types it ranged on average from 0.33 to 0.86. The maximal values of this parameter were observed in the communities formed under extreme environmental conditions, namely, subalpine and high-altitude mountain belts and on the dry slopes of the Black Sea coast (the communities with dominance of the sessile oak and Pallas pine). The minimal values were found under the warmest and most humid

**Table 1.** Characterization of the tree layer in forest phytocenoses

Communities; dominant species (altitude, m)	$n$	$N_i$	$K_1$	$S_i$	$R_e^2$
Low-altitude mountain forests of southern macroslope; <i>Taxus baccata</i> (50–300)	1	18.7	0.33	6.2	0.962
Low-altitude mountain forests of southern macroslope; <i>Pinus pallasiana</i> (50–300)	1	14.9	0.71	3.7	0.942
Low- and medium-altitude riverine forests of both macroslopes; <i>Alnus glutinosa</i> and <i>A. incana</i> (300–800)	9	19.7 (13.5–23.9)	0.63 (0.39–0.83)	3.8 (2.6–5.0)	0.959 (0.852–0.992)
Low-altitude riverine forests of northern macroslope; <i>Carpinus betulus</i> and <i>Fagus orientalis</i> (250–500)	7	19.4 (15.3–28.0)	0.52 (0.35–0.76)	4.8 (3.1–7.6)	0.957 (0.924–0.990)
Low-altitude mountain forests of both macroslopes; <i>Quercus petraea</i> (350–1000)	10	19.7 (8.0–34.6)	0.79 (0.60–0.93)	2.9 (1.8–5.7)	0.972 (0.944–0.999)
Low-altitude mountain forests of northern macroslope; <i>Quercus robur</i> (100–300)	8	22.7 (18.7–27.0)	0.51 (0.44–0.63)	4.7 (3.2–6.3)	0.977 (0.960–0.991)
Medium-altitude mountain forests of northern macroslope; <i>Abies nordmanniana</i> and <i>Fagus orientalis</i> (600–1400)	9	16.0 (10.9–30.1)	0.70 (0.62–0.85)	2.7 (2.3–3.2)	0.956 (0.854–0.994)
High-altitude mountain forests of both macroslopes; <i>Abies nordmanniana</i> and <i>Fagus orientalis</i> (1400–1800)	8	19.8 (13.5–31.8)	0.81 (0.61–0.92)	2.3 (1.4–4.2)	0.981 (0.937–0.999)
Subalpine forests of both macroslopes; <i>Betula litwinowii</i> and <i>Fagus orientalis</i> (1700–2200)	5	37.0 (21.2–67.5)	0.86 (0.70–0.97)	2.5 (1.5–3.7)	0.985 (0.947–0.999)

Note:  $n$  is the number of descriptions;  $N_i$ , mean density of the overall tree stand, i.e., the mean number of trunks per 300 m<sup>2</sup>;  $K_1 = N_1/N_i$ , dominance level, where  $N_1$  is the number of trunks of dominant (first-rank) species;  $S_i$ , mean number of tree species on test sites of 300 m<sup>2</sup>; and  $R_e^2$ , the coefficient of determination demonstrating the matching of the rank structure of species abundance distribution (or logarithm of the abundance) to an exponential (or linear) function.

conditions (the communities with dominance of the pedunculate oak and common yew). A considerable variation in the dominance level was also observed within certain types of communities. The observed correlation between  $K_1$  and  $S_i$  is rather high with a correlation coefficient of 0.852 ( $n = 58$ ,  $p < 0.01$ ).

The species pool size ( $P$ ) in the tree layer of low-altitude mountain forests of various formations varies from 14 to 22 species; in the medium-altitude beech–fir forests it is 12 species; and in high altitude beech–fir, beech, and birch forests it is 7, 4, and 6 species, respectively. The species pool size, dominance level, and local species richness of the tree communities are correlated in a statistically significant manner ( $r = 0.709$  and  $0.626$ , respectively;  $n = 58$ ;  $p < 0.001$ ).

