1. Абиотические основы экосистем

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THE RELATIONSHIP BETWEEN NUMBER AND MEAN FREQUENCY OF SPECIES IN PLANT COMMUNITIES OF THE WESTERN CAUCASUS WITH DIFFERENT ORGANIZATION MODELS

Akatov V.V.
Maikop State Technological University, ul. Pervomaiskaya 191, Maikop, 385000 ***Russia****,* akatovmgti@mail.ru;
Akatova T.V.
Caucasian State Nature Biosphere Reserve, ul. Sovetskaya 187, Maikop, 385000 ***Russia****,* *hookeria@mail.ru*
Eskina T.G.
Caucasian State Nature Biosphere Reserve, ul. Sovetskaya 187, Maikop, 385000 ***Russia****,* trepet71@mail.ru

The ratio between number and the mean frequency of plant species in closed subalpine herbaceous and scrub communities, open plant communities of the alpine screes and low-mountain shoals along rivers, closed and open synanthropic communities on the Western Caucasus were analyzed. The frequency of species was valued in 0.5 m^2 squares within 15-25 m^2 plots. The results show that the ratio between species richness and the mean frequency of species can be defined by different process and be different in plant communities formed by species with different (C-, S- or R-) population strategy types.

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The relationship between number and the mean density (frequency) of species in communities not often becomes the subject of the special analysis in spite of the fact that this ratio can be defined different process and be their indicator.

So, possible expect that type of this ratio in communities is in some degree defined by their organization model. In particular, Cornell and Lawton have separated communities on two groups: interactive and non-interactive (Cornell & Lawton 1992; Cornell 1993). The interactive community is one in which strong interactions take place among species at the same trophic level within a local habitat. In the non-interactive community, species are characterized by feeble or absent interactions, and the population dynamics of each species is completely independent of others. Niches in such communities always remain and colonization their by new species is a random process, independent of the number of species already present (Cornell & Lawton 1992; Cornell 1993; Caswell & Cohen 1993). In Cornell's opinion, non-interactive communities are likely to be common in extreme environments with substantial numbers of open niches, created by reduced population levels due to fluctuations in the abiotic environment.

According to the polymodal concept of plant community organization by Mirkin (1994), communities with intensive interactions among plants (for example, the woods and the meadows) belong to C-S- or C-R-S- models (C – «competitors», S – «stress-tolerators» and R – «ruderals»: Grime, 1977). The communities with non-intensive interactions – 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 of high productive habitats).

In this connection possible expect, that reduction of the species richness in interactive communities (C-S- or C-R-S- models) can be caused by reinforcement in interspecific competition. For example, when the environment quality and/or amount of available resources decreases or when less competitive dominant are replaced by more competitive one (Currie, Paquin, 1987; Wright et al., 1993; Francis, Currie, 1998; McKane et al., 2002; Akatov et al., 2010). Known that communities formed in severe conditions usually are be characterized by the relatively high dominance level and the pattern of the species abundance, corresponding of the geometrical model (Whittaker 1975; Magurran, 1983). This implies that as environmental quality decrease, the competitive asymmetry among the species must increase. Correspondingly, abundance of dominant species must increase, but their frequency must remain unchanged (100%). Other species of these communities (in order of their ranks) begin to utilize greater proportions of available resources, but the absolute density of these plants must decrease. In this case communities with low species richness must be characterized by lower mean frequency of species, than communities with larger number of species (the first scenario) (Akatov, Chefranov, 2014).

The composition of species on sites of non-interactive communities (S-and R- models) represents a random sample from the species pool of the communities and the occurrence of these species in test plots depends on their biological features as well as by many other factors, mainly abiotic, and therefore is a random event (Cornell, 1985, 1993; Ricklefs, 1987; Zobel et al., 1998). In case when populations vary independently within the communities mean frequency of species should remain unchanged as species richness decreases, while the amplitude variation of values of this parameter should increase, since the high richness reduces variability of cenotic parameters through statistical averaging (Tilman et al., 1998; Stevens et al., 2003; Akatov et al., 2013) (the second scenario).

