The relationship between local species richness and species pool: a case study from the high mountains of the Greater Caucasus

Valeriy Akatov[1,*], Sergey Chefranov[1] and Tatjana Akatova[2]

[1]*Maikop State Technological Institute, Pervomaiskaya str. 191, Maikop, 385000, Russia;* [2]*Caucasus State Reserve, Sovetskaya str. 187, Maikop, 385000, Russia; *Author for correspondence (e-mail: akatovmgti@mail.ru)*

Abstract

The causes of linear relationships between local species richness and the size of the actual species pool in closed subalpine meadow communities and open plant communities of the alpine stony substrate (the Greater Caucasus Mountains) were analyzed using a computer simulation model. The results demonstrated that this relationship is insufficient evidence for the variation of local species richness among communities is wholly or partly determined by regional processes (the species-pool hypothesis). A relatively proportional ratio between these variables can also arise where local species richness and the size of the species pool both depend on local processes, or where local species richness is determined by local factors alone while the size of the species pool is determined by both local and regional factors.

Introduction

The species pool of a given community is a set of species potentially capable of coexisting in this community (MacArthur and Wilson 1963; Eriksson 1993; Partel et al. 1996). The problem of correlation between local species richness and the size of the community species pool has been actively discussed over the last few years (Ricklefs 1987; Akatov 1995; Hugueny and Paugy 1995; Partel et al. 1996; Caley and Schluter 1997; Fenchel et al. 1997; Hugueny 1997; Partel and Zobel 1999; Akatov et al. 2002, 2003). This is associated with the following assumptions: (1) variation in species richness among communities is wholly or partly explained by variation in the size of the species pool associated with each particular community; (2) species richness in these communities seldom

reaches an upper limit on small local plots and the local richness often remains unsaturated; (3) the key to the community structure may lie in extrinsic regional processes (speciation, species dispersal, island effect) rather than intrinsic local processes (abiotic fluctuation or disturbance, competition, predation, parasitism).

These assumptions constitute the so-called species-pool hypothesis (Eriksson 1993; Zobel et al. 1998). It is also believed that interactive and non-interactive communities differ from one another in their tendency to be saturated with species (Cornell and Lawton 1992; Caswell and Cohen 1993; 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 open since there is no limit to the number of individuals summed over all the species coexisting in them. Colonization by new species is a random process, independent of the number of species already present (Cornell and Lawton 1992; Caswell and Cohen 1993; Cornell 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 species-pool hypothesis, the upper limit of local species richness must result from species interactions which are a necessary but not sufficient condition for local saturation in ecological time (Cornell and Lawton 1992). Hence, the influence of the species pool size on local richness in interactive communities may vary, but impacts on species richness in non-interactive communities are always very strong, and the latter communities cannot be saturated with species in any case (Cornell and Lawton 1992; Cornell 1993).

In support of this hypothesis, Cornell demonstrated several examples of linear relationships (proportional sampling) between local and regional richness in communities of phytophagus insects (Cornell 1985, 1993; Cornell and Lawton 1992). According to Cornell and Lawton (1992), a direct proportional relationship between local and regional richness reveals unsaturated communities where species interactions are not sufficient to limit local species richness. Deviations from this relationship may be an indicator of species richness patterns consistent with local saturation.

However, further analysis of the local-regional species richness relationship gives ambiguous results (Aho and Bush 1993; Lawton et al. 1993; Kennedy and Guegan 1994; Hugueny and Paugy 1995; Partel et al. 1996; Caley and Schluter 1997; Duncan et al. 1998; Oberdorff et al. 1998; Shurin et al. 2000; Simkova et al. 2001). Moreover, the assumption is sometimes proposed that linear relationships between local and regional richness may be interpreted differently. One of the possible interpretations of this relationship is that richness depends on the species pool size (Cornell's assumption). According to another interpretation of the same phenomenon, the species pool size depends on local richness (Cornell and Lawton 1992; Cornell 1993; Ricklefs and Schluter 1993; Caley and Schluter 1997; Duncan et al. 1998; Herben 2000). If local richness is saturated, then species pool size may be limited by local processes (Cornell and Lawton 1992). In this case both local and regional richness will vary in response to a third variable – namely, environmental conditions (Duncan et al. 1998; Herben 2000). It is very difficult to distinguish between these interpretations and we do not know of any publications devoted specifically to this problem.

We tested these hypotheses in closed subalpine meadow communities and open vegetation of alpine stony substrates (stable and unstable scree and secondary uncovered stony substrates) in the Greater Caucasus Mountains. The purpose of our study was to determine, whether the species-pool hypothesis provides the sole theoretical basis for the linear relationship between local species richness and the species pool size in both open (presumably non-interactive) and closed (presumably interactive) communities.

Material and methods

Study area

The study area is located in the subalpine and alpine zone of the Central and Western Caucasus Mountains, Russia (42°48′–44°03′ N, 39°08′–44°06′ E; altitude: 1700–2900 m above sea level).

Subalpine meadow communities (*Betonici macranthae – Calamagrostietum arundinaceae*, Onipchenko 2002) are typical of the subalpine zone in the altitude range of 1700–2400 m. They occupy mainly slopes with southern exposure. Vascular plant cover is high (95–100%). The diagnostic species set includes *Betonica macrantha* C. Koch, *Leontodon hispidus* L., *Campanula collina* Bieb., *Festuca varia* Haenke, and *Trifolium canescens* Willd. The overall floristic richness of subalpine meadow communities is highest in the high mountain zone. There are about 300 species represented in the study area. These closed communities are presumably interactive.

