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ON THE POSSIBLE ROLE OF LOCAL EFFECTS ON THE SPECIES RICHNESS OF ACIDIC AND CALCAREOUS ROCK GRASSLANDS IN NORTHERN HUNGARY

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Abstract: EWALD (*Folia Geobot.* 38: 357–366, 2003, this issue) stated that in Central Europe the number of calcifrequent species is higher than the number of acidofrequent species, while the range of acidofrequent communities is larger than that of the calcifrequent ones. All the explanations considered in his paper are based on an evolutionary spatial and temporal scale. In this paper we are trying to prove that local effects might also be important.

Five open rock grassland communities on different bedrocks, viz. rhyolite (acidic), andesite (slightly acidic), calcareous sandstone (slightly calcareous), limestone (calcareous) and dolomite (calcareous) were chosen for the analysis. Two parameters of the species-area curve (i.e., local richness and the slope of log area-species richness line) were estimated based on all species and on rock specialist species separately. With this method we could simultaneously study three attributes of diversity: local species number, the slope of log area-species richness line, and species pool size.

We found that the size of the regional species pool is determined by local effects through local richness (slopes do not differ significantly). Consequently, in this case weathering is a more important characteristic for bedrocks than the Ca^{2+} content. The extremely high number of rock species on dolomite is also determined by local effects; the fine, continuously changing pattern of microhabitats makes the role of competition weaker.

The slope of log area-species richness line, calculated for the rock specialist species is unambiguously higher on the calcareous grasslands. The difference can be explained by the smaller species pool on acidic rocks caused by the lower speciation ability. This is supported by the fact that the endemic species of dry habitats are concentrated on the calcareous ones. One possible explanation for the lower speciation ability could be that adaptation to acidic habitats is more difficult than to calcareous ones.

The different behaviour of rock specialist species is the consequence of the limited permeability of the surrounding landsape. Hence, on calcareous habitats the arrival of all species from the larger species pool needs more time.

Keywords: Dolomite, Regional scale, Rocky grasslands, Specialists, Species-area relationship, Species pool

INTRODUCTION

Temperate and arctic plant communities of neutral soils tend to be more species-rich than those of acid soils (GRIME 1979, GRUBB 1987, PEET & CHRISTENSEN 1988, GOUGH et al. 2000). EWALD (2003, in this issue) suggested that this may be due to the so-called species pool effect (ZOBEL et al. 1998), i.e., the number of species that are able to grow in acid soil is limited. He demonstrated the lower species pool of acid soils by the fact that in Central Europe the number of calcifrequent species (according to their Ellenberg indicator values) is higher than the number of acidofrequent species, while the area of acidofrequent communities is larger than that of calcifrequent ones. However, such correlation between local richness and size of species pool cannot be interpreted as evidence of the species pool effect (i.e., HERBEN 2000, BARTHA & ITTZÉS 2001), because local effects can also generate such correlation (HERBEN 2000). In this paper we argue that local effects might also play an important role in the differences in species richness of communities in calcareous and acidic soils.

Local species richness is determined by the size of the species pool (top-down effects) and local interactions (e.g. competition) (GRACE 2001). In the analysis of the relation between species pool size and local species richness, species pool is supposed to be constant and not influenced by local interactions on an ecological time scale (ZOBEL 1997). This is true if species pool is determined by the fundamental niche (habitat requirement in monoculture) of the species. However, in most cases, species pools are determined based on field observations. In such cases, the species pool is influenced by local interactions (bottom-up effect). The first type of species pool is called non-filtered (ZOBEL 1997) or potential (GRACE 2001) species pool, while the second is called filtered (ZOBEL 1997) or observed (GRACE 2001) species pool.

Ellenberg indicator values were determined by field observations, not by monoculture experiments, thus they indicate the realized niche of a species. Consequently, species pool of acido- or calcifrequent species is observed species pool (sensu GRACE 2001), whose size may be influenced by local interactions (LEPŠ 2001).

Based on the above-mentioned reasons, we deem it more appropriate to refer to species of low R indicator value as acidofrequent instead of acidophilous species, since no measurement or observation supports that these species prefer acidic habitats (this would be indicated by the -philous suffix), existing data only show that these species are frequently present in such habitats (this is indicated by the -frequent suffix). For the same reason, we will use the term calcifrequent instead of calciphilous in this paper (JUHÁSZ-NAGY 1984, 1986).