Besides, reduction species richness of communities can be accompanied by density compensation – an increase in the density (frequency) of remaining species conditioned by the improvement of resource supply and alleviation of interspecific competition (MacArthur et al., 1972) (the third scenario). This effect was initially considered to be characteristic mainly with insular (isolated) biotopes (Crowell, 1962; MacArthuret al., 1972). Subsequently it was attributed to factors such as evolutionary youth of communities, their pollution or fragmentation, climate warming, extreme environmental conditions (Hawkins et al., 2000; Dulvy et al., 2002; Kaspari et al., 2003; Chernov, 2005; Belyuchenko, 2005; Morozov, 2009; Gonzalez and Loreau, 2009; Longino and Colwell, 2011). In particular, Kaspari et al. (2003) find that the average density of and species populations in the tropical desert and rain forest habitats of New World is lower than in other biomes. They proposed that these habitats were less likely to disappear during recent glaciation’s events or their populations have faster evolutionary clocks. Chernov (2005) expressed a opinion, that high population abundance in species-poor communities of extreme habitats of tundra and polar deserts can be connected with compensatory phenomena. In Tomiałojć’s opinion, compensatory dynamic is common among plant and animal assemblages which underwent synanthropization (Tomiałojć, 2000).

The purpose of our study is to show how the ratio between number and the mean frequency of species in plant communities of the Western Caucasus differentiate and to define possible reasons of these differences. In particular, we wanted to define whether this ratio is connected with organization model of communities.

Material and methods

Objects of study

The objects of the study were open and closed herbaceous and scrub communities growing in natural (seminatural) and anthropogenic habitats in the low altitude, subalpine and alpine belts of the Western Caucasus, Russia (42°48' - 44°03' N, 39°08' - 44°06' E; altitude: 50-2600 m above sea level). The factual material on natural alpine and subalpine communities was collected in the Caucasian State Nature Biosphere Reserve on the mountain ridges and massifs of the Belaya, Malaya Laba and Bolshaya Laba river basins. In the alpine belt (2300-2600 m above sea level) descriptions were made of the open plant communities of the alpine stable and unstable screes (assoc.: *Veronico minutae-Chaerophylletum humilis* Onipchenko 2002, *Campanulo ciliatae–Chamaesciaduium acaulis* Onipchenko et Minaeva 2002, *Heliantemetum cani* Ermolaeva 2007, according to Onipchenko, 2002 and Ermolaeva, 2007). In the subalpine belt (1700-2450 m) descriptions were made of the communities of mesophytic meadows (assoc. *Betonici macranthae_Calamagrostietum arundinaceae* Onipchenko 2002, according to Onipchenko, 2002) and areas with a long snow period: snowbed meadows (*Hedysaro caucasicae_Geranietum gymnocauli* Rabotnova 1987, according to Onipchenko, 2002) and *Rhododendron caucasicum* scrub communities (assoc. *Lerchenfeldi_Rhododendretum caucasici* Onipchenko et Sennov 2002, according to Onipchenko, 2002). In the low altitude belt (40-250 m) we described closed communities of areas exposed to trampling and motor traffic within the city limits and vicinities of Maikop and Krasnodar, the open communities on shoals of four mountain rivers (Shepsi, Psezuapse, Zapadnyi Dagomys, Belaya) and on annual crop fields (Belaya river basins).