Open stony substrate habitats of the alpine zone in the Greater Caucasus Mountains are characterized by extreme environmental conditions. These include cold climate (frost period

of 5–7 months, vegetative period of 40–70 days), strong temperature fluctuations, a limited number of microhabitats suitable for plants, high disturbance frequency, and low habitat fertility (Shgagapsoev 1988). These factors determine the 'primitive' structure of plant communities. In the study area, plant communities of unstable alpine scree (*Veronico minutae – Chaerophylletum humilis.* Onipchenko 2002) include up to 30 species of vascular plants. Fifteen of these are encountered only or mainly on scree habitat (*Dentaria bipinnata* C.A.Mey., *Lamium tomentosum* Willd., *Oxyria digyna* (L.) Hill, *Veronica minuta* C.A.Mey. et al.). All the others are found in other alpine communities (*Myosotis alpestris* F.W. Schmidt, *Veronica gentianoides* Vahl. and some others). Vascular plants cover less than 10% of the scree surface. Species composition displays low variability among scree communities of various mountain ranges.

Plant communities of stable alpine scree include over 60 vascular species −20 of which occur only on scree habitat, 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). The area of scree covered by plants varies from three to 60%. Plant communities of stable and unstable scree are both at successional stages and climaxes in extreme environmental conditions. The secondary uncovered stony substrates are the result of disturbance activity of wild and domestic animals. Plant communities in these habitats include small numbers of petrophyte species (0–25%); the majority of the species occurs in different alpine communities. These communities represent pioneer stages of secondary succession. According to Shgagapsoev (1986, 1988) and Norin (Norin and Kitsing 1982; Norin 1987), there are no strong species interactions in open plant communities in extreme environmental conditions.

Field sampling

Meadow communities were described on 12 high mountain ranges of the Western Caucasus from 1993 to 1997 during annual field expeditions in July and August. 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 × 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 94–100% of the plant species occurring there. In addition, we also recorded previously unrecorded species within the sites. Altogether, 24 subalpine meadow sites were selected, including 11 sites on isolated and 13 on non-isolated high mountain ranges.

We described the open vegetation of alpine stony substrates on 13 high mountain ranges of the Central and Western Caucasus in the period from 1999 to 2002. Six of these ranges are made up of calcareous rocks (limestone), four of granite, and three of shale. On each high mountain range in the alpine belt we selected relatively homogeneous scree and secondary uncovered stony substrate sites ranging from 50 to 500 m^2 and surrounded by sites of other habitat types. Within these, we randomly placed six to 26 transects with five plots (0.5 × 1 m). We recorded all vascular plants on each sample plot and estimated their total coverage. The larger sites had more transects and sample plots. The density of sample plots at each site was enough to record all plants occurring in the sites. Altogether, we selected 17 sites of stony substrate and sampled 1270 plots including plots without vascular plant species.

Since the variation in species richness per 0.5 m^2 within sites can be determined by substrate quality, the plots with vascular plants from each site was subdivided into groups with similar species composition and approximately equal species number. We used a table method for this purpose. We excluded from the analysis groups including fewer than 20 plots or plots with mainly one species. For each remaining group of open plant communities, we determined the mean plant cover and excluded groups of communities with a mean cover of more than 15%. For the 20 open plant

community groups selected according to this method, and for all subalpine meadow sites, we calculated the following four characteristics: S is the mean number of species of vascular plants per plot (local species richness); N is the total number of species recorded within all plots of each group of open plant communities or 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; Cantero et al. 1999) the actual species pool is the total number of species present in the community or in one stand. In the case of the open plant community, this characteristic is determined on the basis of a different number of plots (20–69). However, there is no positive correlation between the number of plots used and the actual species pool size of open communities ($r = -0.399$, $n = 20$, $p < 0.1$). Hence, one may assume that the sampling effort does not predetermine the size of the species pool. f is the frequency of each species on the plots of each group of open plant community or on subalpine meadow sites; F is the mean frequency of species for each group or for each site.

Some characteristics of the study sites and information about open and meadow plant communities are presented in Tables 1 and 2.

Analysis methods

To determine the causes of the local richness – actual species pool relationships, we used a computer simulation method. 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 or from a decrease in environment quality. A general pattern of species frequency distribution in closed meadow and open plant communities with a large actual species pool (site numbers 5, 6, 9 and 14 in Table 1 and group numbers 11, 15, 18 and 20 in Table 2) and the simple formula of correlation between S, N and F ($S = NF$) (Schluter and Ricklefs 1993) provided the basis of this analysis.

The first scenario corresponds to Cornell's hypothesis and is based on three assumptions: (1) the changes are generated by regional processes, for example, an increase in community isolation; (2) the total number of individuals on the plots is

Table 1. Information about 24 subalpine meadow communities of Greater Caucasus, used in the present study.

