RESEARCH PAPER

Small-scale species richness of plant communities with similar biomass: the influence of habitat types in the context of historical hypothesis (Western Caucasus and Ciscaucasia, Black and Azov Seas, Russia)

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ABSTRACT

We compared the species richness of the plant communities of different habitats on different sites of the biomass gradient. The analysis was based on data on 1089 above-ground biomass samples taken from the sites 0.25 m² of terrestrial herbaceous communities of the Western Caucasus and Ciscaucasia (30–2800 m a.s.l.) and 317 samples taken from the same sites of the macrophytobenthos of the Black and Azov Seas (0.5–10 m depth). Results showed that a certain amount of biomass, sampled in communities of different types, includes, on average, a significantly different number of species. Thus, among terrestrial plant communities, high-mountain communities of the Western Caucasus are characterized by the highest species richness in most ranges of the biomass gradient; communities of herb layer of shaded forests – on the contrary, the lowest richness. The macrophytobenthos of the Black Sea is characterized by lower species richness than most of the terrestrial communities, but higher species richness than the benthic communities of the Azov Sea. We showed that significant difference in the small-scale species richness of these communities can be plausibly explained by the peculiarities of their history.

Keywords: terrestrial plant communities, macrophytobenthos, species richness, above-ground biomass, species-energy hypothesis, historical data

Р Е З Ю М Е

Акатов В.В., Афанасьев Д.Ф., Акатова Т.В., Чефранов С.Г., Ескина Т.Г., Сушкова Е.Г. Локальное видовое богатство растительных сообществ со сходной биомассой: влияние типов местообитаний в контексте исторической гипотезы (Западный Кавказ и Предкавказье, Черное и Азовское моря, Россия). Мы сравнили видовое богатство растительных сообществ разных местообитаний на разных участках градиента биомассы. Для анализа мы использовали данные по 1089 пробам наземной биомассы, отобранным с участков площадью 0.25 м² наземных травяных сообществ Западного Кавказа и Предкавказья (30–2800 м н.у.м.), и по 317 пробам, отобранным с таких же по площади участков макрофитобентоса Черного и Азовское морей (0.5–10 м глубины). Результаты показали, что определенное количество биомассы, отобранной в сообществах разного типа, включает в среднем существенно разное число видов. Так, среди наземных растительных сообществ наиболее высоким видовым богатством на большинстве участков градиента биомассы характеризуются высокогорные сообщества Западного Кавказа; сообщества травяного яруса затененных лесов – наоборот, наименьшим. Макрофитобентос Черного моря характеризуется менее высоким видовым богатством, чем большинство наземных сообществ, но более высоким, чем макрофитобентос Азовского моря. Мы показали, что существенные различия в видовом богатстве этих сообществ можно правдоподобно объяснить особенностями их истории.

Ключевые слова: наземные растительные сообщества, макрофитобентос, видовое богатство, наземная биомасса, энергетическая гипотеза, исторические данные

According to the "species-energy theory" (Wright 1983) and one of its potential mechanisms, the "more individuals hypothesis" (Srivastava & Lawton 1998), the amount of available energy (habitat productivity) may constrain the number of coexisting species by limiting the density of its individuals: more resources available, higher production and biomass of the communities, more individuals, higher probability for more species. The key link in this causal chain is the density of individuals. However, when grass

and macroalgal communities are studied, as a surrogate measure for habitat productivity usually used above-ground biomass (Garsía et al. 1993, Bhattarai et al. 2004, Arenas et al. 2009, Ma et al. 2010, Konar et al. 2010, Twist et al. 2020).

Many studies show that for grassy and macroalgal communities with a wide range of habitats, the relationship between biomass and richness often has a hump-shape with a peak in species richness at intermediate level of production (biomass) (Grime 1973, Tilman 1988, Moore & Keddy

1989, Garsia et al. 1993, Waide et al. 1999, Cornwell & Grubb 2003, Adler et al. 2011, Ma et al. 2010, Bhattarai et al. 2004, Pärtel et al. 2007, Zobel & Pärtel 2008, Fraser et al. 2015, Bhattarai 2017, Twist et al. 2020). According to "species-energy theory", monotonic increase in richness from low to intermediate level of production (biomass) reflects a decrease in the harshness of the environment and increase in resources available. At higher levels of biomass the decline in species richness is believed may to be due to competitive exclusion of poor light competitors or the sampling effect (i.e. plant individuals increase in their size with biomass, leading to the reduction in their abundance and consequently to the reduction in the total number of species) (Grime 1973, Latham & Ricklefs 1993, Oksanen 1996, Bhattarai et al. 2004, Šímová et al. 2013).

Moreover, according to species pool hypothesis, low species richness of plant communities of low and high productive habitats may not be a direct consequence of harsh physical conditions, strong competition or the sampling effect. Simply few species are adapted to such habitats (Zobel et al. 2011, Cornell & Harrison 2014). So, 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 & Ricklefs 1993, Ricklefs et al. 1999, Qian et al. 2003, Qian & Ricklefs 2004). On the other hand, it has been suggested, that high productive habitats in the temperate regions, unlike the tropics, have been scarce historically for speciation. Furthermore, they were rare during ice ages, which may have caused a reduction in the number of species inhabiting them (Taylor et al. 1990; Pärtel et al. 1996, 2007, Schamp et al. 2002, Šímová et al. 2013, Zobel & Pärtel 2008).

However, as follows from many studies the species richness of community sites with similar production (biomass) also vary significantly and this is the reason that the observed relationship between the values of these characteristics is a sort of "filled" hump-shape (Garsía et al. 1993, Venterink 2001, Bhattarai et al. 2004, Adler et al. 2011, Šímová et al. 2013, Fraser et al. 2015). In addition, in some studies it was shown that such a variation at least in some cases cannot be explained only by random processes, since plant communities of different habitats, but with similar production, biomass or density of individuals, are characterized, on average by different species richness (Garsía et al. 1993, Latham & Ricklefs 1993, Ricklefs et al. 1999, Kaspari et al. 2003, Longino & Colwell 2011, Perevozov 2011, Akatov & Chefranov 2014). In particular, Garsía et al. (1993) showed that salt-marsh grasslands of Guadalquivir Delta (SW Spain) have lower species richness than the ruderal communities of this region similar in production (biomass) and explained this difference based on historical hypothesis. In their opinion, this is due to the relatively small size of the species pool of salt-marsh communities, since relatively few plant species are able to tolerate a high salt concentration in the soil solution. But the plants which are able to cope with a harsh condition, benefit from a high availability of water, light and nutrients and may produce a large amount of biomass.