Plant communities of alpine stable and unstable screes are both at successional stages and climaxes in extreme environmental conditions. They are characterized by low plant cover (3-60%), “primitive” structure and feeble or absent species interactions. Several species of these communities occur only on scree habitat (*Dentaria bipinnata* C.A.Mey., *Lamium tomentosum* Willd., *Oxyria digyna* (L.) Hill, *Veronica minuta* C.A.Mey. et al), while the remainer are found in other alpine communities as well (*Carum caucasicum* (Bieb.) Boiss., *Seseli alpinum* Bieb., *Festuca ovina* L., *Pedicularis caucasica* Bieb., *Viola altaica* Ker-Gawl., *Anthoxanthum odoratum*

L., *Polygonum bistorta* L., *Alchemilla retinervis* Bus., *Luzula multiflora* (Ehrh.) Lej., and others). According to the polymodal concept of plant community organization by Mirkin (1994), communities of alpine screes should be belonging to S- or S-R- models.

The meadows, snowbed and scrub communities of subalpine belt are presumably interactive. The main dominants of these communities (*Festuca woronowii*, *Geranium gymnocaulon* DC, *Hedysarum caucasicum* M.Bieb., *Alchemilla retinervis* Buser aggr., *Rhododendron caucasicum*) have large biomass, the high seed production, large seeds and low relative growth rate, which corresponds to the C-strategy. Other species pronounce features of the S- or R-strategy (Onipchenko et al., 1998). Therefore, these communities should be belonging to C-S- or C-R-S- models. Snow accumulation is the main controlling factor of the number and composition of species on their sites.

The closed communities of areas exposed to trampling and motor traffic include mostly species with S- and R-population strategies (*Polygonum arenastrum, Trifolium repens, T. pretense*, *Oxalis stricta, Acalypha australis,* *Convolvulus arvensis* and others). Consequently, these communities can be referred to S-R models. The annual crop fields are frequently disturbed high productive habitats. Therefore, plant communities of these habitats should be belonging to R-models. Finally, shoals of rivers are frequently disturbed, but low productive habitats. Open plant communities of these habitats include species occurring in the surrounding seminatural (*Pyrethrum parthenifolium* Wild., *Stachys officinalis* (L.) Trev, *Geranium robertianum* L., *Linaria pontica* Kuprian., *Hedera helix* L., *Galega officinalis* L. and others) and synanthropic (*Convolvulus arvensis* L., *Crepis setosa* Hall. fil., *Verbena officinalis* L., *Plantago major* L. and others) communities. We suppose that these communities can be referred to R-S-models.

Field sampling

The descriptions of open plant communities of the alpine screes were made in 25 m^2 plots in which 10 small plots (0.5 m^2) were laid down in a regular pattern. The descriptions other communities were performed using 15 (16) m^2 plots, each containing 20 small plots (0.5 m^2) formed by a regular method. The vegetation in the large and small plots was examined to record all plant species and visually evaluate the total coverage of the herbaceous layer and the coverage of individual species, which was expressed in grades: (1) 1–25%, (2) 26–50%, (3) 51–75%, and (4) 76–100%). The descriptions were used as a basis for calculating the following indices: *N* – the number of plant species per 15-25 m^2 plot; *F* – the average frequency of subordinate species in 0.5 m^2 plots within a 15-25 m^2 plot (expressed as a decimal fraction); *C* – the total coverage of vascular plant and *Cd* – the coverage of dominant species in grades. The total number of descriptions was 267, including 97 for alpine screes, 52 for closed subalpine and 21 for closed synanthropic communities, 72 for river shoals, 25 for annual crop fields.

We used statistical tests (the least squares regression method and Pearson correlation coefficient) to estimate the fit of field data to different scenarios of relationship between number and the mean frequency of species in plant communities.

Results and Discussion

The average values of species richness (*N*), mean frequency of plant species (*F*) and the coverage of dominant species (*Cd*) in plant communities of different types are given in Tables 1 and 2. The relationships between these parameters are illustrated in Figure 1, 2 and Table 3.

