"Mass-effect" in alpine communities of the Northwestern Caucasus

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4. "Mass-effect" in alpine communities of the Northwestern Caucasus

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4.1. INTRODUCTION

Spatial heterogeneity in plant communities has several causes, e.g. environmental heterogeneity, several characteristics of plants (distribution, growth, life cycle), interactions between plants and random factors (WATT 1947, WHITTAKER 1970, RABOTNOV 1983).
Many researchers attribute the coexistence of species and their spatial pattern to environmental heterogeneity (GRUBB 1977, SOHLBERG and BLISS 1984, CHUYO 1985). If the environment is more or less homogeneous, the theory of mass effect (SHMIDA and ELLNER 1984, WILSON 1990), i.e. the pool of diasporas from neighbouring habitats supporting populations of rare species and increasing the species variety within a community, is very useful.
The direct measuring of mass effect can be a complex matter. SHMIDA and ELLNER (1984) suggested that mass effect within a community exists if a significant difference in the floristic similarity between plots is found. In this case two neighbouring plots should be more similar than two remote ones.
The proposition is presented that the idea of mass effect can be especially useful when investigating different communities situated close to each other, e.g. for high mountain communities as in the present case. There have been only few investigations of horizontal structure in alpine communities. The aim of this work is the comparision of the horizontal structure of different types of alpine communities under consideration of the mass effect hypothesis.

Acknowledgement
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We also acknowledge the help received from M. Blinnikow, who made useful comments on the text.

4.2. METHODS

4.2.1. Field methods

The investigations were carried out during the summer of 1990 at the high mountain station of Moscow State University in the Teberda reserve. Five sample areas, 25 m^2 each (Fig. 4.1), were laid out within each of four community types, namely alpine lichen heaths (ALH), *Festuca varia* dominated grasslands (FVG), *Geranium gymnocaulon-Hedysarum caucasicum* meadows (GHM) and snow bed communities (SBC). Descriptions of the studied communities are given in Chapter 1.4. The sides of the areas were oriented along the slope. Each area was divided into one hundred square plots (50x50 cm). The plots were arranged in horizontal and vertical rows. The 52 plots within the sample areas (Fig. 4.1) were checked for the presence or absence of all vascular plant species.

4.2.2. Analysis data

For the analysis of our data, the following was obtained:

1. Dependence of floristic similarity between plots on the distance between them. The coefficient of similarity (the Sorensen's coefficient) was calculated to estimate floristic similarity between each pair of plots. The distances between small plots were subdivided into 8 classes. The first class comprised plots 0.5 m apart, the second from 0.5-1 m, the third from 1-2 m, and so on. The average value of Sorensen's coefficient was calculated for each class of distance. The correlation between the average similarity coefficient and the distance class is depicted in a graph.

Table 4.1. Floristic diversity of the alpine communities (average number of species on different plots) and total number of species on five sample plots.
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities.

	plot size				
	0.5 x 0.5 m		5 x 5 m		
type of community	average	standard error	average	standard error	total number of species
SBC	11.6	0.18	23.0	0.15	31
ALH	17.8	0.43	33.0	0.47	42
GHM	17.0	0.6	41.2	2.9	66
FVG	9.2	0.7	41.2	2.2	79

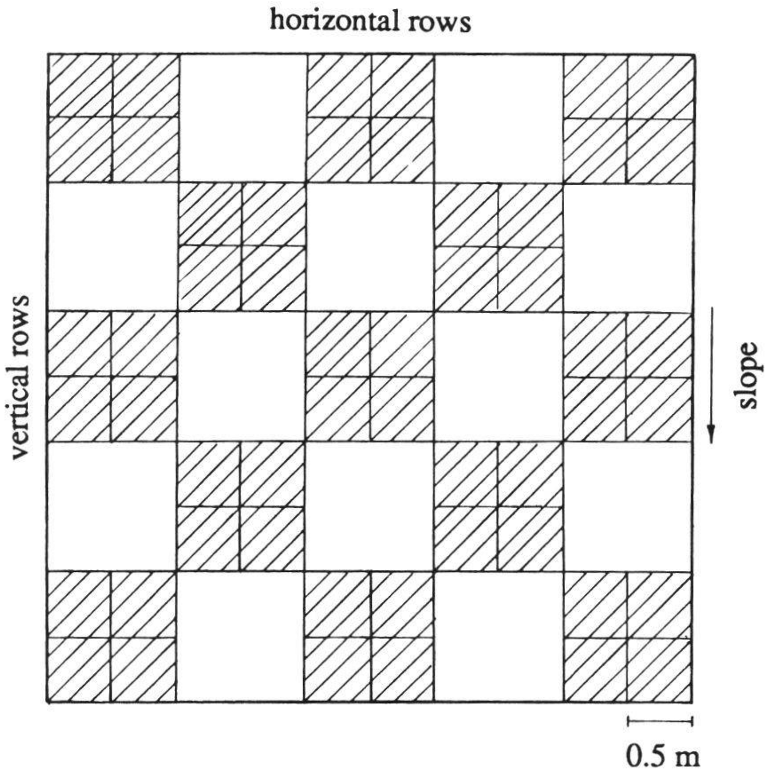

Fig. 4.1. The scheme of the sample area. Only shaded plots were studied.