In turn, Ricklefs et al. (1999) showed that the different species richness of stands of temperate forests in different regions of the world can also be plausibly explained on the basis of a historical hypothesis. In their opinion, the low diversity of temperate forest trees in Europe and western North America resulted also from extinction of taxa during period of cooling climate and glaciations (Late Pliocene and Pleistocene). Eastern North America and eastern Asian apparently suffered no such loss and therefore tree species richness of these regions is higher. Eastern Asian has a higher woody species diversity than eastern North America because higher rates of speciation during the Tertiary (Latham & Ricklefs 1993).

Later, Akatov & Chefranov (2014) associated with historical events the relatively high average number of species per density unit in the stands of the middle-mountain belt of the Western Caucasus (dominated by *Fagus orientalis* and *Abies nordmanniana*) in comparison with the stands of this mountain system located above and below (in the high-mountain belt – the stands dominated by *Betula pubescens* var. *litwinowii*, *F. orientalis* and *A. nordmanniana*, in the low-mountain – *Quercus robur* and *Castanea sativa*). It was suggested that the relatively high constancy and trunk density of tree species in high-mountain stands is a consequence of their evolutionary youth. These stands consist mainly of boreal tree species (*Betula pubescens* var. *litwinowii*, *Sorbus aucuparia*, *Salix caprea*), which appeared in the Caucasus only in Late Pliocene or Early Pleistocene (Maleev 1941, Ratiani 1979, Kleopov 1990). Apparently, historical processes have also negatively affected the low-mountain stands of the Caucasus. It is assumed that due to a periodic decrease in temperature and drying in the Pleistocene, they lost many tree species (Galushko 1976, Ratiani 1979, Dolukhanov 1980). In contrast to the mid-mountain beech and fir forests, which, as is commonly believed, were damaged less significantly in this period (Kolakovsky 1974, Galushko 1976, Ratiani 1979, Dolukhanov 1980).

The historical hypothesis was also used to explain the different relationship between the density of individuals and the species richness in communities of organisms of other taxonomic groups (Kaspari et al. 2003, Longino & Colwell 2011, Perevozov 2011). In particular, Kaspari et al. (2003) found that ant communities of deserts and rain forests of New World have relatively more species per unit abundance than other biomes. They suggested that these biomes were less likely to disappear during recent glaciation events or if their populations have faster evolutionary clocks.

The role of historical effects in the formation of current local patterns of a species richness of plant communities has been discussed over the past three decades. The results suggest that the processes of speciation, dispersal and extinction of species in the evolutionary past do indeed seem to determine the size of the species pool of modern communities, which, in turn, determines their local species richness. In addition, it was assumed that the most favorable conditions for the accumulation of species in species pools are formed mainly in favorable and widespread habitats (Eriksson 1993, Latham & Ricklefs 1993, Onipchenko & Pavlov 2009, Zobel 2016, Onipchenko et al. 2020). As men-

tioned earlier, one of the possible reasons for the low species richness of plant communities of extreme habitats is the need in evolutionary development for mechanisms providing tolerance to harsh environmental factors (Latham & Ricklefs 1993, Ricklefs et al. 1999, Qian et al. 2003, Qian & Ricklefs 2004). The influence of habitat area on the species richness of communities is explained in different ways. First, the communities occupying large territories are usually characterized by a long period of stable evolutionary development, which creates widespread opportunities for speciation. That is, more species are expected to occur in conditions that have been more abundant (in space or time) throughout evolutionary history (Taylor et al. 1990, Schamp et al. 2002, Pärtel et al. 2007, Zobel et al. 2011). Secondly, as populations are distributed more widely in communities with a larger area, they are less likely to suffer catastrophic extinction (Terborgh 1973, Kaspari et al. 2004). Finally, communities that have a limited distribution in the region are usually represented in the landscape by small isolated sites, that are affected by the island effect (MacArthur & Wilson 1963].

And yet, despite significant efforts, knowledge of the role of historical events and processes in determining the current species richness of plant communities remains limited (Harrison & Cornell 2008, Cornell & Harrison 2012, Ricklefs & He 2016, Zobel 2016). Comparison of the species richness of communities with similar production, biomass or density of individuals but with different histories could significantly help in this regard. At the same time, surprisingly little research has been devoted to this issue. We considered it using the widespread plant communities of the Western Caucasus and Ciscaucasia, as well as the macrophytobenthos of the shallow waters of the Black and Azov Seas, as the objects of the study. This region is characterized, on the one hand, by a significant diversity of plant communities, and, on the other hand, by the presence of events in the history of these communities, which could have a significant impact on their modern species richness. In this study, we: (i) tested the significance of the impact of plant community types on small-scale species richness in different parts of the biomass gradient; (ii) identified community types with relatively high and low average small-scale species richness; (iii) discussed the results based on our knowledge of the history of the studied communities (habitats).

MATERIAL AND METHODS
Study area and objects

The study area included the foothills and mountain massifs of the Western Caucasus (between 220 and 2800 m a.s.l.), the Stavropol upland, Kumo-Manych depression, the coastal parts of the Black Sea shelf near the Abrau Peninsula and shallow waters of the Taman Bay of the Azov Sea. The object of the study was herb- and algae-dominated vegetation: alpine grasslands, heaths and snowbeds (AG); subalpine meadows (SAM); typical and steppe meadows of low mountain forest glades (GM); communities of early flowering plants of alder and beech forests (early spring development period) (EFP); late spring herb communities of closed-canopy (shaded) alder, beech and oak forests (LSSF); summer herb communities of such forests (SSF); summer

herb communities of light oak forests (SLF); typical steppes (TST); dry steppes (DST); macrophytobenthos of the upper sublittoral of the Black Sea (MBS) and of the shallow waters of the Taman bay of the Azov Sea (MAS). Plant communities of alpine and subalpine belts were studied within the Caucasian State Nature Biosphere Reserve. The information of the study site locations is given in Figure 1 and Table 1.