In this paper species-area curves are used as a framework, because earlier studies showed that they are solid theoretical bases to consider the relationship between local species richness and size of the species pool (cf. BARTHA & ITTZÉS 2001).

The criteria of habitat selection were

(a) long and well-known acidity gradients within a geographical region,
(b) no substantial influence of human activities,
(c) the presence of species that live only in this habitat.

The second criterion was necessary because human activities may influence the ratio of acido- and calcifrequent species. The third criterion allows us to demonstrate that results strongly depend on whether all species or only the specialist of the habitat are considered. Based on the mentioned criteria, we chose five open rock grassland communities in northern Hungary, which are dominated by *Festuca* species and have developed on different bedrock: rhyolite (acidic), andesite (slightly acidic), calcareous sandstone (slightly calcareous), limestone (calcareous) and dolomite (calcareous). These communities have supposedly been stable for a long time; they have not been heavily influenced by human activities. Their soil is shallow, thus soil acidity is mainly determined by the compound of the substrate (other processes, e.g. leaching, are unimportant). There are many species that occur only in this habitat. In this paper these species will be called "rock specialist species".

SPECIES-AREA RELATIONSHIP

The relationship between species number and area is most often characterized by either the power function suggested by Arrhenius (1921) or by the logarithmic function suggested by Gleason (1922). Neither relationship can be considered generally valid unambiguously based on their fitting to real data (Connor & McCoy 1979), nor based on their relationship to theoretical distributions (Fisher et al. 1943, Preston 1948, 1960, 1962, Williams 1944, 1947). Fortunately, from the viewpoint of our investigations, both functions give qualitatively the same results. We use the logarithmic function ($S = C + z \ln A$, where S = the species number, A = the observed area, C and z are parameters) because parameter C can be interpreted better in this case (i.e., it is the local species richness).

The values in the equations belonging to acidofrequent species are subscripted by a, and the values belonging to calcifrequent species by c. The paradox reviewed by Ewald (2003, in this issue) concerning the species-area relationship can be written as follows:

$$A_c < A_a$$

and

$$C_c + z_c \ln > C_a + z_a \ln A_a$$

From a mathematical point of view, the two inequalities contradict each other if and only if $C_c \leq C_a$ and $Z_c \leq Z_a$. That is, the two inequalities can be valid at the same time only if at least one parameter in the equation relating to calcifrequent species is greater than the corresponding parameter relating to acidofrequent species.

METHODS

Sampling

The relevés for all five investigated communities were taken in northern Hungary, on different substrates in the Pannonian Range, on an area that measures roughly 200 km in the east-west direction and 100 km in the north-south. The climate of the area is relatively uniform; towards the western part it is submediterranean and towards the east the continental characteristics begin to dominate. The maximum distance between the relevés for each substrate is 15–25 km. All communities are open rock grasslands dominated by xerofrequent perennial grasses and all have a southern exposure. The main data of relevés are summarized in Table 1.

The bedrocks

Triassic dolomite weathers slowly chemically and intensively physically. Due to the fast formation of small debris, dolomite mountains have steep slopes. Open rock surfaces are

Table 1. The main data of relevés: bedrock, name of association, location, number of relevés, plot size, author/source. Plot size = 4 m × 4 m.

Bedrock	Name of association	Location	No. of relevés	Author/Source
Dolomite	*Seseli leucospermi-Festucetum pallentis* ZÓLYOMI (1936)1958	Budai Mts.	20	ZÓLYOMI in TÖRÖK & ZÓLYOMI 1998
Limestone	*Campanulo-Festucetum pallentis* ZÓLYOMI 1958	Bükk Mts.	25	ZÓLYOMI in TÖRÖK & ZÓLYOMI 1998
Sandstone	*Cleistogeni-Festucetum pallentis* CSIKY 2002	Nógrád-Heves--Borsodi Wold	28	CSIKY 2002 (10 relevés) and RÉDEI (18 relevés), unpubl. data
Andesite	*Minuartio-Festucetum pseudodalmaticae* (MIKYŠKA 1933) KLIKA 1938	Visegrádi Mts.	30	HORÁNSZKY in TÖRÖK et al. 1994
Rhyolite	*Minuartio-Festucetum pseudodalmaticae* (MIKYŠKA 1933) KLIKA 1938	Zemplén Mts.	39	SIMON 1977

frequent. This favours the formation of rocky grasslands (GAMS 1930, ZÓLYOMI 1942). The soil pH of the rock grasslands is 7.2 on average (in water extract, KOVÁCSNÉ LÁNG 1966).