2. Distribution of plant species among five Raunkiaer's frequency classes. The average frequencies of plant species was calculated for each community type.
3. Besides community structure estimations, the Euclid distance between sample areas within each community type, floristic diversity of the plots and the total number of species on the sample areas were calculated.

4.3. RESULTS

4.3.1. Floristic richness

Table 4.1 displays the floristic diversity values and the total number of species found in each community type. The poorest community type is SBC and the richest FVG. Nevertheless, for small plots, the highest number of species was found on ALHs. The same results were obtained by ONIPCHENKO and SEMENOVA (1988).

A positive correlation between the number of species and the degree of heterogeneity of community spatial structure can be expected. Then the greater the number of species the more heterogeneous the community structure will be. Thus the least heterogeneous community type should be SBC. This assumption can be compared with obtained results, shown in Fig. 4.2.

4.3.2. Degree of heterogeneity

Figure 4.2 represents the dependence of floristic similarity on the distance between plots. This dependence is different in the four studied community types. The inclination of the curve shows the degree of heterogeneity of community structure. In view of the supposed connection between the heterogeneity of structure and mass effect, the steeper the curve, the more important the mass effect is for this type of community. Thus these curves enable an estimation of the degree of mass effect.

The two-way analysis of variance has demonstrated the significant influence of the community type and the distance between plots on floristic similarity. The ALHs and SBCs have the most gently sloping curves. These types of communities are the most homogeneous of those studied, and the species of these communities are equally distributed within them. However, the SBC curve falls more rapidly than that of the ALH. We will discuss the reasons for this later.

Table 4.2. Average floristic similarity (SORENSEN's coefficient, %) between plots in vertical (v) and horizontal (h) rows of sample areas.
ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities.

community type	row	distance between centres of plots, m 0.5	1.5	2.0	2.5	3.5	4.0	4.5
ALH	v	81.8	78.0	78.4	77.8	74.6	75.8	75.6
	h	79.8	78.2	77.6	76.6	77.2	75.4	74.8
FVG	v	62.4	51.2	52.0	51.0	44.6	47.4	48.2
	h	61.0	53.8	52.2	51.2	45.2	48.0	51.6
GHM	v	73.2	67.0	67.0	66.0	63.8	63.2	61.6
	h	72.6	68.0	66.4	65.0	65.2	64.0	62.6
SBC	v	82.8	76.2	76.2	75.2	71.2	72.4	72.0
	h	81.6	77.4	75.6	73.2	69.4	71.4	71.4