The habitats of meadows and herb communities of light oak forests can be considered as the most favorable: high insolation, the average temperature in July is 18–22°C, and the average annual precipitation is 680–1150 mm (Bedanokov et al. 2020). Communities of the other types are formed under continuous exposure to low level of resources or stress factors. For example, the communities of subalpine and alpine belts are subjected to low temperatures – the average temperature in July is less than 14°C (Bedanokov et al. 2020). Besides, floristic composition of alpine communities is controlled by the snow cover duration, in relation with variation in mesorelief: alpine grasslands occupy the most favorable slopes, where the winter snow accumulation is moderate; alpine snowbed communities develop on habitats with considerable snow accumulation and short growing season; plants of alpine heath grow in habitats with a small amount of snow (at the tops of mountains and ridges), where the winter soil temperatures are very low. Communities of early vascular plants of forests are formed under the exposure to low temperature stress, periodic frosts and short growing season; communities of typical and dry steppes – moisture deficit (the average annual precipitation is 550–560 and 432 mm – Gvozdetsky 1963, Anonymous 1971), the herb layer in shaded forests (late spring and summer development periods) – light deficit.

Benthic macrophytes of the Black Sea grow under relatively low salinity (the Black Sea has salinity around 17–18 ‰, whereas the Mediterranean Sea – the source of the
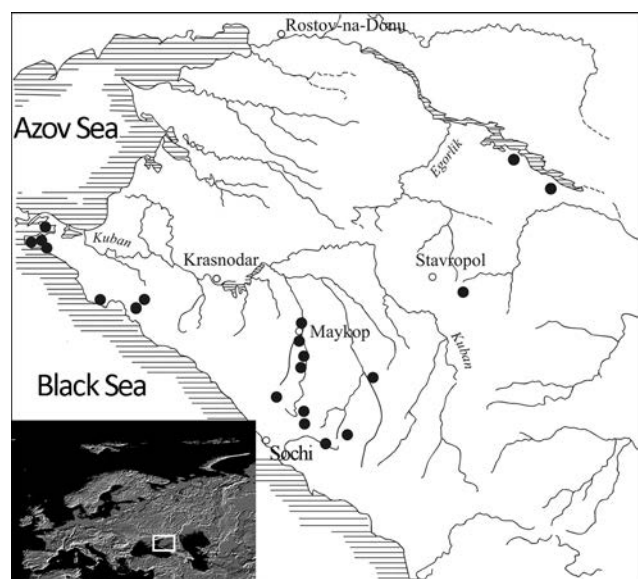

Figure 1 The geographic locations of the study sites

Table 1. The location of sampling plots.

Location	Coordinates	Elevation a.s.l., m	Communities	n
High mountain massifs of the Belaya, Malaya Laba and Mzymta river basins (WC)	43°32.845'–44°01.074'N 39°56.47'–40°42.150'E	1855–2800	AG, SAM	317
Skalistyj Ridge, Belaya River basin (WC)	44°15.464'–44°21.393'N 40°09.587'–40°14.280'E	498–1008	EFP, LSSF, SSF, SLF, GM	155
Lesistyj Ridge, Belaya river basin (WC)	44°35.152'–44°36.122'N 40°01.041'–40°06.399'E	220–300	EFP, LSSF and SSF	226
Mt. Tryu, Malaya Laba river basin (WC)	43°55.54'N 40°40.21'E	845	GM	20
Mt. Akhmedov Post, Bolshaya Laba river basin (WC)	44°13.346'N 41°02.718'E	662	GM	26
Marcoth and Shize Mountains, Abin river basin (WC)	44°38.819'–44°44.508'N 38°02.380'–38°09.283'E	540–714	TST and GM	102
Stavropol' Upland (CC)	44°51.153'N 41°56.285'E	585	TST and GM	55
Kumo-Manychskaya depression (CC)	45°59.833'N 43°14.405'E	30–75	SST	39
Abrau Peninsula, Bol'shoj Utrish Cape, Black Sea	44°45.394'–44°45.150'N 37°22.210'–37°22.391'E	0.5–10 m depth	MBS_1, MBS_2 and MBS_3	143
Taman Bay, Azov Sea	45°11.103'–45°20.970'N 36°35.755'–36°59.425'E	0.5–2 m depth	MAS	174

Here and in Tables 2–4: AG – alpine grasslands, heaths and snowbeds; SAM – subalpine meadows; meadows of mountain forest glades; TST – typical steppes; DST – dry steppes; LSSF – late spring grassy communities of grass layer of shaded forests; SSF – summer grassy communities of grass layer of shaded forests; SLF – summer grass layer of light forests; EFP – communities of early flowering plants of forests; MBS – macrophytobenthos of the upper sublittoral of the Black Sea; MAS – macrophytobenthos of shallow waters of the Azov Sea (Taman Bay); n – number of samples; WC – Western Caucasus; CC – Ciscaucasia

Black Sea flora – 36–38 ‰), low water temperature, relatively low light level and a wide range of their seasonal fluctuations (Afanasyev et al. 2017). In shallow areas the macrophytes are exposed to the powerful waves. However, the conditions of the Azov Sea (and the investigated shallow Taman Bay) are even more severe for phytobenthic communities, than the conditions of the Black Sea: lower and unstable salinity (5–20 ‰), a wider range of seasonal fluctuations of water temperature, lower transparency of water, sandy and muddy bottom, which prevents algae from fixing on it. In fact, the Azov Sea can be considered as the estuary of the Don River.