Table 1. Description of closed herbaceous and scrub communities

Communities; elevation a.s.l., m (no. of plots)	Dominant and constant species*	*N*	*F*	*Cd*
mesophytic meadows; 1700-2450 (22)	*Calamagrostis arundinacea, Festuca woronowii, Bromopsis variegata, Poa longifolia, Brachypodium rupestre, Geranium sylvaticum, Anemone fasciculata*	38.4 (15-51)	0.46 (0.34-0.58)	1.8 (1-3)
snowbed meadows; 1920-2100 (20)	*Geranium gymnocaulon, Alchemilla retinervis, Inula grandiflora, Phleum alpinum, Chaerophyllum rubellum, Rumex alpestris, Anthoxanthum odoratum*	16.9 (5-32)	0.41 (0.27-0.58)	3.5 (2-4)
with *Rhododendron caucasicum*; 1940-2340 (12)	*Rhododendron caucasicum, Vaccinium myrtillus, Oxalis acetosella, Lerchenfeldia flexuosa, Polygonum carneum, Alchemilla retinervis, Solidago virgaurea*	7.9 (3-16)	0.38 (0.28-0.55)	4.0 (4-4)
closed synanthropic; 40-500 м (21)	*Polygonum arenastrum, Trifolium repens, Lolium perenne, Poa trivialis, Convolvulus arvensis, Plantago lanceolata, P. major, Taraxacum officinale, Chenopodium album*	15.8 (5-30)	0.42 (0.26-0.69)	3.2 (1-4)

* Species names are given according to: Zernov, 2006.

Table 2. Description of open herbaceous communities

Communities; elevation a.s.l., m (no. of plots)	Constant species*	*C*	*N*	*F*
on stable screes; 2300-2600 (34)	*Dentaria bipinnata, Corydalis alpestris, Saxifraga sibirica, Oxyria digyna, Chaerophyllum humile, Lamium tomentosum*	3-10	4.7 (1-9)	0.47 (0.12-0.97)
on unstable screes; 2400-2500 (63)	*Oxyria digyna, Veronica telephiifolia, Corydalis alpestris, Draba scabra, Myosotis alpestris, Carum caucasicum, Alchemilla retinervis*	3-60	10.8 (2-25)	0.39 (0.15-0.70)
on shoals; 50-200 (72)	*Polygonum persicaria, Petasites albus, Setaria viridis, Ambrosia artemisiifolia, Erigeron annuus, Bidens frondosa*	5-25	14.2 (5-26)	0.26 (0.12-0.48)
on annual crop fields; 180-220 (25)	*Convolvulus arvensis, Chenopodium polyspermum, Cynodon dactylon, Ambrosia artemisiifolia, Phalacroloma septentrionale*	10-80	20.3 (11-34)	0.40 (0.32-0.50)

* Species names are given according to: Zernov, 2006.

Table 3. The relationship between the mean frequency of species (*F*) and the species richness (*N*) in studied plant communities

Communities	no. of plots	Independent variables	R^2	*r*	*P*
closed subalpine	52	ln *N*	0.164	0.405	<0.01
on screes	97	*N*	0.010	-0.102	-
closed synanthropic	21	*N*	0.046	-0.214	
on shoals	72	*N*	0.132	-0.363	<0.01
on annual crop fields	25	*N*	0.317	-0.563	<0.05

As follows from Tables 1, among closed communities of subalpine belt species diversity reaches the highest level in the mesophytic meadows, then in decreasing order, snowbed meadows and *Rhododendron caucasicum* scrub communities. In addition, this Table demonstrates that the coverage of dominant species (*Cov*) grows as the species richness of communities (*N*) decreases. As follows from Figure 1A and Tables 3, the correlation between species richness (ln*N*) and mean frequency of plant species (*F*) is weak positive, but significant.