Triassic limestone is a karstic rock that dissolves easily chemically. The soil is slightly alkaline with a pH of 7.3–7.6 (in water extract, KOVÁCSNÉ LÁNG 1966).

Oligocene calcareous sandstone weathers quickly, thus the grasslands of steep surfaces are open, and erosion is so rapid that soil formation and leaching cannot start. In the rocky grasslands of the soil pH is 7.2 on average (in water extract).

Miocene andesite is a neutral or slightly alkaline volcanic rock. Leaching can be strong on single standing rocks, leading to the formation of slightly acidic skeletal soils. In the open rock communities soil pH is 6.5 on average (in water extract, HORÁNSZKY 1964).

Miocene rhyolite is an acidic volcanic rock. The soils formed on it are strongly acidic. In the soil of rock grasslands pH is 5.1–5.5 (in water extract, SIMON 1977).

Statistical analysis

Acido/calcifrequent characters of species were described by their R-indicator values according to Ellenberg's system (ELLENBERG et al. 1991) applied to the Hungarian flora by BORHIDI (1995). A low value means acidofrequent species, while a high value means a calcifrequent one.

We ordered the different communities according to their R-value spectrum in order to verify that the acidity gradient of the parent materials can really be observed in the vegetation data. For ordination, concentration analysis was used (FEOLI & ORLÓCI 1979). PRÉCSÉNYI (1995) suggested applying this method to investigate the indicator values instead of the mathematically incorrect averaging of ordinal data. In order to fulfil the conditions of the method, R values 3 (acidofrequent species, mostly in acid soils) and 4 (moderately acidofrequent species), and values 8 (calcifrequent species) and 9 (specialists of basic soils)

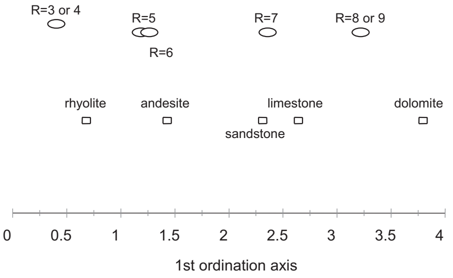

Fig. 1. Ordination of grassland communities and R indicator value categories by concentration analysis according to PRÉCSÉNYI (1995). Importance of axes was tested by randomization (BOTTA-DUKÁT & RUPRECHT 1999, see details in Appendix 1). Only the first axis proved to be significant, therefore other axes were not plotted. Concentration analysis produces parallel ordination of rock grassland communities and species groups based on R indicator values; these are plotted in two different rows.

were merged (c.f. BOTTA-DUKÁT & RUPRECHT 1999). Significance of ordination axes was investigated by a randomization test (BOTTA-DUKÁT & RUPRECHT 1999). (For more details about this analysis see Appendix 1).

In the equations of logarithmic species-area curve (see above), parameter C means the species number in a unit area, and z means the log area-species number slope. In our study, the increase in area was replaced by combining the species list of relevés; the number of relevés was then used as a proxy for area. This was possible because the plot size was constant. In this case parameter z shows the difference of species composition among relevés. Thus the size of the species pool depends on local species richness and the difference in species composition on the different locations. The disadvantage of the method used for increasing the area is that the species numbers belonging to different relevés are not independent of each other, therefore the maximum likelihood estimation of slope by least squares method cannot be applied. Thus linear regression cannot be carried out, because it overestimates the slope. Therefore the species richness of relevés was used for estimating parameter C and Dahl alpha for parameter z (DAHL 1960; cf. Appendix 2). In the first case the communities were compared using a Kruskal-Wallis test with subsequent Dunn post hoc test (ZAR 1999), while in the latter the jackknife method was used for the estimation and calculation of the 95% confidence interval (EFRON 1982). The calculations were carried out for all species and also for rock specialist species only.

RESULTS

Only the first axis of the ordination carried out on the R indicator value spectra proved to be significant (based on the randomization test only the first canonical correlation was significantly higher than the one expected in the random case). The R-values are located on this axis in increasing order. It means that low values on the axis indicate acidic character, while high values indicate basic character. Relevés from dolomite were most basifrequent, this was followed by limestone mildly basifrequent and sandstone slightly basifrequent species pool. The species pool of andesite is slightly, while that of rhyolite is more acidofrequent (Fig. 1).