Field sampling

The biomass of terrestrial communities was sampled from 2014 to 2020 in the relatively homogeneous sites without obvious signs of anthropogenic disturbance in the period when the grass cover was at a peak of development. The biomass of benthic marine communities was sampled in June-August (2012, 2013, 2018 and 2020) when diversity was more likely the highest (i.e. when annual and seasonal-summer species were present: Kalugina-Gutnik 1975). The major part of the samples was collected in a regular pattern along linear transects including ten 0.25 m² plots each. Others were collected in series of three to ten samples per site. In total, we took 1089 above-ground biomass samples from the terrestrial herbaceous communities and 317 macrophytobenthos samples. In each 0.25 m² plot we determined total number of species (S) and number of accompanying species (S_a), as well as dry weight in grams of above-ground biomass of the entire communities (W), the dominant species (W_d) and accompanying species (W_a), i.e. without biomass of the dominant species. The phytobenthos communities are dominated by functionally similar *Gongolaria barbata* and *Ericaria crinita* f. *bosphorica* (*Cystoseira*

sensu lato), as well as *Zostera noltii* and *Z. marina*. Therefore, the W_d values corresponded to the total biomass of these species. The general characteristics of the studied plant communities are presented in Table 2. The nomenclature of all vascular plants mentioned in the article is based on the database of POWO (http: //www. plantsoftheworldonline. org/), the macroalgae – on the global taxonomic database and AlgaeBase nomenclature of algae (Guiry & Guiry 2021).

Data analysis

The biomass gradient of complete communities (W gradient) was divided by us into 7 sites (ranges) of different sizes, the biomass gradient of accompanying species (W_a gradient) – into 6 ranges. The boundaries of the ranges of both gradients roughly corresponded to the boundaries of the predominant distribution of communities of certain types (Tables 3 and 4). Then we compared the S and S_a values of communities of different types for each range of the W and W_a gradients, respectively. We suggested that if the types of habitats (plant communities) do not have a systematic effect on S and S_a values (that is, these values are randomly distributed among different communities), then the species richness of these communities is on average approximately the same. We used the analysis of variance (ANOVA) to test for significant effect of the types of the plant communities on S and S_a values and Tukey's post-hoc test to determine which types of communities are significantly different from each other in this respect. The strength of the influence of the types of the plant communities on S and S_a values was determined as the share of factorial variation (between community types) in the total variation of S and S_a values (h_x^2).

According to the "energy-diversity theory" (Wright 1983) and the "more individuals hypothesis" (Srivastava & Lawton 1998), the variation in species richness of the plant

Table 2. The information about the studied plant communities.

Community, elevation a.s.l. (dominant species)	*n*	*W* mean ± SE (limits)	*S* mean ± SE (limits)
AG, 2000–2800 m (*Alchemilla retinervis, Campanula tridentata, Carex alatauensis, C. capillifolia, C. tristis, Carum caucasicum, Festuca ovina, Geranium gymnocaulon, Hedysarum caucasicum, Leontodon hispidus, Onobrychis bi*ebersteinii, *Pedicularis nordmanniana, Plantago atrata, Ranunculus crassifolius, Sibbaldia semiglabra, Silene dianthoides, Trifolium badium, Veronica gentianoides*)	149	66.8±2.9 (8.2–171.4)	12.0±0.5 (2–28)
SAM, 1850–2450 m (*Alchemilla oxysepala, Betonica macrantha, Brachypodium pinnatum, Calamagrostis arundinacea, Caucasalia pontica, Festuca varia, Inula grandiflora*)	167	155.7±5.7 (46.4–354.4)	16.9±0.6 (5–35)
GM, 490–1008 m (*Bothriochloa ischaemum, Brachypodium pinnatum, Chrysopogon gryllus, Galega orientalis, Geranium sanguineum, Pentanema asperum, Salvia verticillata*)	209	125.0±4.8 (22.2–458.9)	12.8±0.3 (5–29)
TST, 540–714 m (*Agropyron cristatum, Allium denudatum, Psephellus declinatus, Salvia verticillata, Stipa pulcherrima, Teucrium chamaedrys*)	77	79.4±3.2 (27.9–160.4)	14.8±0.8 (5–32)
DST, 30–75 m (*Artemisia lercheana, Carex divisa, Poa bulbosa, Stipa lessingiana*)	39	41.5±3.1 11.3–75.3	9.3±0.2 7–12
LSSF, 220–400 m (*Aegopodium podagraria, Allium ursinum, Helleborus orientalis, Onoclea struthiopteris, Paris incompleta, Scopolia caucasica, Symphytum grandiflorum*)	89	38.2±1.6 (11.8–92.7)	6.4±0.2 (3–14)
SSF, 220–500 m (*Aegopodium podagraria, Carex divulsa, C. pallescens, C. sylvatica, Dryopteris filix-mas, Festuca drymeja, Lamium galeobdolon* subsp. *galeobdolon, Matteuccia struthiopteris, Salvia glutinosa, Symphytum grandiflorum*)	139	24.3±1.7 (0.7–147.2)	4.1±0.1 (2–8)
SLF, 480–510 m (*Carex tomentosa, Betonica officinalis, Lotus corniculatus, Trifolium medium*)	31	25.9±1.0 (14.1–34.6)	12.7±0.5 (8–19)
EFP, 220–400 m (*Arum orientale, Corydalis marschalliana, Doronicum caucasicum, Lamium maculatum*)	42	9.6±0.8 (2.8–22.8)	7.8±0.2 (5–12)
MBS, 0.5–10 m depth (*Ceramium ciliatum, Codium vermilara, Ericaria crinita* f. *bosphorica, Gongolaria barbata, Padina pavonica, Phyllophora crispa*)	143	147.8±8.7 (4.1-507.8)	8.2±0.2 (3-15)
MAS, 0.5–2 m depth (*Zostera marina, Z. noltii*)	174	41.3±2.4 (0.4–170.0)	5.4±0.2 (2–11)

n – number of samples; *W* is dry above-ground biomass of the entire communities (g/0.25 m²), *S* is species richness per 0.25 m², **SE** – standard error.

communities with similar biomass can be associated also with different participation of dominant species in the communities (degrees of dominance, $D = W_d/W$). The higher participation of dominant, the less resources remain for other (accompanying) species, the smaller the number of their individuals appears on sites, the lower the likelihood that they will belong to many species. The comparison of the species richness of the communities on the sites of the biomass gradient of accompanying species makes it possible to minimize the influence of this factor. Therefore we compared the species richness of plant communities on sites of not only the *W* gradient, but also the W_a gradient.