Mountain massif (isolated − +, non isolated − + +), river basin, coordinates	Site number	Elevation (m)	F	S	N
Alous, (+ +), Malaya Laba, 43°48′–43°50′ N, 40°29′–40°32′ E	1	2200	0.36	14.8	41
Yatirgvarta, (+), Malaya Laba, 43°51′–43°52′ N, 40°46′–40°51′ E	2	1810	0.46	28.8	62
	3	1870	0.57	27.5	48
Aspidniy, (+ +), Malaya Laba, 43°50′–44°00′ N, 40°23′–40°25′ E	4	2190	0.47	33.6	71
	5	2275	0.43	36.3	84
Tibga, (+ +), Belaya, 43°52′–43°54′ N, 40°14′–40°17′ E	6	2020	0.49	40.1	81
	7	2000	0.47	32.0	68
	8	2000	0.60	37.6	63
	9	2000	0.45	34.4	77
Pastbishe Abago, (+ +), Belaya, 43°56′–43°57′ N, 40°13′–40°15′ E	10	1885	0.42	27.4	65
	11	1905	0.49	33.2	68
	12	1895	0.45	30.2	67
	13	1890	0.46	29.3	64
	14	1860	0.45	33.2	74
	15	1875	0.44	31.0	71
Pshekish, (+), Belaya, 43°56′–44°00′ N, 40°15′–40°18′ E	16	2060	0.40	25.0	62
	17	1950	0.50	32.0	64
Bsik, Belaya, (+), 43°54′–43°57′ N, 40°02′–40°05′ E	18	1870	0.57	23.8	42
Armyanskiy, (+), Belaya, 43°54′–43°55′ N, 40°01′–40°02′ E	19	1900	0.60	32.5	54
Kud, Shahe, (+), 43°52′–43°54′ N, 39°46′–39°48′ E	20	1980	0.46	21.3	46
Malaya Chura, (+), Shahe, 43°51′–43°52′ N, 39°08′–40°02′ E	21	2000	0.51	30.3	59
Huko, (+), Shahe, 43°55′–43°57′ N, 39°48′–39°50′ E	22	1870	0.63	24.0	38
	23	1890	0.58	29.5	51
Achishko, Mzimta, (+), 43°42′–43°45′ N, 40°06′–40°11′ E	24	2250	0.54	35.8	66

Table 2. Information about 20 open plant communities on the alpine stony substrate of Greater Caucasus, used in the present study.

Mountain range, river basin, coordinates, lithology	Group number	Elevation (m)	Unstable (+), stable (++) screes, secondary uncovered stony substrates (+++); floristic composition	No. of plots	F	S	N
Kivnchoh, Alagir, 42°53′–42°55′ N, 43°58′–44°01′ E, limestone	1	2660	(+), *Dentaria bipinnata**, *Corydalis alpestris*, *Saxifraga sibirica*	29	0.33	2.3	7
Musostau, Cherek-Besengiyskiy, 43°03′–43°06′ N, 43°05′–43°08′ E, granite	2	2660	(+), *D. bipinnata*, *C. alpestris*, *Viola biflora*	26	0.52	4.7	9
	3	2670	(+), *Oxyria digyna*, *Chaerophyllum humile*, *Lamium tomentosum*, *Arabis caucasica*	39	0.25	2.5	10
Kachtantau, Cherek-Besengiyskiy, 43°06′–43°08′ N, 43°08′–43°12′ E, granite	4	2880	(+), *C. humile*, *L. tomentosum*, *Senecio karjaginii*	22	0.40	2.4	6
Djentu, Bolshay Laba, 43°47′–43°50′ N, 40°46′–40°12′ E, limestone	5	2415	(+), *D. bipinnata*, *C. alpestris*, *S. sibirica*	27	0.66	2.0	3
Magisho, Malaya Laba, 43°45′–43°47′ N, 40°44′–40°49′ E, granite	6	2415	(+), *D. bipinnata*, *C. alpestris*, *C. humile*	46	0.50	3.0	6
	7	2415	(+), *D. bipinnata*, *C. alpestris*, *Myosotis alpestris*	38	0.46	4.6	10
	8	2450	(++), *O. digyna*, *Veronica minuta*, *M. alpestris*	61	0.23	1.6	7
Alous, Malaya Laba, 43°48′–43°50′ N, 40°29′–40°32′ E, granite	9	2440	(++), *O. digyna*, *V. minuta*, *Carum caucasicum*	45	0.41	3.3	8
	10	2340	(+++), *Festuca ovina*, *Luzula spicata*, *Carex sempervirens*	27	0.43	2.3	7
Yatirgvarta, Malaya Laba, 43°51′–43°52′ N, 40°46′–40°51′ E, limestone	11	2730	(+++), *F. ovina*, *Seseli alpinum*, *Veronica gentianoides*	22	0.31	5.5	18
Tibga, Belaya, 43°52′–43°54′ N, 40°14′–40°17′ E, shale	12	2460	(++), *Alopecurus sericeus*, *Ranunculus oreophilus*, *Alchemilla retinervis*	32	0.24	3.3	14
Abago, Belaya, 43°54′–43°56′ N, 40°08′–40°10′ E, shale	13	2465	(+), *D. bipinnata*, *C. alpestris*, *C. humile*	36	0.30	2.1	7
Oshten, Belaya, 43°58′–44°01′ N, 39°54′–39°59′ E, limestone	14	2360	(+++), *F. ovina*, *Alchemilla caucasica*, *V. gentianoides*	21	0.27	3.6	13
	15	2360	(+++), *F. ovina*, *R. oreophilus*, *Viola altaica*	23	0.23	5.0	22
	16	2540	(+), *D. bipinnata*, *C. alpestris*, *L. tomentosum*	41	0.42	2.5	6
	17	2540	(+), *D. bipinnata*, *C. alpestris*, *Iberis taurica*	38	0.45	4.5	10
Pshechasu, Belaya, 43°58′–44°01′ N, 39°51′–39°54′ E, limestone	18	2450	(++), *D. bipinnata*, *C. alpestris*, *M. alpestris*	32	0.26	5.5	21
	19	2450	(+), *C. alpestris*, *S. sibirica*, *Poa alpina*	28	0.66	2.0	3
	20	2490	(++), *C. humile*, *C. caucasicum*, *Ar. caucasica*	38	0.36	6.2	17