Table 2 shows the characteristics of the insectivorous bird communities. It is evident from Table 2 that the population density of insectivorous birds ( $N_i$ ) varies in the range of 20 to 843 individuals/km<sup>2</sup>. The values averaged for biotopes vary from 108 individuals/km<sup>2</sup> in alpine meadows to 526 in the medium-altitude beech–fir forests. The effect of  $N_i$  on the species richness of insectivorous bird communities is more pronounced, as compared with the tree layer of forests: the pairwise correlation coefficient for  $N_i$  and  $S_i$  is 0.565 ( $n = 61$ ,  $p < 0.001$ ).

The average dominance level in the patches of West Caucasian insectivorous bird communities ( $K_1$ ) varies

from 0.22 in the medium-altitude mountain beech–fir forests to 0.72 in alpine meadows. In general, the  $K_1$  value for the forest communities varies in the range of 0.14–0.61, and in the high-altitude communities (alpine and subalpine zones) it falls in the range of 0.40–1.0. The pairwise correlation coefficient for  $K_1$  and  $S_i$  is 0.626 ( $n = 61$ ,  $p < 0.001$ ).

The species pools of the insectivorous bird communities of the low-altitude mountain zone comprise up to 31 species; for the medium-altitude zone, 28; high-altitude mountain forest and subalpine zones, 20–25; and alpine, 16 species. This parameter, dominance level, and local species richness of bird communities display a statistically significant correlation ( $r = 0.674$  and  $0.788$ , respectively;  $n = 58$ ;  $p < 0.001$ ).

#### *Matching between the Species Abundance Distribution Structure of the Studied Communities and GSM*

As demonstrated above, the niche preemption hypothesis of Whittaker implies the strictest correspondence between the  $K$  values for the first-rank species and the species of subsequent ranks. Thus, it is of interest at the first stage of analysis to estimate the degree of matching between the actual data on the studied communities and Motomura's model (GSM). This model implies that the rank distribution of species significance follows the law of geometric series

**Table 2.** Characterization of the population of insectivorous birds

Communities; dominant tree species (altitude, m)	$n$	$N_i$	$K_1$	$S_i$	$R_e^2$
Low-altitude mountain forests of southern macroslope; <i>Cas-tanea sativa</i> and <i>Fagus orientalis</i> (50–300)	7	377.7 (139–465)	0.32 (0.20–0.45)	14.9 (12–16)	0.933 (0.907–0.978)
Low-altitude mountain forests of northern macroslope; <i>Quercus petraea</i> (350–850)	5	502 (424–613)	0.31 (0.23–0.40)	21.4 (17–24)	0.959 (0.937–0.980)
Low-altitude mountain forests of northern macroslope; <i>Quercus robur</i> (100–300)	4	376 (280–461)	0.24 (0.15–0.32)	20 (17–22)	0.945 (0.911–0.962)
Medium-altitude mountain forests of both macroslopes; <i>Fagus orientalis</i> (600–1400)	7	486 (257–743)	0.29 (0.24–0.41)	19 (16–25)	0.948 (0.909–0.963)
Medium-altitude mountain forests of northern macroslope; <i>Abies nordmanniana</i> and <i>Fagus orientalis</i> (650–1400)	6	525.8 (253–843)	0.22 (0.14–0.30)	16.5 (12–22)	0.954 (0.923–0.981)
High-altitude mountain forests of both macroslopes; <i>Abies nordmanniana</i> and <i>Fagus orientalis</i> (1400–1800)	9	431.7 (307–612)	0.28 (0.17–0.61)	15.4 (10–21)	0.937 (0.896–0.955)
Subalpine forests of northern macroslope; <i>Betula litwinowii</i> (1700–2200)	8	325.4 (111–515)	0.27 (0.17–0.40)	17.3 (12–23)	0.949 (0.858–0.971)
Subalpine meadows of both macroslopes (1800–2500)	4	139.3 (56–203)	0.62 (0.40–0.83)	6.8 (5–10)	0.887 (0.770–0.956)
Alpine meadows of both macroslopes (2500–3000)	11	108 (20–225)	0.72 (0.39–1)	4 (2–7)	0.925 (0.740–0.992)

