Does "semi-island effect" influence on the species richness in subalpine plant communities of Mount Bolshoy Tkhach (Western Caucasus)?

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If Equilibrium theory (MacArthur, Wilson, 1963) is correct, species richness in communities should be dependent on extinction and colonization rates. If the communities are relatively isolated and small, the probability of extinction of their typical plant species will be high, and probability of recolonization will be low. Species richness in these communities seldom reaches an upper limit and is unsaturated (Terborgh, Faaborg, 1980; Akatov, Akatova, 1999). Therefore small isolated communities are sensitive to abiotic fluctuations, nature and anthropogenic disturbances. They must be placed under especially strong protection in the reserve area.

Subalpine meadow communities (*Betonici macranthae-Calamagrostietum arundinaceae*, Onipchenko, 2002) are typical of the subalpine zone on Western Caucasus in the altitude range of 1700 to 2400 m. The diagnostic species set includes *Betonica macrantha* C. Koch, *Leontodon hispidus* L., *Campanula collina* Bieb., *Festuca varia* Haenke, and *Trifolium canescens* Willd. (vascular plant nomenclature is based on checklist for the alpine vegetation of the Teberda reserve, Northwestern Caucasus: Onipchenko, 2002). Floristic richness of subalpine meadow communities is highest in the high mountain zone of Western Caucasus. Overall, we registered 301 vascular plant species in this association. The number species for 16 m^2 plot was estimated as 15-64 (Akatov et al., 2003).

Mount Bolshoy Tkhach is northwestern part of a high mountain range Peredovoy (42°03'-44°04' N, 40°25'- 40°26' E; maximum altitude: 2368 m above sea level). On this mountain the subalpine meadow communities are common within altitude range of 1800-2000 m. and are developed on slopes varying exposure and stepness. Local richness of these communities is very high. The number species for 16 m^2 plot was estimated as 19-63, however, overall, we registered only 157 species in 150 releves. It is possible to assume that relative low size of the species pool of these communities are caused by regional processes, for example, their isolation. The subalpine meadow communities of Mount Bolshoy Tkhach connected with similar communities of other high mountains by narrow "isthmus". Therefore these phytocenoses may be considered true "habitat semi-island". This suggests that plant species occurring exclusively on these phytocenosis are less persistence to the environmental variability or disturbance then species of other non isolated communities. The purpose of our study was to determine, whether semi-island effect influence on species richness in subalpine meadow communities of Bolshoy Tkhach.

Material and methods

Study area and Field sampling
The study area is located in the subalpine zone of the Western Caucasus Mountains, Russia (43°45' - 44°03' N, 40°06' - 40°26' E; altitude: 1700-2400 m above sea level). Meadow communities were described on Mount Bolshoy Tkhach and other 14 high mountain ranges of the Western Caucasus. On eight ranges these communities are isolated from meadow communities of other high mountain ranges by subalpine beech or mixed coniferous-broadleaf forests. The area of non-woody vegetation on these mountains ranges from 0.01 to 36.5 km^2. On

other high mountain ranges, these communities are not isolated by forest communities. One to six relatively homogeneous subalpine meadow sites (about 0.25 ha) were selected on each high mountain range. Within these, five transects with five plots (4 x 4 m) were systematically located. We recorded all vascular plants on each sample plot. The number of sample plots at each site was sufficient to record 94 to 100% of the plant species occurring there. In addition, we also recorded previously unrecorded species within the sites. Altogether, 34 subalpine meadow sites were selected, including 6 sites on Bolshoy Tkhach, 12 sites on isolated and 16 on non-isolated high mountain ranges.

For all subalpine meadow sites, we calculated the following four characteristics:

S – the mean number of species of vascular plants per plot (local species richness);

N – the total number of species recorded within all plots in meadow sites. We consider this characteristic to be the size of actual (= community) species pools of plant communities. According to Partel and Zobel (Partel et al. 1996; Zobel et al. 1998) the actual species pool is the total number of species present in the community or in one stand.

f – the frequency of each species on subalpine meadow sites;

F – the mean frequency of species for each site.