*Vascular plant nomenclature is based on checklist for the alpine vegetation of the Teberda reserve Northwestern Caucasus (Onipchenko, 2002).

independent of environmental conditions and has no upper limit; (3) species with low frequency are more likely to disappear from the local species pool as a result of these processes than frequent species.

In the literature there is a lot of theoretical and factual evidence in support of the third assumption (MacArthur and Wilson 1963; Dzwonko and Loster 1989; Zacharias and Brandes 1990; Cutler 1991; Kwiatkowska 1994). The consecutive disappearance of the most rare species and then species with intermediate and high frequency from the pool have no influence on the frequency of remaining species.

The second scenario is based on assumptions that (1) the changes are caused by regional processes; (2) the total number of individuals in plots has a limit; (3) the environmental conditions are constant and, hence, the total number of individuals in plots is constant as well. 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 third 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 limited; (3) frequency of all the 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 statistical tests (the least squares regression method and Pearson correlation coefficient) to estimate the fit of field data to these models.

Results

The results of computer analyses of the ratio between species pool (N), mean species frequency (F), and local species richness (S) are graphed in Figures 1 and 2. Curves were obtained using polynomial regressions. Tables 3 and 4 show equations and determine coefficients of polynomial and linear regressions.

According to the first scenario (Cornell's hypothesis), the mean frequency of species (F) increases and expected local species richness (S) decreases as N decreases (Figure 1, Tables 3, 4). However the relationship between N and S is more curvilinear than linear.

According to the second 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).

According to the third 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 4).

Thus, the results of the computer simulation allow us to assume that the significant negative correlation between F and N indicates that the species pool together with local species richness (the first scenario) or the species pool alone (the second scenario) change as a result of regional processes. Absence of significant negative correlation between these parameters indicates that both the species pool and local species richness are mainly determined by local processes (the third scenario). This test is insufficient to discriminate between the first and second scenarios since both predict a significant negative correlation between F and N. However, this is possible using the analysis of the ratio between N and S. The second scenario is correct if these variables do not show significant positive correlation where N is greater by certain relatively small values (approximately 45 species for meadows and seven species for open communities). The positive relationship between S and N should indicate that the first and third scenarios fit better with our data than the second one.
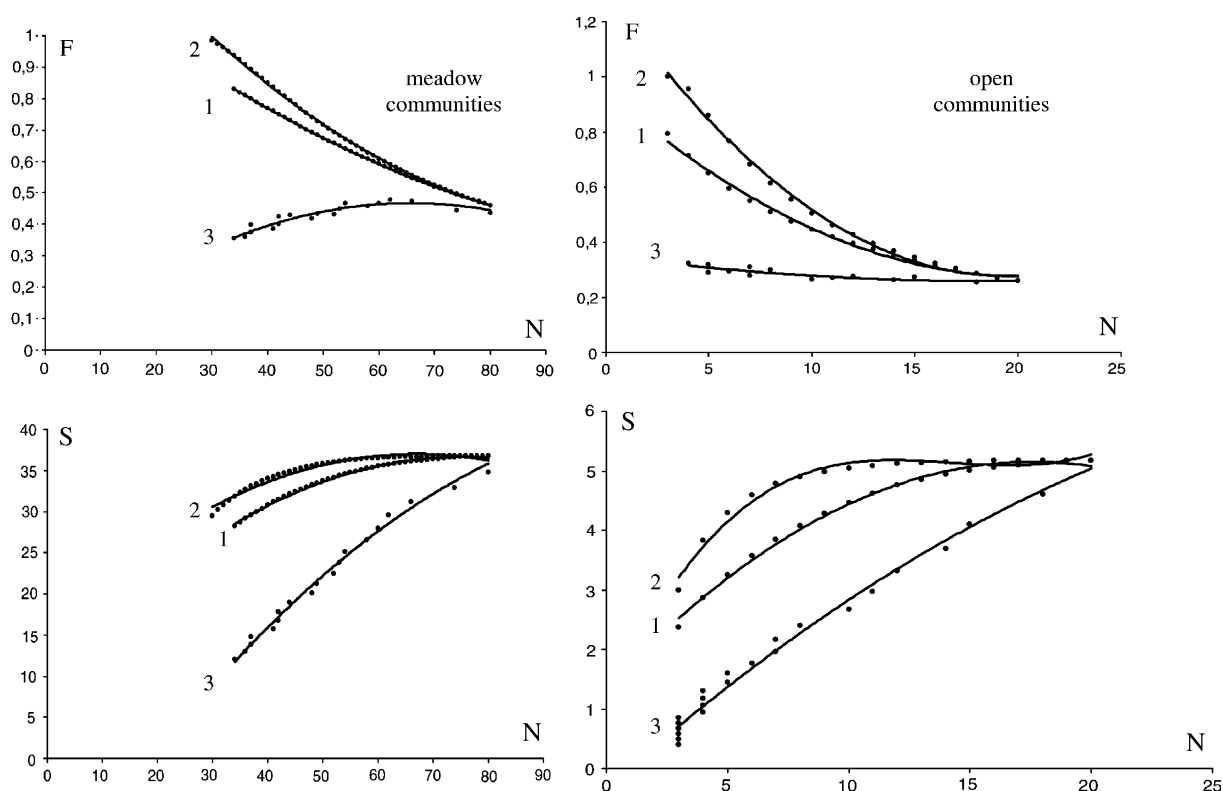
Figure 1. The results of computer simulation of the probable scenarios of changes in F/N and S/N ratios for the subalpine meadow communities and alpine open communities are caused by local and regional processes. Curves 1, 2 and 3 correspond to the first, second and third scenarios.