Note:  $n$  is the number of route surveys;  $N_i$ , mean population density (individuals/km<sup>2</sup>);  $K_1 = N_1/N_p$ , dominance level;  $S_i$ , mean number of birds per route survey; and  $R_e^2$ , the coefficient of determination demonstrating the matching of the rank structure of species abundance distribution (or logarithm of the abundance) to an exponential (or linear) function.

described by an exponential function in a direct (rank/abundance) scale and a linear function in a semilogarithmic (rank/logarithm of abundance) scale (Whittaker, 1980; Lebedeva and Krivolutskii, 2002). Therefore, the degree of matching between the actual data and the GSM can be estimated via the matching of the empirical series and the abovementioned functions using the determination coefficient. In this process, the match can be regarded as conditionally good if these functions (exponential or linear) describe over 95% of the variations in species abundance and satisfactory in the case of 90–95%. The values of the determination coefficient, demonstrating the matching between species abundance rank structure and exponential function ( $R_e^2$ ), are listed in Tables 1 and 2. As is evident from these tables, the average matching of the actual data on the tree layer can be regarded as good in West Caucasian forest phytocenoses and satisfactory in the insectivorous bird communities. Table 3 and Fig. 2 also suggest that the  $K$  values of the first-rank species and species of several subsequent ranks (for example, second and third), which utilize a considerable part of the community resources, are correlated in a statistically significant manner.

Possible reasons underlying the deviations of  $K_{2,3}$  values from  $K_1$  can be determined by comparing Figs. 1 and 2. In particular, the deviations of species abundance distribution structure from the GSM in the communities of both taxonomic groups with high  $K_1$

values is connected with relatively low  $K_{2,3}$  values, as compared with  $K_1$ , which suggests that this structure is close to a hyperbolic model. In the arboreal communities with medium  $K_1$  values (0.6–0.7), considerable deviations of the  $K$  values for the second- and third-rank species can be associated with the shift of species abundance structure toward both the hyperbolic and MacArthur models; in the avian communities with a low dominance level, toward the lognormal model. In addition, a satisfactory match of the actual species abundance structure to a particular model should suggest that species have reached a competitive equilibrium (Huston, 1979; Puzachenko, 2006; Ulrich, 2008), although it is known that the majority of communities are actually in a nonequilibrium state (Huston, 1979). However, independently of the underlying reason, these deviations do not contradict the statement that, the larger the fraction of community resources utilized by the dominant species, the larger the amount of remaining resources utilized on average by the group of most abundant concomitant species (Table 3) and the smaller the part remaining for the small-population species.

#### *Dominance Level and Local Species Richness: Analysis of the Causes Underlying the Correlation*

The mean values of the analyzed parameters for real West Caucasian arboreal and avian communities, as well as the ranges of their variation, are listed in

**Table 3.** The ratio of the  $K$  values for the first-rank species and species of subsequent (second and third) ranks

Communities	Species rank	$n$	$r$	$p$	$b$
Trees					
Total	Second	58	0.740	<0.001	0.702
	Third	42	0.657	<0.001	0.961
With high $R_e^2$	Second	20	0.941	<0.001	1.052
	Third	13	0.950	<0.001	1.145
With low $R_e^2$	Second	20	0.543	<0.05	0.556
	Third	13	0.292		0.317
Birds					
Total	Second	61	0.767	<0.001	0.602
	Third	59	0.765	<0.001	0.603
With high $R_e^2$	Second	20	0.927	<0.001	0.922
	Third	18	0.904	<0.001	0.907
With low $R_e^2$	Second	20	0.612	<0.01	0.373
	Third	20	0.684	<0.001	0.500

Note:  $n$  is the number of route surveys;  $r$ , Pearson's correlation coefficient;  $p$ , confidence level;  $b$ , slope coefficient of linear regression equation; and  $R_e^2$ , the coefficient of determination demonstrating the matching of the rank structure of species abundance distribution (or logarithm of the abundance) to an exponential (or linear) function.