Among the investigated relevés the slightly acidic andesite grasslands were significantly the richest in species (Fig. 2a). These were followed by dolomite and sandstone grasslands,

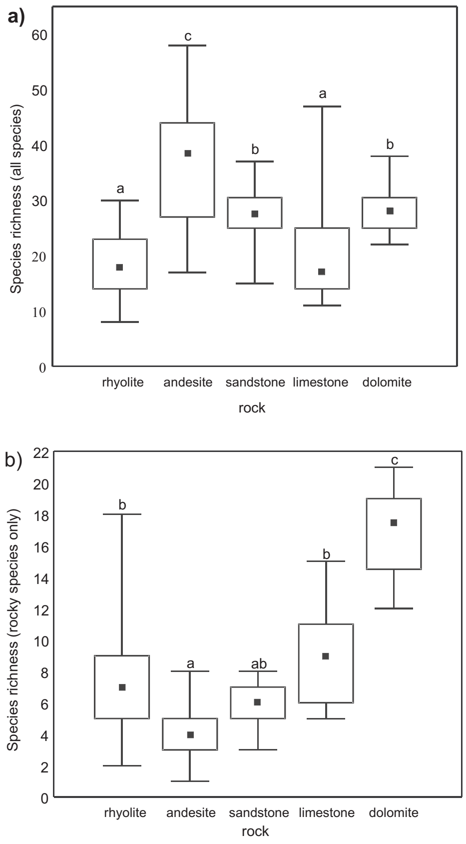

Fig. 2. Local species richness in 4 × 4 plots (median, inter-quartile range, range) in the five rock grassland communities: (a) all species, (b) rock specialist species only. Communities were compared using Kruskal-Wallis test, then Dunn post hoc test. The same letter above bars indicates that there are no significant differences between communities. The box encloses the middle 50% quartiles, while the median is indicated by the black square and range of values by the lines.

which cannot be distinguished from each other significantly. The poorest in species are rhyolite and limestone grasslands, which also do not differ significantly from each other.

There are significant differences between the relevés as regards the number of rock specialist species in relevés, but these differences cannot be explained by the acido- and calcifrequent character of communities (Fig. 2b). The number of rock specialist species is lowest on andesite grasslands, and highest on dolomite. The other three communities, that is acidic rhyolite, the basic limestone, and sandstone show intermediate values, and do not differ from each other significantly (the last one does not differ from andesite significantly either).

If we plot the total species number as a function of the proportion of rock specialist species, then the dolomite grasslands sharply separate from the others (Fig. 3) due to the medium-high species number with a high proportion of rock specialist species. The proportion decreases slightly, but not significantly (slope = -0.17, t = 1.94, n.s.) with an increase in species number. The grasslands of the other four substrates form a sickle-like sequence on the graph, where a decrease in species number entails an increase in rock specialist species. Among them the andesite grasslands are characterized by a rather low proportion of rock specialist species and the high species number; there is a significant, strongly negative correlation between them (slope = -0.89, t = 3.26, P < 1%). On sandstone, the low proportion of rock specialist species accompanies a medium species number with significant negative correlation (slope = -0.35, t = 2.49, P < 5%). On limestone and rhyolite, the low species number is accompanied by a higher proportion of rock specialist species, and correlation is significantly negative on limestone (slope = -0.26, t = 2.27, P < 5%), while on rhyolite it is also slightly negative, but not significant (slope = -0.09, t = 1.41, n.s.).

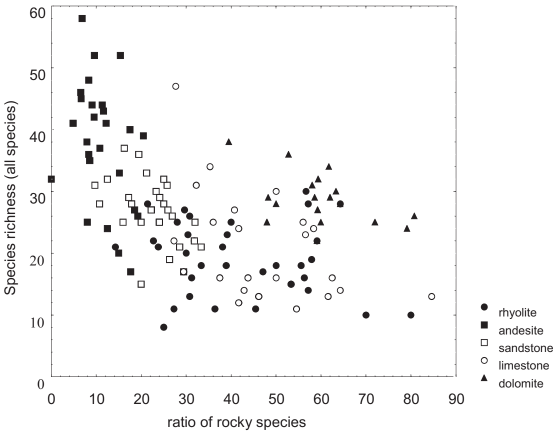

Fig. 3. Relationship between the species richness and the proportion of rock specialist species.