The relationship between species richness (S) and the size of the actual species pool (N) of subalpine meadow and open communities of the alpine stony substrates is shown in Table 5 and in Figure 2. In the case of both full and partial data, there is a significant positive linear relationship. Curvilinearity was tested by inclusion of a quadratic term in the regression of the local richness on the species pool. This test showed that the fit of both the linear and second-order polynomial regressions to field data is practically the same (Table 5). Thus, these results disagree with the second scenario and disagree rather than agree with the first one.

For full data on subalpine meadow communities as well as for open plant communities there is a significant negative correlation between F and N (Table 6). This suggests that the species pool and local species richness (or only species pool) are, at least partly, dependent on regional factors. However, most meadows and open communities

tend to have values S and F lower than expected according to the 1st or 2nd scenarios, but they are higher than expected according to the 3rd scenario. Thus, none of the three scenarios gives an adequate model of the F/N and S/N relationship (Figure 2).

It is important to note that open plant communities of different habitat types and meadow communities located on isolated and non isolated high mountain ranges have different distributions in $S(N)$ and $F(N)$ spaces.

The majority of the communities of unstable scree have a relatively high S and F, and they are located above curves 3 (Figure 2). Thus, it is possible to assume that the actual species pool and local species richness of these communities (or only species pool) depend on regional factors. A significant negative correlation between F and N supports this assumption (Table 6).

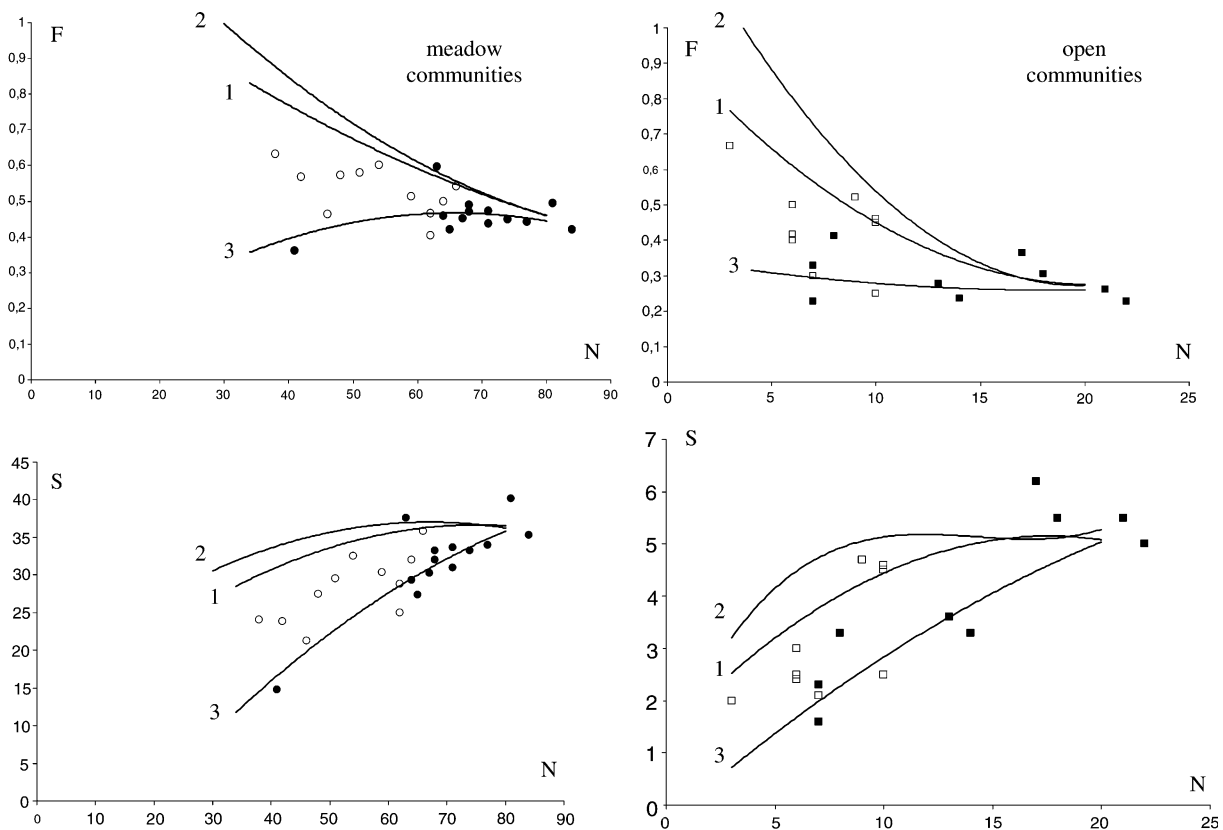The communities of stable scree and secondary uncovered stony substrates have relative low S and