**Table 4.** Mean values and variation ranges of the analyzed parameters for tree and bird communities

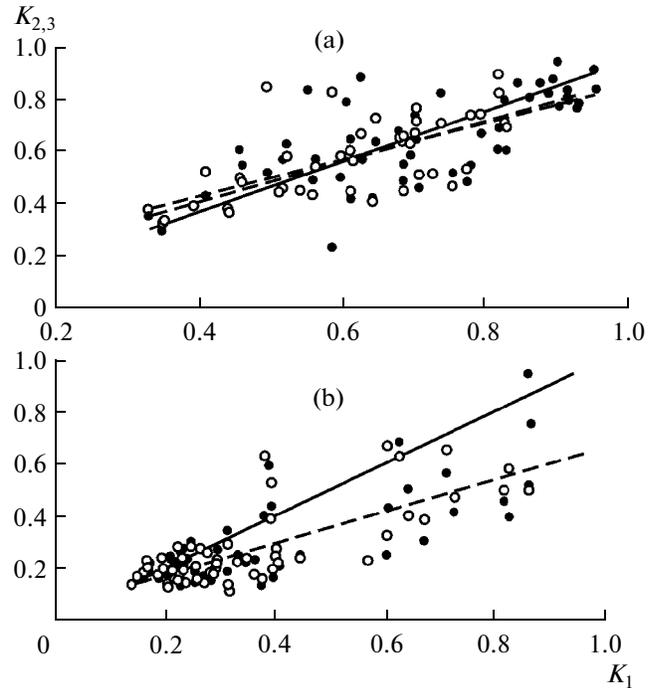
Communities	$n$	$K_1$	$N_s$	$S_s$	$P$	$R_e^2$
Trees						
Total	58	0.68	6.5	2.4	12.7	0.968
		(0.33–0.96)	(0.9–18.1)	(0.8–6.6)	(4–23)	(0.852–1.00)
With high $R_e^2$	20	0.72	6.6	2.5	11.5	0.993
		(0.35–0.95)	(1.4–18.1)	(0.4–6.6)	(4–18)	(0.978–0.999)
With low $R_e^2$	20	0.64	6.1	2.3	14.0	0.939
		(0.33–0.96)	(0.9–14.5)	(0.5–5.2)	(6–18)	(0.852–0.985)
Birds						
Total	61	0.37	243.8	13.3	24.1	0.938
		(0.14–0.96)	(4–773)	(1–24)	(16–31)	(0.740–1.00)
With high $R_e^2$	20	0.36	245.5	14.4	25.0	0.969
		(0.15–0.87)	(6.7–462.3)	(2–24)	(16–31)	(0.953–0.991)
With low $R_e^2$	20	0.40	227.3	12.1	22.3	0.896
		(0.17–0.83)	(3.7–434.5)	(3–21)	(16–28)	(0.740–0.940)

Note:  $n$  is the number of descriptions;  $N_s$ , mean density of the overall tree stand, i.e., the mean number of trunks per 300 m<sup>2</sup>;  $K_1$ , dominance level of the first-rank species, where  $N_s$  is the mean number of trunks of all concomitant species on test sites of 300 m<sup>2</sup>;  $S_s$ , mean number of concomitant tree species on test sites of 300 m<sup>2</sup>;  $P$ , species pool size of communities; and  $R_e^2$ , the coefficient of determination demonstrating the matching of the rank structure of species abundance distribution (or logarithm of the abundance) to an exponential (or linear) function.