RESULTS

Figure 2 shows the relationship between the biomass and species richness for the studied terrestrial communities and macrophytobenthos in general. As seen from this Figure 2, the biomass in the studied terrestrial and benthic marine communities varies approximately within the same limits: from several grams to slightly more than 500 g per 0.25 m². The species richness of terrestrial herb communities ranged from 1 to 35 species per 0.25 m² plot, macrophytobenthos – from 2 to 15 species. The highest species richness of terrestrial communities (32–35 species) corresponds to intermediate values of dry biomass (70–140 g). In macrophytobenthos relatively high species richness (13–15 species) is observed in a wide range of biomass gradient (45–370 g). At the same time, the sites of both terrestrial and marine communities with similar biomass are characterized by significantly different species richness.

Table 2 indicates that the communities of subalpine meadows and forest glades have highest average biomass. Among other terrestrial communities, the communities of

alpine belt and typical steppes are most productive. The communities of dry steppes, late spring and summer herb communities of shaded and light forests have lower biomass. The communities of early flowering plants are the
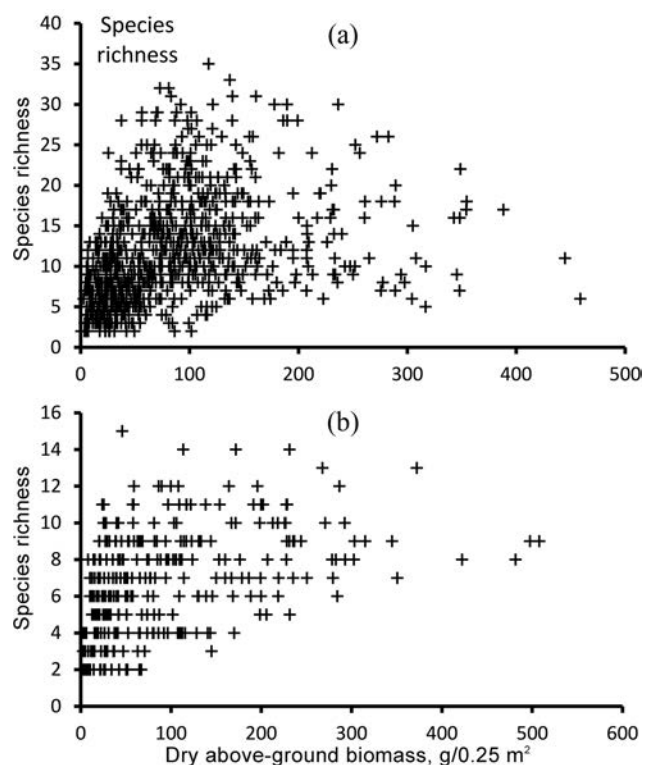

Figure 2 The relationship between dry above-ground biomass (*W*, g/0.25 m²)) and species richness (*S*, per 0.25 m²) for the studied terrestrial communities in general (a) and macrophytobenthos in general (b)

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least productive. At the same time, let us note that the biomass of communities of the most types varies in a wide range. Therefore, the ranges of variation of this characteristic in the communities of different types overlap.

Table 2 also indicates that species richness is the highest in the communities of subalpine meadows and typical steppes. It is slightly lower in the communities of alpine belt, herb communities of light forests and forest glades; even lower – in communities of dry steppes, early flowering plants and late spring herb communities of shady forests. The smallest number of species per site was found in the herb communities of shaded forests. In addition, Table 2 shows that the macrophytobenthos of the Black Sea is characterized, on average, by higher biomass and higher species richness than the benthic communities of the Azov Sea.

Table 3 shows the average values of the species richness per 0.25 m² of terrestrial and marine (benthic) plant communities in different ranges of the biomass gradient. One-way ANOVA detected significant differences average S values among terrestrial communities of different types in each of seven ranges of W gradient. In particular, among low production communities, the communities of the alpine belt and the herb communities of light forests are characterized by the highest average S. The Tukey's post-hoc test suggests that in the range of W gradient from 20 to 40 g / 0.25 m² differences in this regard between the communities of these two types are not significant at the 0.05 level. Among the other communities, meadows of forest glades, dry steppes and communities of early flowering plants are more rich species. The communities of late spring and summer herb communities of shady forests are characterized by the lowest average species richness. Among the communities with relatively high biomass (more than 60 g / 0.25 m²), subalpine meadows are characterized by the highest average S. Among other communities with such biomass, meadows of forest glades, typical steppes and communities of alpine

belt are more rich species. In the range of W gradient from 100 to 150 g / 0.25 m² the average S values of communities of subalpine meadows, forest glade and typical steppes are approximately the same. The communities of dry steppes are characterized by the lowest average S. In general, the influence of plant community types on S values is stronger in less production sites of habitats. Thus, the types of terrestrial communities determine 50–80 % of the total variation of S values in the ranges of biomass gradients less than 20 g, 20–40 g and 40–60 g / 0.25 m², but only 8 and 10 % in the range of 100–150 and 150–300 g / 0.25 m².