Dahl alpha values calculated for all species did not differ significantly for the five communities (Fig. 4a). In the case of Dahl alpha calculated for rock specialist species (Fig. 4b), however, the differences can probably be connected to the characteristics of the substrate. The value is lowest on strongly acidic rhyolite, and significantly higher on the slightly acidic andesite and the calcareous sandstone, which do not differ significantly from each other. It is highest on the strongly calcareous limestone and dolomite, whose alpha values are significantly higher than that of other communities, but do not differ significantly from each other.

The estimated species pool (estimated number of species in 100 relevés) is much higher in andesite than in the other four communities, which do not differ considerably (Fig. 5a). The estimated pool of rock species (Fig. 5b) increased with decreasing soil acidity from rhyolite to limestone (andesite and sandstone do not differ considerably). The pool of rock species is even higher in the dolomite grassland than in limestone, however these two communities do not differ considerably in soil pH.

DISCUSSION

Because different mechanisms can generate the same pattern, a hypothesized mechanism cannot be verified by observing the pattern that can be generated by this mechanism (HERBEN 2000). Therefore, in discussing our results, we can only say that a certain mechanism is possible (i.e., we can only point out the possible importance of local effects).

A hypothesized mechanism, however, can be falsified by observing patterns; i.e., if the observed pattern cannot be generated by this mechanism. In our opinion, the effects of large-scale mechanisms linked to soil acidity (and consequently the patterns generated by them) should be the same within communities of either acidic or calcareous, or it should change gradually. It allows us to falsify the hypothesis that the observed species richness patterns are generated by large-scale mechanisms linked to soil acidity.

In what respect are calcifrequent rock-grasslands more diverse?

We can say that based on our results summarized in Table 2, the species richness indicators obtained from different scales and set of species differ in their response to the acidic-basic character of the substrate.

The species number in the relevés can be only partly explained by the number of specialists. Andesite grasslands were poorest in rock specialist species, while they were most

Table 2. Comparison of the studied communities in parameters of soil and species richness. Rows that share the same letter do not differ significantly at $\alpha = 0.05$.

Substrate	pH of soil	Average species number of relevés		Slope of species-area relationship		Estimated species pool of 50 relevés	
		all species	rock specialists only	all species	rock specialists only	all species	rock specialists only
rhyolite	5.1-5.5	18.9^{a}	7.1^{b}	24.9	2.2	116.4	15.6
andesite	6.5	36.6^{c}	4.2^{a}	35.5	6.8	175.4	30.6
sandstone	7.2	27.3^{b}	5.9^{ab}	23.8	6.4	120.5	30.9
limestone	7.3–7.6	20.6^{a}	9.3^{b}	21.1	12.5	103.2	58.1
dolomite	7.2	28.5^{b}	16.7^{c}	21.3	13.6	111.7	69.8

species-rich. Sandstone, which is also poor in rock specialist species, is also rather rich in species. The phenomenon is explained by the ratio of total species number and rock specialist species number. While on dolomite, limestone, and rhyolite this ratio is rather high and (except for limestone) does not correlate significantly with species number, on sandstone and andesite the relatively low ratio has a strong negative correlation with species number. This shows that the species richness of the two latter rocky-grasslands is not caused by the high number of their specialists (rock specialist species), but probably by the higher habitat-diversity within sampling plots. The surface forms on these substrates do not favour formation of really connected rocky-grassland communities, but they make a mosaic with steppe patches of deeper soil even inside the 4 m × 4 m plots . Therefore, the relevés are rich in dry grassland generalists. Among the three highly rocky grasslands the dolomite has higher both species number and ratio of rock specialist species. Several dolomite specialists are added to the pool of calcifrequent rock specialist species, thus increasing the number of rock specialist species. Species requiring deeper soil play a less important role. This results in the outstanding ratio of rock specialist species.

Altogether it can be said that none of the two indicators of local species richness (total species number and rock specialist species number) can be explained definitely by the acidic or alkaline state of the substrate; i.e., neither they are homogeneous within acidic and within calcareous communities, nor do they change gradually along the acidity gradient.