Table 2; the results of their analysis are presented in Table 5. It is evident from Table 5 that the number of individuals belonging to concomitant species,  $N_s$ , has the most pronounced effect on the local species richness in both types of communities, when one considers the total set of data. This factor determined approximately 50–60% of the variations in  $S_s$  values. The effects of the specific species abundance structure ( $K_1$ ) and species pool of communities ( $P$ ) on this characteristic ( $S_s$ ) are considerably weaker and approximately equal (10–20% each). Note that the value of standard regression coefficient ( $Beta$ ), demonstrating the relative effect of  $K_1$  on the number of concomitant species ( $S_s$ ), in the bird communities is somewhat higher than in the tree communities.

To obtain a clearer understanding of the role of  $K_1$  in determining the number of concomitant tree and bird species in local sites ( $S_s$ ), we analyzed in an analogous manner the groups of both tree and bird communities with a high and low match to the GSM. For this purpose, we divided the communities of both organism groups according to the similarity in the number of individuals of concomitant species ( $N_s$ ) into five classes; we then selected four patches with the best match and four patches with the worst match of the species abundance structure to the GSM (estimated according to the parameter  $R_e^2$ ) from each class. Thus, two groups of 20 test sites each with high and low  $R_e^2$  values were formed for both the tree and bird communities. For each of these groups, the relative effects of the factors  $K_1$ ,  $N_s$ , and  $P$  on the number of concomitant species ( $S_s$ ) was determined by multiple regression analysis. We assumed that, if the relative contributions of these factors to determining  $S_s$  did not considerably differ in the groups of communities with high and low  $R_e^2$  values, then this could be regarded as an argument in favor of the hypothesis on the insignificant effect of the species abundance structure on the local species richness of communities. On the contrary, the presence of such an influence would suggest that the role of  $K_1$  in the communities with high  $R_e^2$  values would be more significant, whereas the role of  $P$  would be weaker, as compared with the communities with low  $R_e^2$  values.

Table 4 shows the characterization of the arboreal and avian communities with relatively good and relatively poor matches of the species abundance structure to the GSM. As is evident from Table 4, the considered groups of communities differ significantly in the  $R_e^2$  values yet remain similar in other characteristics. In addition, it follows from Table 3 that the communities with high  $R_e^2$  values display a very good correlation between the  $K$  values for the first-rank species and the species of several subsequent ranks (second and third),



**Fig. 2.** The ratios between the  $K$  values of the first-rank species ( $K_1$ ) and the two species with subsequent ranks (second and third) in the studied (a) tree and (b) bird communities. Black circles denote the second-rank species; white circles, third-rank species; dashed lines, regression lines for these dots; and solid line, complete matching between the  $K$  values of the first-rank species and the species of two subsequent ranks.

whereas the correlation of  $K_1$  with  $K_2$  and  $K_3$  in the communities with low  $R_e^2$  values is considerably weaker.

The results of data analysis are listed in Table 5. It is evident that the factors  $K_1$  and  $N_s$  have a statistically significant effect on the number of concomitant species in the tree communities displaying a good matching of their species abundance structure to the GSM, while the factors  $N_s$  and  $P$  have a statistically significant effect in the communities with another structure. In the bird communities with high  $R_e^2$  values, only  $N_s$  has a statistically significant effect on the number of concomitant species ( $S_s$ ). However, the values of the standard regression coefficient ( $Beta$ ) and the coefficient of separate determination ( $d^2$ ) for  $K_1$  are still higher in these communities, as compared with  $P$ ; the communities with low  $R_e^2$  values display the opposite pattern. Note that in the last case the effect of  $P$  on  $S_s$  is statistically significant and comparable to the effect of  $N_s$ . In addition, the factor  $N_s$  in the tree and bird communities with a good matching of the species abundance structure to the GSM determines the number of concomitant species to a greater degree

**Table 5.** The effects of dominance level ( $K_1$ ), number of individuals belonging to concomitant species ( $\ln N_s$ ), and species pool size ( $P$ ) on the number of concomitant species ( $\ln S_s$ ) in tree and insectivorous bird communities