Table 4 shows the average S_a values in different ranges of the W_a gradient for terrestrial and marine communities. It follows that One-way ANOVA detected significant differences average S_a values among terrestrial communities of different types in each of six ranges of W_a gradient. The highest Sa values in range of the W_a gradient less than 10 g / 0.25 m² are observed in the communities of dry steppes and meadows of forest glades. Among the rest, communities of alpine belt and early flowering plants are more rich species. In other ranges of the W_a gradient, the highest S_a values are observed in the communities of the alpine and subalpine belt, glade meadows and typical steppes, herb communities of light forests. Moreover, in many of these ranges, the differences in the average S_a values between these communities are not significant at the 0.05 level (Tukey's post-hoc test). Late spring and summer herb communities of shaded forests are characterized by the lowest average Sa values in different ranges of the W_a gradient. In general, the influence of plant community types on S_a values is stronger in sites of habitats with relatively low biomass of accompanying species.

It is also seen from Tables 3 and 4 that in most of the ranges of the gradient W, as well as W_a, the values of S and S_a, respectively, are higher in the macrophytobenthos of the Black Sea than in the Azov Sea. Note also that the species

Table 3. The average species richness per 0.25 m² for terrestrial and marine benthic communities of different types in different ranges of dry above-ground biomass gradient.

Community	Dry above-ground biomass (g/0.25 m²)						
	< 20	20 – 40	40 – 60	60 – 80	80 – 100	100 – 150	150 – 300
Terrestrial plant communities							
EFP	7.8±0.2						
SLF		12.7±0.5a					
LSSF		6.2±0.2b	6.3±0.3				
SSF	4.0±0.2	4.3±0.2	3.7±0.3				
DST	9.1±0.3		9.3±0.4	9.1±0.3			
AG	12.4±0.4	12.7±0.9ab	13.4±1.2	12.1±0.9a	10.4±0.8	10.5±1.3	
GM		9.2±0.5b		12.8±0.6a	12.8±0.8	14.9±0.6b	11.6±0.7
TST				12.1±1.3a	16.7±1.6	17.7±1.4a	
SAM				21.3±1.9	22.3±1.1	16.0±0.9ab	15.4±1.0
F	162.1*	60.16*	27.25*	10.06*	22.03*	6.30*	9.92*
h_x^2	0.80	0.58	0.50	0.28	0.40	0.10	0.08
Phytobenthic communities							
MBS	4.7±0.4		9.1±1.1		8.8±0.6	8.9±0.4	8.8±0.3
MAS	4.2±0.3	6.2±0.3	6.2±0.4	5.4±0.6		4.2±0.2	
F	0.64		9.06*			73.45*	
h_x^2	0.01		0.19			0.65	

F, actual values of the Fisher criterion, one-way ANOVA (*– actual values exceed critical for $P < 0.05$). The same letters show no significant differences between the DSS values at the 0.05 level (Tukey's post-hoc test)

richness of macrophytobenthos of the Black Sea is lower than that of many terrestrial communities with a similar biomass of all or only accompanying species. Finally, note that the strength of the impact of community types on S values in the ranges of the W gradient is on average higher than on Sa values in the ranges of the W_a gradient.

DISCUSSION

Thus, we found that a certain amount of biomass, sampled in communities of different types, includes, on average, a significantly different number of species. Since the strength of the impact of community types on S values in the ranges of the W gradient is on average higher than on S_a values in the ranges of the W_a gradient, the difference in the species richness of communities of different types partially can apparently be explained by the difference in the average participation of dominant species in them. However, despite this, the structure of S and S_a values in the ranges of W and W_a gradients is approximately the same. So, among terrestrial communities in ranges of the gradients with relatively low W and W_a values, the communities of the alpine belt and the herb communities of light forests are characterized by the highest average S and S_a values; among more productive communities – subalpine meadows. At many sites of the W_a gradient, the difference in the species richness of these communities is statistically insignificant. Among other terrestrial communities, typical and dry steppes, meadows of forest glades and communities of early flowering forest plants are richer in species. The communities of late spring and summer herb communities of shady forests are characterized by the lowest average S and S_a values in almost all sites of the W and W_a gradients. In general, the influence of plant community types on S and S_a values is stronger in sites of habitats with relatively low biomass of all or only accompanying species. That is, low production

communities of different types are characterized by more different species richness than communities with relatively high production. The macrophytobenthos of the Black Sea is characterized by lower species richness than most of the terrestrial communities, but higher species richness than the benthic communities of the Azov Sea with similar biomass.

Our results raise several questions. Four of them seem to us the most interesting. Why, among the plant communities with similar biomass, the communities of the alpine and subalpine belts of the Western Caucasus, formed in relatively cold conditions, are characterized by the highest species richness? Why is currently widespread herb communities of shady forests characterized by lower species richness in comparison with herb communities of light forests, as well as meadow and steppe communities, with similar production? Why is the species richness of benthic communities of the Black and Azov Seas lower than that of many terrestrial communities with approximately the same biomass? Why is the species richness of benthic communities in the Azov Sea lower than in the Black Sea?

Following other authors, we will try to answer them based on our knowledge of the vegetation history of the study area. So in many works, it has been suggested that unusually high biodiversity of high-mountain ecosystems are the result of reflects the interplay of multiple evolutionary mechanisms, including long evolutionary history of species adaptation to steep environmental gradients, enhanced speciation rate, as well as high topographic diversity, which contributes to a high level of specialization (Musciano et al. 2018, Muellner-Riehl et al. 2019, Rahbek et al. 2019). This may be true, among other things, in relation to the high-mountain flora of the Greater Caucasus. Most botanists consider it historically ancient, formed mainly in the Tertiary period (Tolmachev 1948, Fedorov 1952, Altukhov 2017). At the same time, in the opinion of many authors, the presence of young regional species closely related to modern landforms

Table 4. The average number of accompanying species per 0.25 m² for the communities of different types in different ranges of gradient of the dry biomass of such species.