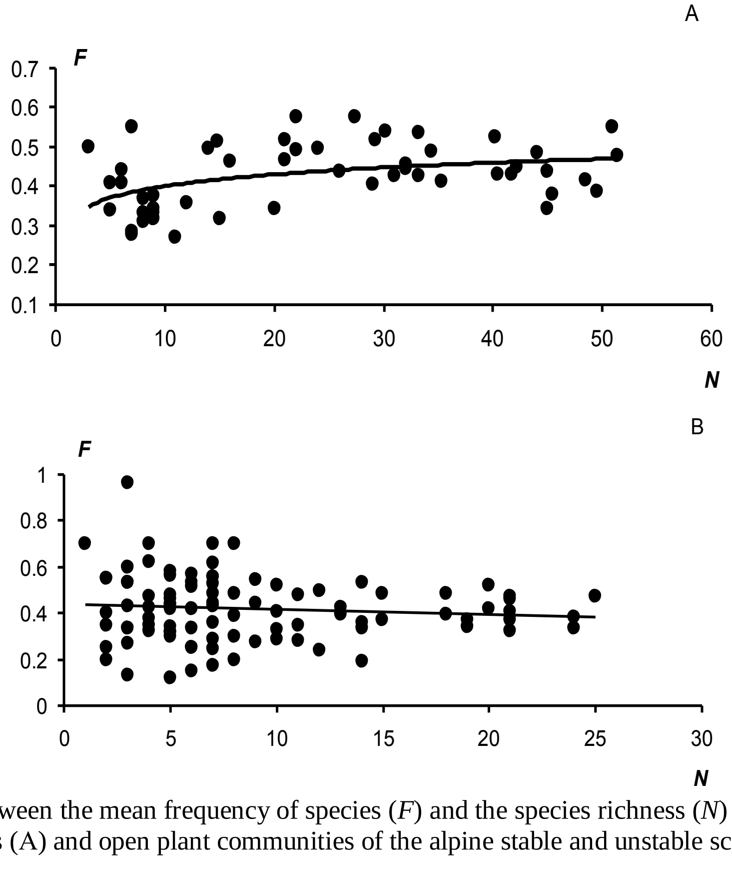

Figure 1. The relationship between the mean frequency of species (*F*) and the species richness (*N*) for closed subalpine plant communities (A) and open plant communities of the alpine stable and unstable screes (B).

Figures 1B, 2A and Table 3 show that: 1) there is no significant correlation between species richness (*N*) and mean frequency of plant species (*F*) in open plant communities of alpine screes and closed synanthropic communities; 2) the amplitude of variation in *F* values is higher in species-poor communities, than in species-rich communities.