Communities	$n$	$\ln N_s$		$K_1$		$P$		$\ln N_s + K_1 + P$	
		<i>Beta</i>	$d^2$	<i>Beta</i>	$d^2$	<i>Beta</i>	$d^2$	$R$	$R^2$
Trees									
Total	58	<u>0.642</u>	0.574	-0.187	0.159	<u>0.160</u>	0.106	0.915	0.838
With high $R_e^2$	20	<u>0.598</u>	0.571	<u>-0.318</u>	0.299	0.136	0.096	0.982	0.965
With high $R_e^2$	20	<u>0.460</u>	0.408	-0.278	0.242	0.291	0.216	0.931	0.866
Birds									
Total	61	<u>0.524</u>	0.483	<u>-0.237</u>	0.208	<u>0.252</u>	0.204	<u>0.947</u>	0.896
With high $R_e^2$	20	<u>0.617</u>	0.592	-0.231	0.214	0.146	0.129	<u>0.967</u>	0.935
With high $R_e^2$	20	<u>0.441</u>	0.380	-0.238	0.189	<u>0.419</u>	0.317	<u>0.941</u>	0.885

Note:  $R$  is the coefficient of multiple correlation;  $R^2$ , coefficient of multiple determination; *Beta*, standard regression coefficient; and  $d^2$ , coefficient of separate determination; the statistically significant (for 5% and higher levels) values of  $R$  and *Beta* are underlined.

(approximately, 60%), as compared with the communities with another structure (approximately, 40%).

## DISCUSSION

Thus, the obtained results can be reduced to the following.

The dominance level of the most abundant species in the West Caucasian arboreal and avian communities varies in a wide range both among and within the types of communities or habitats. The dominance level and local species richness display a significant correlation associated with several factors.

The number of individuals belonging to concomitant species determines the species richness of communities to the greatest degree. This can suggest that the main factor underlying the correlation between the dominance level and the number of species in small patches of the studied cenoses is a reduction in the resources available for other species caused by the dominants. In addition, this factor determines the number of concomitant species in the tree and bird communities with a good matching of the species abundance structure to the GSM (i.e., in the communities displaying a strict correspondence between the  $K$  values of the first-rank species and the species of subsequent ranks), better than the communities with another structure.

Since the dominance level of the strongest competitor in a considerable number of test sites of the West Caucasian tree and insectivorous bird communities reflects to a certain degree the overall species abundance distribution structure, this has a certain effect on their species richness. Considering the total set of patches of the examined communities, this factor determines about 15–20% of the variation in the num-

ber of species; this value increases to approximately 20–30% in the sites displaying the best matching of the species abundance structure to the GSM.

The effect of the species pool size on the local species richness of communities is also determined to a considerable degree by the species abundance distribution pattern: it is almost absent in the sites with a good matching of this structure to the GSM and is significant in the case of another structure. This result suggests that the correlation between the dominance level and species richness in the communities with a poor matching of the species abundance structure to the GSM (to a greater degree for the avian communities and to a lesser degree for arboreal communities) reflects the dependences of both characteristics on the species pool size.

Correspondingly, the results of analysis suggest that the key moment determining the relative contributions of different mechanisms to establishment of the correlation between the dominance level and species richness in communities is the matching of the species abundance structure to the geometric series model. In the patches displaying such matching, the species richness is determined to a considerable degree (over 80%) by the number of individuals belonging to concomitant species and the factor  $K$ , reflecting the pattern of niche space distribution, i.e., local processes. In the patches with a poor matching of the species abundance structure to the GSM, both the local environmental conditions and the species pool size of communities influence this characteristic. The contribution of the local factors in this case decreases to 57% in the bird communities and to 65% in the tree layer of forests.