Figure 2. The expected and observed relationships between mean frequency of species (*F*), mean local species richness (*S*), and the size of the actual species pool (*N*) for subalpine meadow communities and alpine open communities. Curves 1, 2 and 3 correspond to the first, second and third scenarios of the changes in *F/N* and *S/N* ratios, described in the text. The community types: (□) – open communities on unstable scree; (■) – open communities on stable scree and secondary uncovered stony substrates; (○) – meadow communities located on isolated high mountain ranges; (●) – meadow communities located on non isolated high mountain ranges.

are located not far from curves 3. The Pearson correlation coefficient between *F* and *N* is negative but non significant. Thus, the third scenario fits with these data quite well. This suggests that the size of the species pool and local species richness of these communities depend mainly on environment factors. Plant communities from these habitats include many species occurring in the surrounding alpine communities. Therefore their isolation and, consequently, regional influences on their local richness and actual species pool is relatively low or absent.

The subalpine meadow communities located on non isolated high mountain massifs are not far from curves 3 (Figure 2) and a positive non significant correlation between *F* and *N* is found (Table 6). The subalpine meadow communities located on isolated ranges have higher *S* and *F* relative *N*, and are between curves 1, 2 and 3.

There is a significant negative relationship between the mean frequency of species and actual species pool of these communities (Table 6). 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 (or the size of their species pool alone) may also depend on regional processes.

Discussion

Thus, we find that:
(1) there is a linear significant positive relationship between species richness (*S*) and the size of the actual species pool (*N*) of subalpine meadow and alpine open communities;
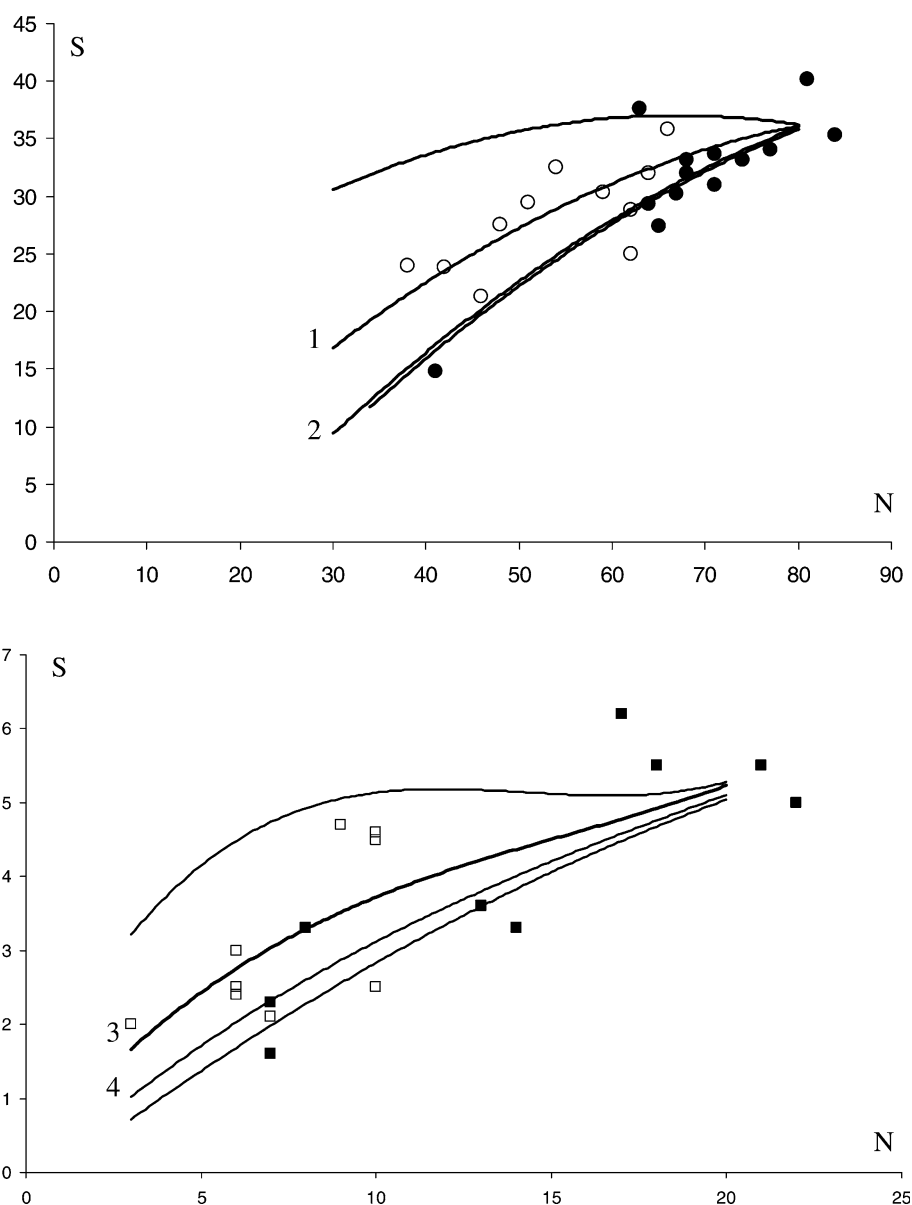
Figure 3. The curves are constructed on the basis of the equations (4) and (5) for the factual data: 1 – for the meadow communities located on isolated high mountain ranges (○); 2 – for the meadow communities located on non isolated high mountain ranges (●); 3 – for the open communities on unstable scree (□); 4 – for the open communities on stable scree and secondary uncovered stony substrates (■). They are compared with the curves corresponding to the second and third scenarios of the changes of S/N ratios.