Analysis methods

To test "island effect" some authors analyze "species richness-area" and "species richness-isolation" relations (MacArthur, Wilson, 1963; Kelly et al., 1989; Sukhova et. al., 1997). According to the Equilibrium theory, the relation between area and species richness should be positive, and relation between isolation and species richness should be negative. However, this method can not be used to test "semi-island effect" since the area and the isolation of "semi-islands" can not be exactly measured. The comparative studies of the species richness in meadow communities of Mount Bolshoy Tkhach and in non isolation communities, growing under similar ecological conditions, may be of substantial help here. However, the problem is that it is very difficult to choose such communities since it is always possible to challenge the statement that ecological conditions are similar.

Therefore to determine, whether "semi-island effect" influence on species richness in subalpine plant communities of Bolshoy Tkhach we used a computer simulation method (Akatov et al., 2005). We simulated probable scenarios of change in F/N and S/N ratios resulting from a decrease in size of the actual species pool caused by regional processes ("island" or "semi-island effect") or from a decrease in environment quality. A pattern of species frequency distribution in subalpine meadow phytocenoses with a largest actual species pool (Mount Abadzesh, Pshekha river basin, 2150 m, $N = 113$, $S = 49.5$ species) and the simple formula of correlation between S, N and F ($S=NF$) (Schluter, Ricklefs 1993) provided the basis of this analysis.

The first scenario is based on assumptions that (1) the changes are generated by regional processes, for example, an increase in community isolation; (2) the environmental conditions are constant; (3) the total number of individuals and vascular plant cover in plots are constant as well; (4) species with low frequency are more likely to disappear from the local species pool as a result of regional processes, than frequent species. In the literature there is a lot of theoretical and factual evidence in support of the third assumption (MacArthur, Wilson 1963; Dzwonko, Loster 1989; Zacharias, Brandes 1990; Kwiatkowska, 1994; Cutler, 1991). According to these assumptions, the consecutive disappearance of certain species from the pool is accompanied by increase in the frequency of remaining species, except for species with 100% frequency.

The second scenario is based on the assumption that: (1) changes are caused by a decrease in environment quality, for example, reduction of the vegetation period, an increase of the environmental variability, frequency of environmental disturbance and so on; (2) the total number of individuals in plots is constant; (3) frequency of one species with 100% frequency is constant; frequency of other species decreases under the influence of environmental factors by equal values at each step of change, independent of the population size. In this case, the relative

change in frequency of high density species is smaller than that of rare species. This assumption is substantiated by the fact that rare and wide-spread species differ in degree of their tolerance to environmental changes: rare species are usually more sensitive to the effects of environmental factors (Braun, 1984). When the species frequency drops to zero, a species is considered to be eliminated from the species pool.

We used Pearson correlation and the least squares method to estimate the fit of field data to these models.