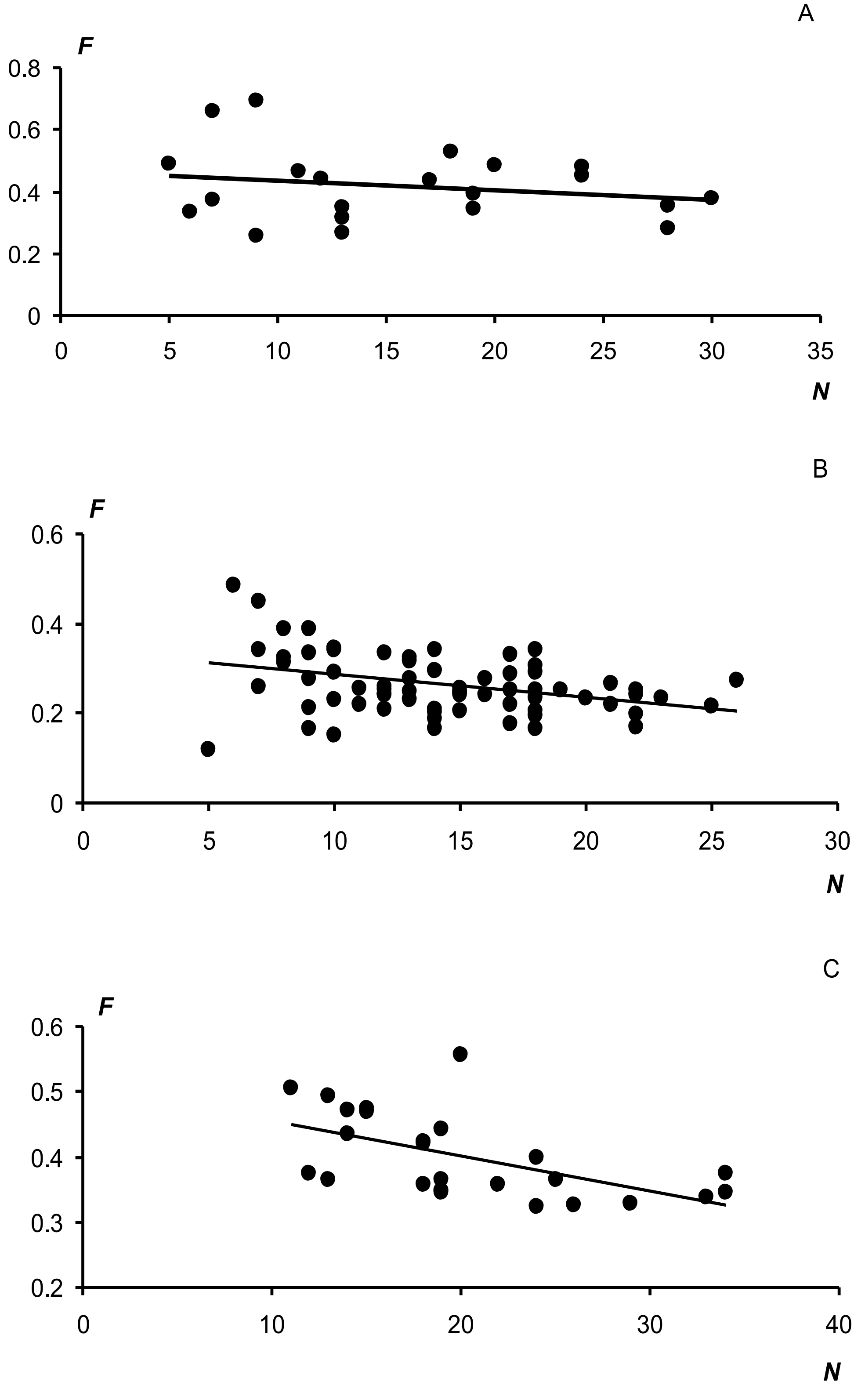

Figure 2. The relationship between the mean frequency of species (*F*) and the species richness (*N*) for plant communities of the low altitude belt (A – on areas exposed to trampling and motor traffic, B – on shoals of mountain rivers, C – on annual crop fields).

As follows from Figure 2B and Tables 3, there is weak negative correlation between *N* and *F* in the open plant communities of river shoals. Figures 2B also show that as *N* decreases, the amplitude variation of values *F* increases.

Figure 2C and Table 3 demonstrate a significant negative correlation between the species richness (*N*) and the mean frequency of plant species (*F*) in the plant communities of annual crop fields. Thus, the mean frequency of plant species (*F*) is higher in species-poor communities of this type than in species-rich ones. Figure 2C also shows that the amplitude of variation in *F* values is not greatly higher in species-poor communities, than in species-rich communities.

Thus, we find that relationship between number and the mean frequency of species in plant communities of the Western Caucasus is different and this difference can be connected with organization model. In particular, in closed communities of C-S- or C-R-S- models, reduction of the species richness is accompanied by some decrease in the mean frequency of species. The species-poor open alpine communities end closed synanthropic communities of S- or S-R- models are characterized by high variation of the mean frequency of species. In open communities of *R*- model reduction of the species richness is accompanied by significant increase in the mean frequency of species; in open communities of *R-S*- models – as some increase in *F* values, so and increase amplitudes of their variation.