We experienced significant differences between the behaviour of the slope of species-area relationship calculated for all species and for rock specialist species only. Dolomite and limestone grasslands have a higher slope of rock specialist species and thus they appear more diverse. It is important to note that significant flora-geographical differences cannot be shown within the different relevé groups. The differences among the rock specialist species were masked by the homogeneity of the accompanying generalists when all the species were involved. Thus, the slope of species-area relationship calculated for specialists is the only feature that is clearly higher on the strongly calcareous habitats.

On rhyolite, the same few acidofrequent rock specialist species appear in all relevés. On andesite and sandstone, the low number of rock specialist species found is chosen randomly from the slightly larger pool of primarily neutral or slightly acidofrequent or calcifrequent rock specialist species; this increases the difference between the relevés. The limestone

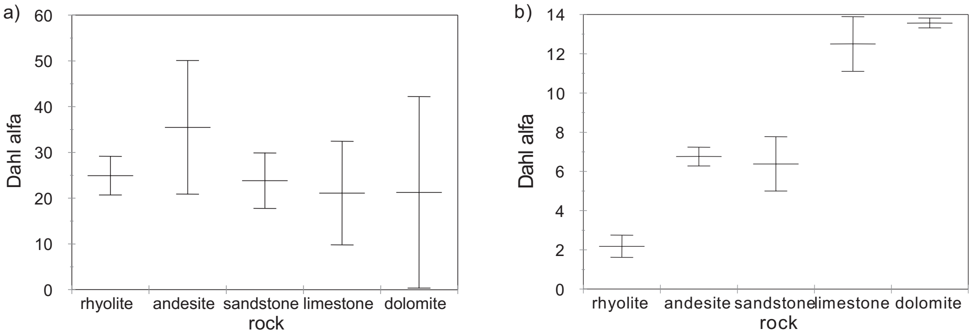

Fig. 4. Dahl alpha in the different rock grassland communities (estimated value and 95% confidence interval calculated by jack-knife method) calculated for all species (a) and rock specialist species only (b).

relevés, which contain rock specialist species in similar numbers to rhyolite, prove to be much more diverse in this respect, and thus have a much bigger pool of rock specialist species. The high number of rock specialist species per relevé and the high diversity on dolomite mean an exceedingly large pool of rock specialist species.

The smaller species pool in strongly acidic habitats may be also due to physiological constraints. The low pH value influences nutrient uptake of plants in many ways (LUCAS & DAVIES 1960). Acidofrequent plants have developed several mechanisms for warding off this effects, which point to strong, more time-demanding specialization, thus limiting the number of specialists.

Top-down or bottom-up effects?

Two types of causation can be considered between the shape of the species area curve and the size of the species pool:

(1) bottom-up effect: the shape of the species-area curve is determined by local effects and the size of species-pool depends on this;

(2) top-down effect: the size of the species-pool is determined by global effects (e.g. vegetation history) and it influences the shape of the species-area curve.

Most often both effects may take place, but their importance varies. If all species are considered, species-pool – which in this case is mainly made up of xerofrequent, generalist species that can be found in other habitats – is significantly higher than local species number. Thus, in our opinion, it does not limit the species richness of communities. The observed differences between the studied communities suggest that the species number is primarily determined by the weathering characteristics of the substrate that is not simply related to the calcium content of bedrock. This local effect, however, probably has an influence by changing the size of the (filtered) species pool (bottom up effect), i.e., many xerofrequent generalists can establish on andesite and sandstone, where habitat conditions are not too extreme, and shallow and deep soil patches pattern up at a scale that is finer than the size of a relevé.

There is no difference between calcareous and acidic rock grasslands in the local number of rock specialist species; however, the number is exceedingly high on dolomite. Due to the peculiar weathering characteristics of dolomite, the spatial pattern of soil depth differs from that of the other rock grasslands, where a rougher mosaic of soil pouches and rock surfaces is characteristic. In contrast, on dolomite this pattern is extremely fine-grained and the patches of deep fertile layers, the so-called soil pouches, are missing. Conditions are fairly favourable in soil pouches, but competition is stronger as well (GRIME 1979, GOLDBERG & NOVOPLANSKY 1997), excluding weaker competitors, thus greatly reducing diversity. Soil pouches do not form on dolomite, and plants root among the debris, thus forming a finer pattern. Since there are no favourable patches on dolomite, the aggregation of species, and thus competition is far less important. Intensive erosion and the resulting quick rearrangement of vegetation pattern (BARTHA et al. 1998) further reduce the importance of competition (HUSTON 1979). The species pool of this heavily stressed, but weakly competitive habitat, is rather large; this is partly explained by the high persistence (survival of relic species), and partly by the high speciation (formation of endemisms) rate (ZÓLYOMI 1942, 1950, 1958). Thus the high species pool on dolomite is a consequence of a long-term cumulative local effect (low competition). Dolomite is locally very rich in rock specialist species partly due to the larger species pool, and partly directly due to the low competitive intensity.