Thus, the obtained result can be considered in a broader ecological context, namely, in connection with the question on the relative contributions of local processes and species pool size in the establishment of

the structure and species richness of communities in small patches. The discussion of this question was brought about by the abovementioned assumption on the nonexistence of the upper limit in species richness in small patches and on the dependence of species richness on the size of the community species pools. The linear dependence between the species pool size and local richness of cenoses was considered as an argument (Cornell, 1985; Ricklefs, 1987). However, further testing of this hypothesis gave ambiguous results (Lawton et al., 1993; Aho and Bush, 1993; Hugueny and Paugy, 1995; Duncan et al., 1998; Shurin et al., 2000; Simkova et al., 2001). In addition, the strictness of this test was repeatedly considered dubious due to ambiguity in determining the dependent and independent variables (Srivastava, 1999; Herben, 2000; Lepš, 2001; Akatov et al., 2002, 2005; He et al., 2005). Thus, the role of the species pool size of communities in the determination of their local species richness is still vague.

Our results suggest that this factor in the West Caucasian arboreal and avian communities influences both the local richness and the dominance level. However, this influence is on the average rather moderate. Moreover, it is almost absent in the communities with the species abundance rank pattern matching the GSM. This inference is not fundamentally new. In particular, it has been assumed that the contributions of the local processes and species pool size to the species richness of biological communities depend on the intensity of interspecific interactions (Cornell, 1985; Cornell and Lawton, 1992). In the interactive communities, the local processes play a significant role. As for the noninteractive communities, their niche space is always open, the effect of local processes is limited, and the species pool size comes to the fore (Cornell, 1985; Cornell and Lawton, 1992). According to Cornell, the noninteractive communities are more frequently formed under environmental conditions where the local species extinctions result from abiotic factors and disturbances rather than from biotic interactions. According to the polymodal concept of plant community organization by Mirkin and Naumova (1998), they belong to either the abiotic *S*-model (communities of extreme conditions, almost lacking any competition, where each constituent species follows its own population patterns) or the *R*-model (frequently disturbed communities and the open communities of the first succession stages). However, note that a geometric mode of species abundance distribution, which as we found out limits the effect of species pool size on the species richness, is more frequently observed in the same community types; i.e., the communities at the first succession stages, as well as the communities of extreme environmental conditions and frequently disturbed habitats (Able and Noon, 1976; Whittaker, 1980; Sugihara et al., 2003; Panchal and Pandey, 2004; Hea and Tangb, 2008; Kuznetsova, 2009). This can mean that either our concepts on the

competition intensity among species in communities of different types (first and foremost, plant communities) remain limited, or a low intensity of biotic interactions is not a sufficient condition for a significant effect of regional processes on local species richness (Akatov et al., 2005; Akatov and Akatova, 2008).

Thus, what is the mechanism underlying establishment of the species abundance pattern that fits the GSM? The relevant literature has no definite answer to this question. In particular, the niche preemption hypothesis, based on the a priori concepts of different "powers" of individual species in their interaction within a community, is an exquisite yet rather formal explanation (Levich, 2007). Its stochastic variant is the dominance preemption model, which implies that each new species entering a community redistributes the resource utilized by the least abundant species; however, the portion of the resource taken is not strictly fixed but rather randomly varies within a certain range specified by the model (Ferreira and Petere, Jr., 2008). Several works substantiate the statement that a geometric distribution of species abundance is observed in the communities where a single resource is consumed and the demands of individual species are linearly distributed (Puzachenko, 2006; Levich, 2007).

According to Kolasa and Waltho (1998), a disadvantage of the models oriented exclusively toward resource distribution is insufficient attention to the other ecological factors potentially influencing species abundance. The hypothesis of the hierarchical structure of communities was proposed as an alternative (Kolasa and Biesiadka, 1984; Kolasa, 1989). According to this hypothesis, the hierarchical nature of habitats plays the leading role in species abundance distribution. Each fragment of a habitat can be divided into smaller fragments according to biologically meaningful criteria. The hierarchical levels of habitat fragments determine the levels of species specialization. Some species (generalists) occupy and utilize relatively large parts of habitats and are abundant, whereas others (specialists) occupy only small parts and are less abundant. According to a prediction following from this hypothesis, the species abundance distribution within small patches of communities should match the geometric series model, whereas the lognormal model describes the distribution in large sets of species (Kolasa, 1989). Recently, attention to the hierarchical organization of the environment and its effect on the species richness of communities has increased (Puzachenko, 2006; Azovskii et al., 2007; Gelashvili et al., 2007).