Community	Dry above-ground biomass (g/0.25 m²)					
	1 – 10	10 – 20	20 – 30	30 – 50	50 – 100	100 – 150
Terrestrial plant communities						
EFP	6.8±0.2b					
SLF		11.8±0.6a				
LSSF	5.0±0.3c	5.3±0.4	5.9±0.5	5.6±0.3		
SSF	3.2±0.1	3.5±0.3				
DST	8.2±0.3a	8.3±0.2c	8.4±0.5			
AG	6.4±0.6b	10.1±0.8b	13.1±0.8a	13.6±0.8a	17.1±1.8a	
GM	8.0±0.5a	8.6±0.4c	11.6±0.4	13.2±0.6a	13.4±0.7	12.6±0.8
TST	5.0±0.4c			14.1±1.3a	17.6±1.1a	
SAM		10.7±1.6ab	14.8±1.5a	16.8±1.1	15.8±0.9a	18.5±1.4
F	35.51*	23.92*	13.13*	9.92*	3.57*	13.20*
h_x^2	0.48	0.46	0.34	0.21	0.06	0.2
Phytobenthic communities						
MBS	6.9±0.3	6.8±0.4		7.3±0.5		
MAS	4.5±0.3	7.1±0.6		5.4±0.6		
F	39.18*	0.27		4.94*		
h_x^2	0.22	0.01		0.17		

F, actual values of the Fisher criterion, one-way ANOVA (*– actual values exceed critical for $P < 0.05$). The same letters show no significant differences between the DSS values at the 0.05 level (Tukey's post-hoc test).

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indicates active speciation also in the Quaternary period (Tolmachev 1958, Fedorov 1952, Galushko 1976, etc.). According to Altukhov (2017), the flora of vascular plants in the high-mountainous belt of the Western Caucasus within the Caucasian Reserve (the area of biomass sampling by us) includes 967 species. This is more than in the corresponding floras of the Eastern and Western Sayan (south of Siberia), or Stanovoy Highlands (Russian Far East) (Altukhov 2017). As follows from the reviews by Onipchenko (Onipchenko & Semenova 1995, Onipchenko et al. 2005, 2020), alpine communities of the Western Caucasus have approximately the same local species richness as the communities of the Central Alps developing under similar ecological conditions. But they have a higher species richness than analogous communities of the Krkonoše Mountains (Czech Republic), Altai and Priokhot'e (Russian Far East), Mt. Kenya (East Africa), Japan and New Zealand.

It is surprising that the herb communities of shady forests, that are now widespread in the Western Caucasus, are characterized by a very low small-scale species richness. In particular, it is lower than the species richness of the herb communities of light forests with the same biomass, as well as communities of the alpine belt and steppes, developing in cold or dry, but well-lit habitats. In this regard, we draw attention that in Late-Miocene low-mountain mesophytic forests of the Western Caucasus, like forests of central Europe, were nearly subtropical. They consisted of two tree layers with mainly deciduous Arcto-Tetriary species dominating in the canopy, and the mainly evergreen Palaeotropical species concentrated in the understory. During the Pliocene they developed generally by changes in species composition in the upper tree layer, by reduction of the evergreen understory and by the increase of herbs (Dolukhanov 1980, Peters 1997). In the Western Caucasus this process also continued in the Pleistocene (Galushko 1976, Dolukhanov 1980). However the mostly cool and dry Pleistocene climate as well as the high density of large herbivores, contributed to the formation of open landscapes, including predominantly well-lit, dry habitats with soils characterized by neutral or not too high pH. This circumstance should have contributed, on the one hand, to the accumulation of species preferring such environmental conditions, and, on the other, to the extinction of species with opposite preferences (Pärtel 2002, Ewald 2003, Chytrý et al. 2007, Smirnova et al. 2020).

It should also be noted that the forests with evergreen understory and poor development herb layer are still widespread in the Western Caucasus. At the same time, they are characterized by a very low diversity of vascular plants. For example, in the Belaya River basin (area where we sampled the biomass of forest herb communities) the flora of forests with evergreen understory (dominated by *Buxus colchica*) includes only 65 species (Bondarenko 2011). The flora of shady floodplain and mesophytic beech forests with herb cover includes more species – 192 and 276, respectively, but much less than the flora of light oak forests – 429 species (Bondarenko 2011).

One would expect that for at least two reasons, the species richness of macrophytobenthos in certain ranges of gradients W and W_a should be higher than in most terrestrial communities. Firstly, resource availability in a three-dimensional aquatic environment should be higher than in terrestrial habitats. Secondly, large thalli of the dominants of benthic communities (for example, *Cystoseira* sensu lato) can be used by other species as an additional substrate alongside with other surfaces, such as rocks and boulders. However, our results showed that the species richness of macrophytobenthos of the Black Sea is lower than the species richness of many terrestrial communities with a similar biomass. It can be assumed that this may be caused not only by relatively unfavorable environmental conditions, but also by the history of this sea, namely by full (about 7–10 thousand years ago) or partial (currently) isolation from other seas and oceans. According to the latest data, the balance of fresh and saltwater inflow, as well as the Black Sea water salinity, which are more or less close to modern ones, were achieved only 3–6 thousand years ago (Ivanova et al. 2012). The coastline of the Black Sea, close to the present, was formed in the middle of the Holocene era or later (Hiscott et al. 2007). Thus, the overwhelming number of species of the modern Black Sea flora penetrated into the Black Sea from the Mediterranean through the Sea of Marmara and the system of straits only over the past 3–9 thousand years, and they continue to penetrate (Kalugina-Gutnik 1975, Afanasyev & Korpakova 2008, Afanasyev & Ruban 2013). However, due to the significantly lower salinity and temperature of the Black Sea, only about 30 % of Mediterranean algal species can thrive here – in the Mediterranean there are 1124 macrophyte algae species (Coll et al. 2010), while in the Black Sea there are only about 330 (Kalugina-Gutnik 1975). Among approximately 50 species of *Cystoseira* sensu lato dominate the Mediterranean shelf and adjacent areas of the Atlantic, only five species are found in the Black Sea and only two species have been recorded in its northeastern part (Afanasyev et al. 2017).