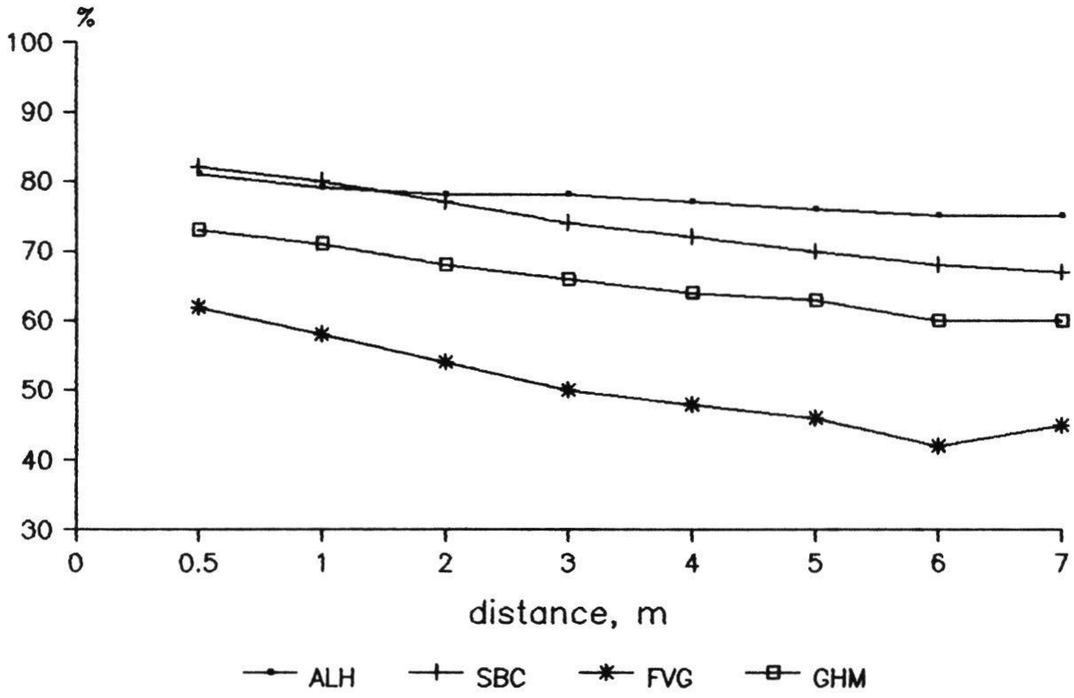

Fig. 4.2. The floristic similarity as a function of distance between plots.
X-axis = distance (m) between small plots, Y-axis = average value of SORENSEN's coefficient (%). ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities.

The FVG possesses the steepest curve, which shows the highest level of heterogeneity of horizontal structure. The curve for GHM lies slightly higher. The results allow the conclusion, that the mass effect is most important for FVG, and least important for ALH. We can see, that these results do not precisely coincide with the assumption presented above.

4.3.3. Dependence on orientation along slope

As mentioned before, the large plots were oriented along the slope. It is suggested, that the distribution of diasporas depends on the slope processes. Then the large part of the diaspora pool will flow down the slope. Therefore, the degree of mass effect should differ in two directions; along the slope and across it.

So the comparison of floristic similarity values for vertical and horizontal rows of plots may say if mass effect depends on orientation. In this case two plots, one below the other, would have different coefficients of similarity than two plots on the same level. However, no significant differences were found

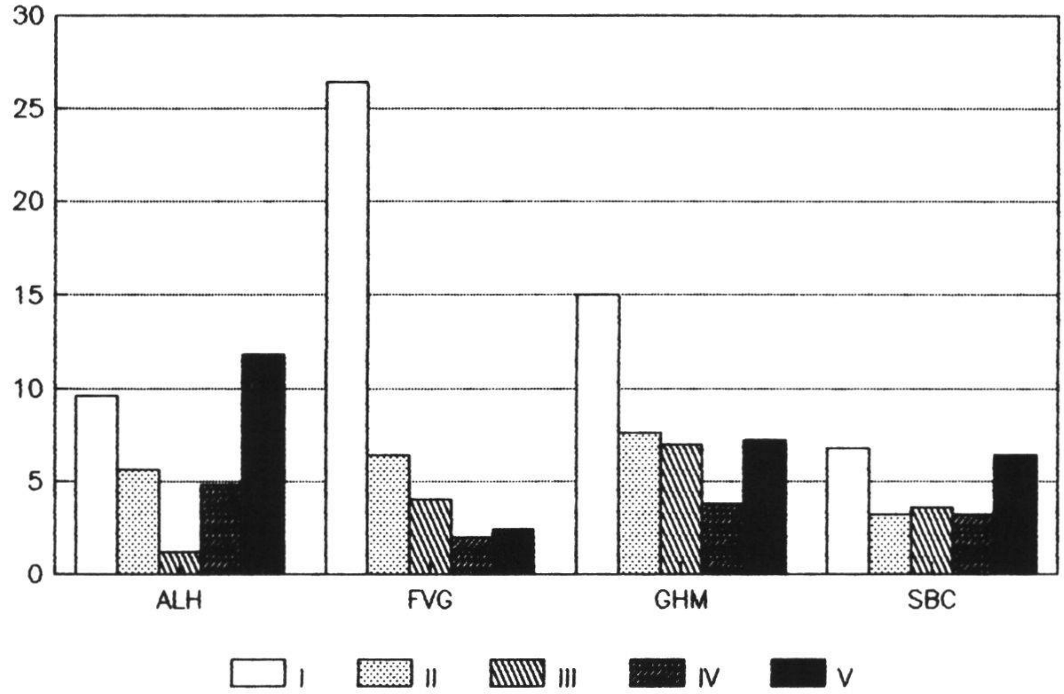

Fig. 4.3. The distribution of species among RAUNKIAER's frequency classes. Y-axis = number of species. Frequency classes of RAUNKIAER: I = 0-20%, II = 20-40%, III = 40-60%, IV = 60-80%, V = 80-100%. ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon - Hedysarum caucasicum* meadows, SBC = snow bed communities.