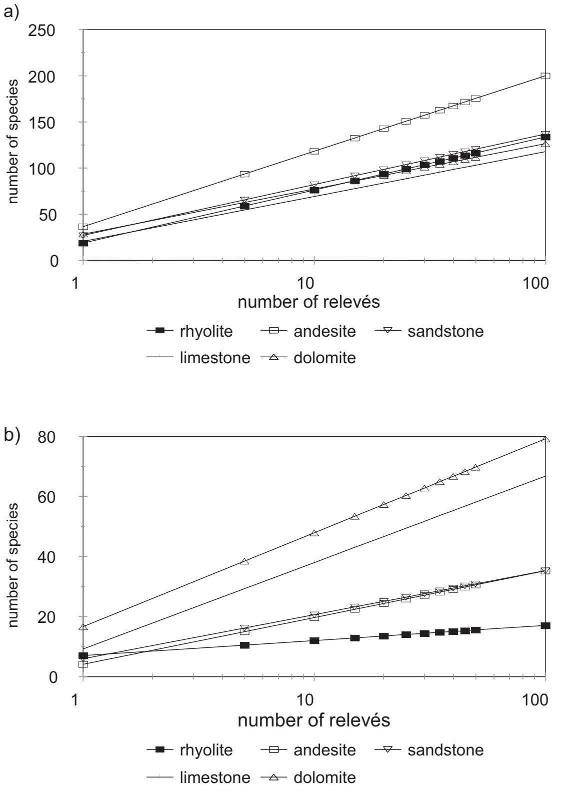

Fig. 5. The species-area curves based on the estimated parameters (*C* and *z*) for all species (a) and rock specialist species only (b).

Significant differences can be found in the slope of species-area relationship (the *z* value) calculated for rock specialist species in favour of the calcareous habitats. Mathematically, the species pool size is determined by the local species number and slope together. From a biological viewpoint, however, the interplay among the three measures is not so simple. For example, local species richness may be restricted by low species pool size, but the observed species pool is the sum of species in local assemblages. Dependent or independent variables are therefore hard to define. The difference in slopes of species-area relationships could be explained by the difference in the ratio of local species richness and species pool size or by the different heterogeneity of habitats at a macro scale (e.g. mineralogical heterogeneity). However, we have not found any proof for the heterogeneity of calcareous habitats being larger at a macro scale. The lower slopes of rock specialist species in silicate-rock grasslands is caused by the low species pool.

The different behaviour of rock specialists is explained by the fact that the surrounding area, which is more or less permeable for generalists, has an isolating effect for rock specialists. This results in a lower settlement rate (MACARTHUR & WILSON 1967). In the case of large species pools, characteristic of calcareous communities, the low settlement rate increases the difference between relevés significantly, while the limited species pool of silicate- and sandstone-rock grasslands arrive much earlier even at the same colonization rate.

CONCLUSIONS

EWALD (2003, in this issue) studied the role of evolutionary space and time-scale processes in the formation of species pools. In our article we wanted to draw attention to the fact that the role of local effects cannot be excluded. Our investigations have shown that the obtained results heavily depend on whether all species or just a selected set of species (i.e., specialists of the habitat) are investigated, and that habitats formed on calcareous and acidic substrate cannot be handled as separate but uniform groups, and that there can be significant differences within the groups.

From the viewpoint of local species richness determined based on the full species list, the differences between the rocky grasslands are at least partly caused by local effects. The relative importance of this effect cannot be determined from the data included in this study, because most of the species appear not only in rocky grasslands but also in other communities as well. If the rock specialist species only are investigated, then the high local species number of dolomite and its high species pool can both be connected to local processes (low competition) as well. For the other four rocky grasslands it is rather the evolutionary or vegetation history that causes the difference in species pool, and this low species pool causes the low local species number of acidic rocky grasslands. In Hungary the vegetation histories of the two types of habitats were not so different as in Central Europe, because during the glaciations there was no ice cover in the Carpathian Basin. Thus the scenario described by Ewald is not very likely here. In our opinion it is rather the much higher speciation rate that is responsible for the high species pool of calcareous rock grasslands, which is supported by the high number of endemisms as well.