Results and Discussion

The results of computer analyses of the ratio between species pool (N) and local species richness (S) are graphed in Figures 1. Curves were obtained using polynomial regressions. Tables 1 show equations and determine coefficients of polynomial and linear regressions.
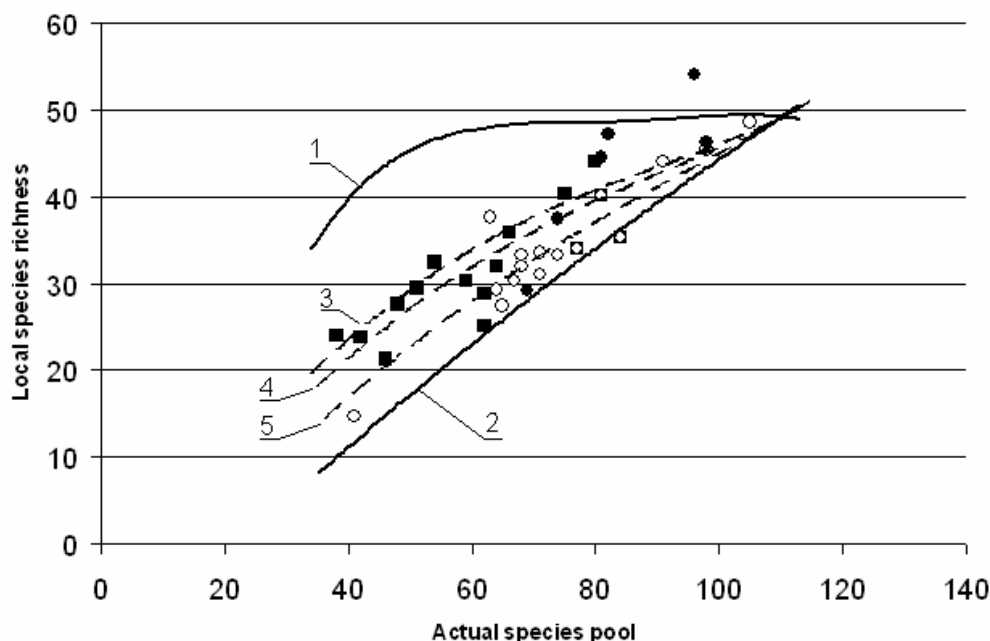

Figure 1. The expected and observed relationships between mean local species richness (S), and the size of the actual species pool (N) for subalpine meadow communities.

Curves 1 and 2 correspond to the first and second scenarios of the changes in S/N ratios, described in the text.

Curves 3, 4 and 5 are constructed on the basis of the equations (4) and (5) for the factual data: 3 - for the meadow communities located on Mount Bolshoy Tkhach (●); 4 - for the meadow communities located on isolated high mountain ranges (■); 2 - for the meadow communities located on non isolated high mountain ranges (○).

According to the first scenario the mean frequency of species (F) increases as N decreases; the expected local richness (S) remains relatively stable until the frequency of the majority of the remaining species becomes 100% and then S decrease. Thus, according to this scenario, N is determined by regional processes while S is mainly determined by local processes (where N is greater than a certain small value).

Table 1. **The relationship between the local species richness *(S)* and the size of the actual species poo*l (N)* in the subalpine meadow communities according to the results of the computer simulation**

Scenario	Model			
	Polynomial		Linear	
	Equation	R^2	Equation	R^2
First	$S = -2E06N^4 + 0.0008N^3 - 0.1N^2 + 5.5933N - 68.651$	0.999	$S = 0.1960N + 32.539$	0.694
Second	$S = -0.001N^2 + 0.6887N - 14.794$	0.992	$S = 0.55N - 10.374$	0.990

According to the second scenario, both species pool and local species richness are determined by local processes. Computer analysis shows relative constancy in the values of *F* and an approximately proportional decrease in *S* and *N*. The fit of both, the second-order polynomial and linear regressions, to the expected values is very good and almost the same (Table 1).

Thus, the results of the computer simulation allow us to assume that the first scenario is correct if the ratio between *N* and *S* do not show significant positive correlation where *N* is greater by certain relatively small values (approximately 50 species). The positive relationship between *S* and *N* should indicate that the second scenarios fit better with our data than the first one.

Table 2. **The relationship between the local species richness *(S)* and the size of the actual species poo*l (N)* in the subalpine meadow communities (field data)**

Sites	No. of sites	Correlation coefficient		Determination coefficient (R^2)	
		r	P	Linear model	Second-order polynomial model
all sites	34	0.881	< 0.001	0.777	0.779
with $N > 50$	29	0.832	< 0.001	0.692	0.701
on Bolshoy Tkhach	6	0.851	< 0.05	0.725	0.928
on isolated massifs	12	0.838	< 0.001	0.702	0.758
on non isolated massifs	16	0.930	< 0.001	0.864	0.872

The relationship between species richness (*S*) and the size of the actual species pool (*N*) of subalpine meadow communities is shown in Table 2 and in Figure 1. In the case of both full and partial data, there is a significant positive linear relationship. Thus, these results disagree with the fist scenario and agree rather than disagree with the second one. However, it is important to note that meadow communities located on isolated, non isolated high mountain ranges and on Mount Bolshoy Tkhach have different distributions in *S(N)* spaces.