As it was noted above, conditions for macrophytes in the Azov Sea are even less favorable than in the Black Sea. In particular, it is well known, that salinity of 5–8 ‰ is critical zone for both marine and freshwater species which is characterized by minimum number of benthic species (Remane 1958). Besides, the Azov Sea is characterized by constant changes of salinity due to short- and long-term fluctuations of the Don's flow. In addition, due to small depth of the sea (maximum 14 m) it has an extremely wide range of daily, seasonal and annual fluctuations of sea level, temperature, turbidity etc (Afanasyev & Korpakova 2008). Apparently, these factors are a significant obstacle to speciation. Finally, the Azov Sea is characterized by a small area and is isolated from similar reservoirs by marine ecosystems of other types. Thus, the Azov Sea is a young, small in area, isolated ecosystem with an ecological regime not favorable for speciation. Perhaps that is why the flora of macroalgae of this reservoir includes significantly less species than the Black Sea (97 versus 330) and there are no species, that can be found only in the Azov Sea (Afanasyev & Korpakova 2008). Therefore, from the standpoint of the historical hypotheses, the higher species richness of the macrophytobenthos of the Black Sea in comparison with

the macrophytobenthos of the Azov Sea, similar in biomass, is not a surprise.

Thus, the historical hypothesis provides a plausible explanation for our results. They are consistent with the existing idea that one of the conditions for high species richness of plant communities is their long-term stable evolutionary development. However, it is conceivable that some other factors can also cause variations in the species richness of the community with the similar productivity. So, for example, all communities that we used as objects of study are widespread in the study area. We deliberately did not consider communities with a limited distribution in the region (for example, communities of subalpine fens, salt marshes, etc.) because they are usually represented in the landscape by small isolated sites that are affected by the island effect (MacArthur & Wilson 1963). In this case, it is very difficult to separate the impact on communities of historical and regional factors. However, it cannot be ruled out that the lower species richness of low mountain meadows (widespread in the study area), than the communities of the alpine and subalpine belts, may be due to their confinement to forest glades isolated from each other. Moreover, it is known that the steppe vegetation of the Ciscaucasia and the lower mountains of the Western Caucasus has been exposed to human impact for a long time and is largely fragmented (Belonovskaya & Yasin 1990).

Secondly, in accordance with the "species-energy theory" and the "more individuals hypothesis" (Wright 1983, Srivastava & Lawton 1998), density of individuals is a positive function of production and species richness is a positive function of density. As we mentioned above, the key link in this causal chain is the density of individuals. Moreover number of individuals in the plots depends not only on the weight of the biomass, but also on their size. The herb communities of relatively productive habitats, including subalpine and low-mountain meadows, typical steppes, are, as a rule, characterized by a similar size of individuals. However low production communities can be formed either by a large number of small individuals or by a small number of large ones. The first group includes, for example, the low-herb communities of the alpine belt (grasslands, heaths and snowbeds) and early spring herb communities of forests. The second group includes late spring and summer herb communities of shady forests. Therefore a difference in the species richness of these low production communities may be due, among other things, to the sampling effect. Perhaps this is another reason why the influence of plant community types on small-scale species richness is stronger in less productive sites of habitats.

Third, the herb layer of forests is part of the forest community as a whole, the different components of which (layers of tall and low trees, shrubs, etc.) are presumably closely related. So, Li et al. (2018) showed that the relationship between species richness and aboveground biomass in the tall tree layer of primary *Pinus kesiya* forest (Yunnan Province, China) directly and indirectly affects the relationship between species richness and aboveground biomass in other layers, including the herb layer. Therefore, it cannot be ruled out that the low species richness with respect to biomass of the herb layer of shady forests of the Western Caucasus is associated, among other things, with this circumstance. However, in general, knowledge about the mechanisms that determine the relationship between biomass and species richness in different layers of forest communities is very limited.

On the other hand, note that the small area of the sampling plots (0.25 m²) means that our findings pertain only to a small spatial scale. However there is evidence that the species richness of small sites of plant communities are less dependent on the species pool size and accordingly on historical or regional effects than the species richness of large sites (Terborgh & Faaborg 1980, Shurin et al. 2000, Akatov et al. 2005, He et al. 2005, Šímová et al. 2013, Onipchenko et al. 2020). In particular, interesting results in this respect were recently obtained by Onipchenko et al. (2020). They compared the α-diversity of plant communities in five mountain regions (Mount Kenya, the European Alps, the Caucasus, Tibet, the New Zealand Alps) and found that percentage of richness variability, explained by mountain system size, increased with spatial scale from 47 % for 1 m² plots up to 69 % for 500 m² area. In this regard note, that only about 30 % of the algal species of the Black Sea can grow in the Azov Sea. At the same time the species richness of the benthic communities of the Azov Sea on plots of 0.25 m² is on average more than 65 % of the species richness of the communities of the Black Sea (Table 2). Therefore, it is quite possible, that some communities, which within certain ranges of the biomass gradient have similar species richness on plots of 0.25 m², will include significantly different numbers of species in the larger plots. That is it can be expected, that the type of communities and habitats will have a more significant impact on the local species richness of communities, if it is estimated on plots with an area larger than 0.25 m².

CONCLUSION

We tested the significance of the impact of plant community types on small-scale species richness in different ranges of the above-ground biomass gradient. The objects of research were widespread plant communities of the Western Caucasus and Ciscaucasia (alpine communities, subalpine and low mountain meadows, steppes, herb layer of light and shady forests, etc.), as well as macrophytobenthos of the shallow waters of the Black and Azov Seas. The results showed that a certain amount of biomass, sampled in communities of different types, includes, on average, a significantly different number of species. In particular, high-mountain communities of the Western Caucasus are characterized by the highest species richness in most ranges of the biomass gradient; communities of herb layer of shaded forests and macrophytobenthos of the Black and Azov Seas – on the contrary, the lowest richness. At the same time, we noticed that the high-mountain communities of the Western Caucasus presumably have a longer evolutionary history than the communities of the other two types. In particular, the period of existence of the Black and Azov Seas as marine reservoirs is limited to only a few millennia. In addition, herb communities of shady forests presumably

had a limited distribution in the Pleistocene. Therefore, we concluded that significant difference in the small-scale species richness of these communities in different parts of the biomass gradient can be plausibly explained by the peculiarities of their history.

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