(Tab 4.2). The obtained results are even more interesting, as the studied communities are situated on the slopes of different steepness from 1-3 up to 40 degrees.

4.3.4. Distribution among frequency classes

The studied community types have differing species distribution values among five Raunkiaers's classes of frequency (Fig. 4.3). FVGs are characterized by a low number of species with a high frequency and a considerable number of species with low frequency. SBCs and ALHs possess many species with high frequencies. Species of medium frequency (III class) are comparatively common in GHMs.

4.3.5. Results of Euclid distance calculating

An interesting body of results was obtained by the calculation of Euclid distance between sample areas within one community. It enabled the evaluation of variation within a community. The FVGs were the least variable, which means that the sample areas were more uniform there than the plots. The similar results are found in PALMER (1990).

4.4. DISCUSSION

Based on the present research alpine community types of the Northwestern Caucasus can be characterized in the following way.

ALHs are polydominant communities, developing under the severe, snow free conditions of mountain crests (GRISHINA et al. 1986). The floristic diversity of the plots is quite high here, and there are many species with a high frequency. These communities are most homogeneous among the four studied types, and the mass effect is negligible.

The following explanation for this phenomenon is suggested: The species belonging to this community are equally distributed because the low height and only slight competitive ability of these plants set no obstacles for the settlement of the species of this community. Still, this assertion is correct perhaps only on a large scale, e.g. our sample area. In contrast, the presented data (Chapter 8) allow the statement that root competition of ALH plants can prevent other plants from growing in ALHs. Severe conditions prevent the invasion of plants from the neighbouring communities, so mass effect is negligible. There were some observations that the severe environmental conditions can be the greater on influence the establishment of seedlings than competition (see RYSER 1990).

FVGs are highly productive monodominant communities dominated by large tussocks grasses. They are the richest in species, but there are only few species with a high frequency. FVGs are the least homogeneous among the studied communities, thus the mass effect is strongly expressed there. We suppose, that the main dominants, *Festuca varia* and *Nardus stricta*, which form a tough sod, prevent other species from settling in the community. It is possible, that the input of diasporas from neighbouring communities, i.e. mass effect, can enable many species with low frequencies to survive on FVGs. These species, spreading vegetatively, form patches scattered among *Festuca* and *Nardus* tussocks. Burrowing activity of rodents and other mammals (FOMIN et al. 1989), although not very intensive here, can ease the survival of such species.

The GHM is another example of the alpine community type with a high pro-

duction and a considerable total number of species. Species with a middle frequency prevail here. Burrowing activity of animals has a great effect on this community type (FOMIN et al. 1989). The dominants, *Geranium gymnocaulon* and *Hedysarum caucasicum*, which produce a high phytomass (ONIPCHENKO 1990), may prevent settlement of other species. Although this community is rather heterogeneous, the degree of mass effect here is lower than that on FVGs. We suspect, that intensive disturbance caused by digging animals, lowers the impact of dominating species, and facilitates the settlement of the territory by other plant species. Investigations of mountain communities with differing degrees of disturbance were also conducted by LEPS and STURSA (1989). In the latter work, different results were obtained. For example, they show that the most disturbed community has the lowest number of species on small plots and the highest on large ones. Thus the authors conclude that disturbance leads to more heterogeneity, contrary to the present supposition and other works on the subject. The vegetation of SBCs must withstand a very short vegetation season (ONIPCHENKO et al. 1987). This community type is the poorest in species, yet it is less homogeneous than the ALH. This fact may be explained as caused by a slight difference in the time of snow melting during the vegetation season, which significantly effects the SBC structure.
Among other factors responsible for the heterogeneity of the community structure, the complexity of soils (OLSVIG-WHITTAKER 1988) must be mentioned. Unfortunately, no data is available at the time which takes this factor into account.

SUMMARY

Four alpine communities of the Northwestern Caucasus differ considerably from each other in the principal features of their horizontal structure.
Alpine lichen heath with predominance of fruticose lichens and snow bed communities with predominance of rosette forbs are communities which develop under severe conditions. "Mass-effect" has no great influence on the spatial structure of these phytocoenoses. The alpine grasslands are monodominant communities with predominance of large tussock plants. Here, "mass-effect" is an important factor in maintaining species diversity. The meadows take the intermediate position, in which the digging activity of animals plays a very important role, possibly decreasing that of "mass-effect" there.
The degree of mass-effect does not significantly depend on orientation to the slope. Thus, the floristic similarity/distance dependence closely corresponds to species distribution among Raunkiaer's classes of frequency. On the other hand, structural heterogeneity does not strongly depend on the number of species.
The method used in this work seems very promising and could prove a useful tool in the study of the spatial structure of vegetation.