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APPENDIX 1

Analysis of indicator values by concentration analysis

Concentration analysis was developed by Feoli & Orlóci (1979) for analyzing the relationship between the groups of species and the groups of relevés. Précsényi (1995) pointed out that if species are divided into groups based on their indicator values, the pattern of indicator values can be analyzed by this method.

The main point of the method is the following: f_{jk} is the total number of occurrences of species belonging to species-group j in relevés belonging to relevé-group k. The value of f_{jk} depends on the sizes of species-group j and relevé-group k. Eliminating this effect the corrected values (F_{jk}) have to be used in the analysis (Orlóci & Kenkel 1985):

$$F_{jk} = \frac{f_{jk}}{p_j q_k} \cdot \frac{\sum_{g=1}^{n} \sum_{h=1}^{m} f_{gh}}{\sum_{g=1}^{n} \sum_{h=1}^{m} \frac{f_{gh}}{p_g q_h}}$$

where:

n = number of species-groups
m = number of relevé-groups
p_j = number of species belonging to group j
q_k = number of relevés belonging to group k.

In the analysis we regard F as a contingency table, although this matrix may contain fractions. First, the independence of species grouping and the grouping of relevés is statistically tested. If they are independent of each other F will not significantly differ from F^0:

$$F_{jk}^0 = \frac{\sum_{j=1}^{n} F_{jk} \cdot \sum_{k=1}^{m} F_{jk}}{\sum_{j=1}^{n} \sum_{k=1}^{m} F_{jk}}$$

This hypothesis can be tested by χ^2- (Feoli & Orlóci 1979) or G^2-test (Précsényi 1995). If F significantly differs from F^0, the matrix F will be analyzed by correspondence analysis. The scores of species and relevé groups in the same $\min\{m,n\}-1$ dimensional ordination space and the canonical correlation coefficients between scores are obtained this way. The sum of canonical correlation coefficients are connected with the χ^2 value computed earlier:

$$\chi^2 = F_{..} R_1^2 + F_{..} R_2^2 + \ldots + F_{..} R_s^2$$

where:

S = $\min\{m,n\}-1$,
R_1 = canonical correlation between first scores of species-groups and first scores of relevé-groups,
$F_{..}$ = the grand total of F

The χ^2 value can be taken to components. The values of canonical correlation coefficients show the importance of the axes. If the value of $F_{..} R_j^2$ is smaller than the appropriate critical value of χ^2 distribution with $(m-1)(n-1)$ degree of freedom, the jth axis may be left out of consideration.

Botta-Dukát & Ruprecht (1999) showed that decreasing the number of species groups increases efficiency of pattern recognition, because due to the decreasing number of groups the probability of fulfilling the preliminary conditions of χ^2-test increase. They suggested that the significance level of canonical correlation should be tested by randomization (by the so-called "random group size" method) instead of the comparison critical values obtained from χ^2 distribution, because it results in correct significance levels, even if the preliminary conditions of the use of χ^2 distribution are not fulfilled. During this randomization indicator values are assigned to the species randomly with the constraint that all indicator values have to be assigned at least one species.

APPENDIX 2

Estimation of the slope of Gleason species-area relation by Dahl alpha

Dahl alpha (DAHL 1960) was originally introduced to estimate the α parameter of logarithmic distribution. It is calculated by

$$\alpha = \frac{S_n - \overline{S}}{\ln n}$$

where:
$\overline{S}$ = average species number of relevés
S_n = number of species in the pooled species list of n relevés.

Theorem:
Expected value of α is the z parameter of Gleason species-area relationship: $E(\alpha) = z$.

Proof:
(1) As a starting point for our proof we use the following identity:

$$E(\alpha) = \frac{E(S_n) - E(\overline{S})}{\ln n}$$

(2) Let the size of all relevés be the same, and let us measure the area by the number of relevés, then A = 1 for single relevés and A = n for the pooled species list.

(3) By Gleason equation $E(\overline{S}) = C + z \ln 1 = C$,

(4) and $E(S_n) = C + z \ln n$.

(5) By using relations (1), (3) and (4) it is easy to see that $E(\alpha) = \dfrac{C + z\ln n - C}{\ln n} = z$.

Thus the theorem is proved.