(2) none of the model curves fully agrees with all field data and, hence, no hypothesis can explain independently the relationship between the actual species pool and the species richness of the communities studied;
(3) the test results are similar for closed and open communities.

To explain these results we want to emphasize the fact that scenarios 2 and 3 are not alternates, since they are based on the same assumption that the total number of individuals on plots of the communities is limited. Therefore, curves 2 and 3 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

Table 3. The relationship between the mean frequency of species (*F*) and the size of the actual species pool (*N*) in the subalpine meadow communities and the alpine open communities according to the results of the computer simulation.

Community	Scenario	Model				
		Polynomial			Linear	
		Equation	R^2		Equation	R^2
Meadow	First	$F = 0.00006 N^2 - 0.015N + 1.260$	1.00		$F = -0.008 N + 1.085$	0.99
	Second	$F = 0.0001 N^2 - 0.022N + 1.577$	1.00		$F = -0.011 N + 1.275$	0.98
	Third	$F = -0.0001 N^2 + 0.014N - 0.0036$	0.89		$F = 0.002 N + 0.324$	0.56
Open	First	$F = 0.0016 N^2 - 0.066N + 0.949$	1.00		$F = -0.029 N + 0.778$	0.93
	Second	$F = 0.0028 N^2 - 0.111 N + 1.365$	1.00		$F = -0.043 N + 1.018$	0.92
	Third	$F = -0.0009 N^2 + 0.019 N + 0.187$	0.23		$F = 0.002 N + 0.248$	0.04

Table 4. The relationship between the local species richness (*S*) and the size of the actual species pool (*N*) in the subalpine meadow communities and the alpine open communities according to the results of the computer simulation.

Community	Scenario	Model				
		Polynomial			Linear	
		Equation	R^2		Equation	R^2
Meadow	First	$S = -0.0048 N^2 + 0.723N + 9.5$	1.00		$S = 0.175 N + 24.236$	0.90
	Second	$S = -0.0047 N^2 + 0.632N + 15.859$	0.97		$S = 0.113 N + 29.111$	0.75
	Third	$S = -0.0043 N^2 + 1.017N - 17.816$	0.99		$S = 0.526 N - 4.802$	0.98
Open	First	$S = -0.0123 N^2 + 0.434N + 1.337$	1.00		$S = 0.150 N + 2.637$	0.87
	Second	$S = 0.0016 N^3 - 0.067 N^2 + 0.929 N + 0.985$	0.98		$S = 0.084 N + 3.867$	0.59
	Third	$S = -0.0048 N^2 + 0.365 N - 0.335$	0.99		$S = 0.267 N + 0.010$	0.98

and *S* can be presented as the parameters of certain functions with an unknown structure:

$$N = N(c, p) \qquad (1)$$

$$S = S(c, p). \qquad (2)$$

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

According to scenarios 2 and 3 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

$$S = S(c) \qquad (3)$$

Therefore, the considerable variation of *S* relative to the model curves (Figure 2) is most likely

Table 5. The relationship between the local species richness (*S*) and the size of the actual species pool (*N*) in the subalpine meadow communities and the alpine open communities (field data).

Community	No. of sites (groups)	Correlation coefficient		Determination coefficient (R^2)	
		r	*p*	Linear model	Second-order polynomial model
Meadow					
All sites	24	0.788	< 0.001	0.62	0.63
With $N > 45$	20	0.628	< 0.01	0.39	0.38
On isolated massifs	11	0.705	< 0.01	0.50	0.50
On non isolated massifs	13	0.846	< 0.001	0.72	0.77
Open					
All groups	20	0.822	< 0.001	0.68	0.69
With $N > 7$	11	0.615	< 0.05	0.38	0.38
On unstable screes	11	0.726	< 0.05	0.53	0.56
On stable substrates	9	0.869	< 0.01	0.76	0.79

Table 6. Correlation coefficient (r) of the the mean frequency of species with the size of the actual species pool in the subalpine meadow communities and the alpine open communities (field data).