Comparison of the observed *N/F* relationships with expected ones, corresponding to one of three considered above scenarios, allows us to do some suggestions. In particular, our results allow to assume that in studied closed subalpine communities (C-S- or C-R-S- models) the frequency of species are mainly determined by biotic interactions; in open alpine and closed synanthropic communities (S- or S-R- models) – by random processes; in open communities of river shoals (*R-S*- models) – by random and compensatory processes; in the segetal communities (*R*- model) – mostly by compensatory processes.

The observed differences can be connected as with peculiarity of factors, limiting species richness of communities, so and with special features of species with different population strategies. So, comparatively low mean frequency of species in species-poor communities of C-S- or C-R-S- models can be conditioned by ability of species with C-strategy to intensify competitive advantage over other species in the response to decrease in the environment quality and/or the amount of available resources. The high variation of values of this parameter in species-poor communities of S- or S-R- models – relatively independent population dynamic of species with S-strategy and them slow reaction to resource availability. The relatively high mean frequency of species in species-poor communities of *R*- model – them rapid reaction to resource availability on frequently disturbed high productive habitats (Onipchenko et al., 1998).

Conclusion

Thus, our results demonstrate that the relationship between number and the mean frequency of species in plant communities of the Western Caucasus with different organization models is different and it can be connected with special features of species with different population strategies. If this conclusion proves to be correct, then given relationship can be used as indicator of the processes defining the pattern of the species abundance in communities. For example, our results have not confirmed the suggestion that extreme conditions itself can be a reason of density compensation in natural plant communities. Besides, it is possible to assume that relatively high average values of species frequency in some low-diversity closed synanthropic communities are more likely accounted for by random rather than compensatory processes. However, it is necessary to note that the models of studied communities were determined with approximation and our results are based on factual material limited in volume and geography. Therefore additional work it needed in this direction.

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REFERENCES

1. Akatov V.V., Akatova T.V., Eskina T.G., Sazonets N.M., Chefranov S.G. Is there a density compensation effect in plant communities of anthropogenic habitats? // Russian Journal of Ecology. 2013. V. 44. № 6. P. 445–454.

2. Akatov V.V., Chefranov S.G., 2014 Density compensation effect in arboreal communities of the West Caucasus // Zh. Obshch. Biol., V. 75. № 1. P. 48–61 (*in Russian*).

3. Caswell, H. & Cohen, J. E. 1993. Local and regional regulation of species - area relations: a patch - occupancy model. pp. 99-108. In: Ricklefs, R. E. & Schluter, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Chicago University Press, Chicago.

4. Chernov, Yu.I. Species diversity and compensation phenomena in communities and biological systems // Zool. Zh. 2005. V. 84. № 10. P. 1221–1238 (*in Russian*).

5. Cornell, H. V. 1985. Species assemblages of cynipid gall wasps are not saturated. The American naturalist 126: 565-569.

6. Cornell, H. V. 1993. Unsaturated patterns in species assemblage: the role of regional processes in setting local species richness. pp. 243-253. In: Ricklefs, R. E. & Schluter, D. (eds), Species diversity in ecological communities: historical and geographical perspectives. Chicago University Press, Chicago.

7. Cornell H. V. & Lawton J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal 0f Animal Ecology 61: 1-12.

8. Crowell K.L. Reduced interspecific competition among the birds of Bermuda // Ecology. 1962. Vol. 43. P. 75–88.

9. Currie, D.J. & Paquin, V. 1987. Large – scale biogeographical patterns of species richness of trees. Nature 329: 326-327.

10. Dulvy, N.K., Metcalfe, J.D., Glanville, J., et al., Fishery stability, local extinctions, and shifts in community structure in skates, *Conserv. Biol.*, 2002, vol. 14, pp. 283–293.

11. Francis, A., Currie, D. J. 1998. Global patterns of tree species richness in moist forests: another look. Oikos 81: 598-602.