The subalpine meadow communities located on non isolated high mountain massifs are not far from curves 1 (Figure 1). The subalpine meadow communities located on isolated ranges and on Bolshoy Tkhach have higher *S* relative *N,* and are between curves 1 and 2. It means that the size of the actual species pool and local species richness of meadow communities of non isolated high mountain ranges are mainly determined by environmental factors. The size of the species pool and local species richness of communities of isolated ranges and Bolshoy Tkhach (or the size of their species pool alone) may also depend on regional processes. Thus, the test results are more similar for communities of Bolshoy Tkhach and isolated ranges, then Bolshoy Tkhach and non isolated ranges.

We want also to emphasize the fact that scenarios 1 and 2 are not alternates. Therefore, curves 1 and 2 are presumably two extremes of a continuum defined by the correlation between the role of local and regional processes in determining the local species richness and actual species pool of the studied communities. Then N and S can be presented as the parameters of certain functions with an unknown structure:

$$N=N(c, p) \tag{1}$$
$$S=S(c,p). \tag{2}$$

where c is the parameter determined by local processes and p – the parameter determined by regional processes.

According to scenarios 1 and 2 under N more than a certain small value, the changes S are determined by local processes alone. In this case the equation (2) must be presented as

$$S=S(c) \tag{3}$$

Therefore, the considerable variation of S relative to the model curves (Figure 2) is most likely the result of local species richness of plant communities being determined mainly by the local processes, while the actual species pool is determined by both local and regional processes.

In the simplest case, the result of the joint effect of local and regional processes on the local-regional species richness relationships can be determined as the weight sum:

$$S \ (N) = \acute{a} \ S_2 \ (N) + (1 - \acute{a}) \ S_1 \ (N) \ , \tag{4}$$

where $S_2 \ (N)$ is the component $S \ (N)$ determined by local processes (c); $S_1 \cdot (N)$ – the component $S (N)$ determined by regional processes (p); α - the weight coefficient determining the relative contribution of these factors to the relationship between S and N.

On the basis of equation (4), the families of the model curves reflecting the $S(N)$ relationship under different α can be constructed. Curves 1 and 2 reflect an extreme variant, where α is equal to 0 or 1. For factual data, the weight coefficient can be determined using the least squares method:

$$\alpha = \frac{\sum_{i=1}^{n} [S_1(N_i) - S_2(N_i)] \cdot [S_1(N_i) - S_e(N_i)]}{\sum_{i=1}^{n} [S_1(N_i) - S_2(N_i)]^2} , \tag{5}$$

where S_e is factual local richness under N_i ; S_1 and S_2 are expected local richness under N_i according to the first and second scenarios (they can be determined on the basis of regression models of these scenarios: Table 1).

For the subalpine meadow communities located on non isolated high mountain ranges, the weight coefficient is equal to 0.80. For subalpine meadow communities located on isolated high mountain ranges, α equals 0.65; for the communities located on Bolshoy Tkhach - 0.56. Thus, the relative contribution of environmental conditions and regional processes (semi-island effect) in determining the relationship between S and N of subalpine meadow communities of Bolshoy Tkhach equals 56 and 44% accordingly.

Since variation of $S(N)$ relationships is the result of greater sensitivity of the actual species pool to regional processes in comparison to local species richness, coefficient α may be an indicator of the mean level of the saturation of the actual species pool. Consequently, subalpine meadow communities located on non isolated high mountain ranges are characterized on the

average with a greater level of species pool saturation in comparison with subalpine meadow communities, located on isolated high mountain ranges and on Mount Bolshoy Tkhach. These results correlate with the Equilibrium theory of insular biogeography (MacArthur, Wilson, 1963) and show that "semi-island effect" influence sensitively on species richness in subalpine plant communities of Mount Bolshoy Tkhach.

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