Another cause underlying a geometric distribution of species abundance can be the presence of feedbacks in communities, when the species with a higher competitive ability are more abundant than other species not only because they seize better habitats and a larger amount of resources due to their specific bioecological features, but also since a high population enhances a further increase in population. Earlier, Vasilevich

(1991) paid attention to this phenomenon as the reason for the existence of dominants in plant communities. In this case, the deviation from the GSM toward the hyperbolic model can suggest an increase in the role of double feedbacks in the community organization (Markov and Korotaev, 2007). There are also other approaches to substantiation of the rank distribution patterns (Puzachenko and Puzachenko, 1996; Levich, 2007; Ferreira and Petreire, Jr., 2008). However, as Sugihara et al. (2003) underline, unfortunately our general understanding of the causes underlying the species abundance distribution patterns in cenoses, one of the deepest aspects of the cenotic structure, still remain superficial despite the importance of clarifying the corresponding fundamental factors.

### CONCLUSIONS

Thus, a considerable number of factors, including specific bioecological features of several of the most abundant species, particular circumstances formed in individual patches, the pattern of ecosystemic processes in general, and species pool size, can determine the dominance level in communities. Correspondingly, the correlation between the dominance level and species richness in communities is most likely determined by a set of factors. In particular, our results suggest that this correlation results to a considerable degree (50–60%) from a mere redistribution of resources from concomitant species to the dominant. However, the ecosystem-level processes in general, which determine the overall pattern of resource and habitat distribution among species, play a certain role, as well as the regional and historical processes that act in an indirect manner via the species pool size, which influences both the species richness in communities and the number of potential dominants. In these processes, the contributions of different mechanisms to determination of the correlation between the dominance level and species richness in communities depends on the degree of matching of the species abundance rank structure to the geometric series model. In the patches displaying such matching, the species richness is to a considerable degree determined by the number of individuals belonging to concomitant species and the parameter  $K$ , which reflects the pattern of niche space distribution, i.e., by local processes. In the patches with poor matching of the species abundance structure to the GSM, this characteristic is influenced not only by the local environmental conditions but also by the species pool sizes of communities. In addition, the joint impact of ecosystemic and regional processes on this characteristic can also be regarded as significant. In the studied communities, the contribution of these processes to the correlation between the dominance level and species richness amounts to 25–40%. In the communities of other types, the role of these factors can be even larger. This can mean a relative independence of the species rich-

ness of cenoses from the population size of particular dominants. Presumably, that is why the artificial removal of dominant species from some communities does not lead to a rapid and noticeable growth in species richness, as has been demonstrated for several West Caucasian alpine phytocenoses (Aksenova et al., 2004; Cherednichenko, 2004; Akhmetzhanova, 2008).

Note in conclusion that the species abundance distribution pattern, as well as the relative contributions of different factors to the formation of species richness in cenoses, depends to a considerable degree on the scale used to estimate the phenomena (Schmida and Wilson, 1985; Kolasa, 1989; Wilson et al., 1998; Mirkin and Naumova, 1998; Akatov et al., 2002; Ulrich, 2008; Wang et al., 2009; Akatov, 2010). In particular, when the patch size in the tree layer of West Caucasian forests was increased from 300 m<sup>2</sup> to 0.3 ha, the contribution of the dominance level to the species richness variation decreased from 64 to 21%; the contribution to species pool variation increased from 10 to 30% (Akatov, 2010). Therefore, it is necessary to underline that the results described here are applicable only to the community patches of a relatively small size, whose species richness can be regarded as local.

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