12. Gonzalez A., Loreau M. The Causes and Consequences of Compensatory Dynamics in Ecological Communities // Annu. Rev. Ecol. Evol. Syst. 2009. Vol. 40: P. 393–414.

13. Grime J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory // Am. Nat. Vol. 111. № 982. P. 1169-1194.

14. Hawkins, C.P., Norris, R.H., Hogue, J.N., and Feminella, J.W., Development and evaluation of predictive models for measuring the biological integrity of streams, *Ecol. Appl.*, 2000, vol. 10, pp. 1456–1477.

15. Kaspari M., Yuan M., Lecanne A. Spatial grain and the causes of regional diversity gradients in ants // Amer. Natur. 2003. Vol. 161. № 3. P. 459–477.

16. Belyuchenko I.S. Evolutionary and ecological approaches to the plants introduction in practice / I.S. Belyuchenko // The North Caucasus Ecological Herald, 2005. V. 1. № 2. C. 104–111.

17. Longino J.T., Colwell R.K. Density compensation, species composition, and richness of ants on a neotropical elevational gradient // Ecosphere. 2011. Vol. 2(3):art29. doi:10.1890/ES10-00200.1

18. MacArthur R.H, Diamond J.M, Karr J.R. Density compensation in island faunas // Ecology. 1972. Vol. 53. P. 330–342.

19. Magurran, A. E. 1983. Ecological Diversity and its measurement. Univ. Press Cambridge.

20. McKane, R.B., Johnson, L.C., Shaver, G.R., et al., Resource-Based Niches Provide a Basis for Plant Species Diversity and Dominance in Arctic Tundra, *Nature*, 2002, vol. 415, pp. 68–71.

21. Mirkin 1994 Which plant communities do exist? // J. Veget. Sci. V.5. № 2. P. 283-284.

22. Morozov N.S. 2009. A city as an object for synecological studies: a search for density compensation among birds breeding in urban woodlands // Species and Communities in Extreme Environments *Festschrift towards the 75th Anniversary and a Laudatio in Honour of Academician Yuri Ivanovich Chernov*, Yu.I. Chernov), Babenko, A.B., Matveeva, N.V., Makarov, O.L., Golovach, S.I., Eds., Pensoft Publishers & KMK Scientific Press Sofia–Moscow. pp. 459-520.

23. Onipchenko, V. G. 2002. Alpine vegetation of the Teberda Reserve, The Northwestern Caucasus. Veroffentlichungen des Geobotanischen Institutes der ETH, Stifung Rubel, Zurich.

24. Onipchenko V.G., Semenova G.V., van der Maarel E. Population strategies in severe environments: alpine plants in the northwestern Caucasus // J. Veg. Sci. 1998. Vol. 9. P. 27–40.

25. Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science 235: 167-171.

26. Stevens M.H.H., Petchey O.L., Smouse P.E. Stochastic relations between species richness and the variability of species composition // Oikos. 2003. Vol. 103. P. 479–488.

27. Tilman D., Lehman C.L., Bristow C.E. Diversity stability relationships: statistical inevitability or ecological consequence? // Am. Nat. 1998. Vol. 151. P. 277–282.

28. Tomiałojć, L. (2000). An East-West gradient in the breeding distribution and species richness of the European woodland avifauna. – Acta Ornithologica. 35: 3-17.

29. Whittaker R., 1975. Communities and Ecosystems, New York: Macmillan.

30. Wright, D.H., Currie, D.I., and Maures, B.A., Energy Supply and Patterns of Species Richness on Local and Regional Scales, in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D., Eds., Chicago: Univ. Chicago Press, 1993, pp. 66–75.

31. Zernov A.S., Flora Severo_Zapadnogo Kavkaza (The Flora of the Northwestern Caucasus), Moscow: KMK, 2006 (*in Russian*).

32. Zobel, M., van der Maarel, E. & Dupre, C. 1998. Species pool: the concept, its determination and significance for community restoration. Applied Vegetation Science 1: 55-66.