Community	No. of sites (groups)	r	p
Meadow			
All sites	24	−0.419	< 0.01
On isolated massifs	11	−0.567	< 0.1
On non isolated massifs	13	0.247	
Open			
All groups	20	−0.612	< 0.01
On unstable screes	11	−0.612	< 0.05
On stable substrates	9	−0.322	

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 size of the species pool and, accordingly, on the local-regional species richness relationships can be determined as the weight sum:

$$S(N) = \alpha S_3(N) + (1 - \alpha)S_2(N), \quad (4)$$

where $S_3(N)$ is the component $S(N)$ determined by local processes (c); $S_2(N)$ – 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 2 and 3 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:

$$\alpha = \frac{\sum_{i=1}^{n}[S_2(N_i) - S_3(N_i)] \cdot [S_2(N_i) - S_e(N_i)]}{\sum_{i=1}^{n}[S_2(N_i) - S_3(N_i)]^2}, \quad (5)$$

where S_e is factual local richness under N_i; S_2 and S_3 are expected local richness under N_i according to the second and third scenarios (they can be determined on the basis of regression models of these scenarios: Table 4).

For the subalpine meadow communities located on isolated high mountain ranges, the weight coefficient is equal to 0.63. Thus, the relative contribution of environmental conditions and regional processes in determining the relationship

between S and N of these plant communities equals 63 and 37% accordingly. For other studied communities, α equals 0.99 for the subalpine meadow communities located on non isolated high mountain ranges; 0.62 for the unstable alpine scree plant communities; 0.88 for stable alpine scree plant communities and communities of secondary uncovered stony substrates. Curves reflecting $S(N)$ ratios for these communities were obtained using polynomial regressions, however, in all cases the fit of the second-order polynomial and linear regressions to the data is very good and almost the same ($R^2 = 0.965 - 1$).

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 and communities of stable scree and secondary uncovered stony substrates 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 unstable scree communities. These results correlate with the Equilibrium theory of insular biogeography (MacArthur and Wilson 1963).

It is important to stress that the relative influence of local and regional processes on the actual species pool of open and closed communities and, consequently, on the local – regional richness relationships was determined with approximation. The reasons are that the initial assumptions about the mechanisms of changes in species frequency were simplified and the factual data used to generate the reference curves were arbitrarily chosen. However, these results seem to be quite logical and the hypothesis of 'combined impact' of local and regional factors on the $S(N)$ ratio better fits our field data than the initial three hypotheses, including the species pool one. In particular, there are several reasons why our data disagree rather than agree with the species pool hypothesis.

First, there is a linear significant positive relationship between species richness and the size of the actual species pool of the subalpine meadow and alpine open communities. The results of the computer simulation show, however, that according to Cornell's hypothesis the expected relationship between local and regional richness is rather

curvilinear than linear. Earlier, similar results of the simulation were obtained by Caley and Schluter (1997). They concluded that the relationship between these variables is linear only in those cases when the sample size is large. Therefore, the smallest areas used by Caley and Schluter to represent local species richness were 2500 km^2. However, this approach was contested by Westoby (1998). In his opinion, is few would expect convergence of species richness due to within-community interactions to operate on a large scale. Most species would be simply separated onto different landscape elements (Westoby 1998).

On the contrary, our results show that if the sample size is small, proportional sampling is most likely to arise when local species richness and the size of the species pool depend on local processes or when local species richness is determined by local factors while the size of species pool is determined by local as well as regional factors.

Second, the species-pool hypothesis leaves open the question of why there is a considerable variation in the size of the actual pool communities with equal local species richness and vice versa. But this variation can be logically explained by the hypothesis of 'combined impact' of local and regional factors.

Finally, the assumption of the first scenario that the number of individuals in the small plots of both open and closed communities has no limit seems to be quite unrealistic. But if it is finite, then there are two factors that can limit the diversity of the communities even with weak species interactions: these are small population size and abiotic fluctuations. As the size of the species pool and hence local richness increases, average population sizes will decrease to local extinction because of abiotic fluctuations matching the rate of species immigration (MacArthur and Wilson 1963; Sale 1977; Tilman and Pacala 1993). Thus non-rigid limits to richness in small plots can arise due only to the physical environment, without strong species interactions. Presumably therefore, the test results are similar both for closed (mainly interactive) and open (mainly non-interactive) communities.

Thus, our results show that the species-pool hypothesis does not provide a unique theoretical basis for the linear local species richness-species pool relationships in both closed and open plant communities. Further studies are of course needed to verify or falsify this assumption. If it proves to be correct, then the influence of the species pool on local species richness can be determined to compare only communities located on sites with equivalent conditions of abiotic and biotic environments, but characterized by the species pool of a different size. The problem is that it is very difficult to choose such sites. It is considered, that comparative studies of communities growing under similar ecological conditions but in different geographical regions may be of substantial help here (Ricklefs 1987; Onipchenko and Semenova 1995; Hugueny 1997). However, it is always possible to challenge the statement that such sites are similar (Francis and Currie 1998).

The analysis of the local and regional richness of the communities on island habitats located under similar climatic conditions but characterized by a different area and, hence, by a different size of the species pool may prove to be the toughest test of the species pool hypothesis (Terborgh and Faaborg 1980; Hugueny and Paugy 1995; Duncan et al. 1998). But even in this case, higher local and regional richness of the communities on large islands (island habitats) can result from the fact that the habitats on these islands are more 'favorable' and hence supported more species than similar habitats on smaller islands (Kelly et al. 1989).

Thus, although the species-pool hypothesis seems to be very attractive, the results of its testing do not look unequivocally obvious, and therefore it needs further thorough examination.

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