# Species diversity of plant communities on calcareous screes: the role of intermediate disturbance

## Druhová diverzita rostlinných společenstev na vápencových sutích: význam intermediární disturbance

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Dedicated to the memory of Emil Hadač

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The intermediate disturbance hypothesis predicts that species diversity in biotic communities should peak at intermediate levels of disturbance. The vegetation of eight calcareous screes in the Northern Calcareous Alps, Austria was studied to test this hypothesis. Data on total vegetation cover and on cover of individual species were obtained from 0.25 $m^2$, 0.5 $m^2$, and 1.0 $m^2$ plots. An index [100 – vegetation cover (%)] was used as a surrogate for direct quantification of disturbance (movement of stones and destruction of biomass). Its suitability was substantiated by the observation of position changes of marked stones after two years. In agreement with the intermediate disturbance hypothesis, significant unimodal responses of both species richness and species diversity to disturbance were found using plots of all three sizes. However, the maxima of species richness- and species diversity-disturbance curves were shifted towards higher vegetation cover (= lower disturbance) with increasing mean diameters of the scree-building stones. This shift can be interpreted either as a synergistic effect of disturbance frequency combined with disturbance intensity/extent, or as a result of an increase in spatial heterogeneity promoting species coexistence in successionally more advanced patches of vegetation.

Keywords: Alps, patch dynamics, species coexistence, species richness, substrate instability, succession, successional mosaic

## Introduction

Using the broadest available definition provided by ecologists, a disturbance is an event that alters the niche opportunities available to the species in a system (Shea et al. 2004). In the context of plant community ecology, disturbance is usually defined as a partial or complete destruction of biomass, leading to the increase of available resources that can be utilized by new individuals (Grime 1979, van der Maarel 1993). Herbivores, digging animals, storms, fires, draughts, floods, landslides, cryoturbation, and avalanches are among the best known agents of natural disturbance in terrestrial systems (Mooney & Gordon 1983, Tilman 1983, Rejmánek 1984, Collins 1992, Komárková 1993, Guno 1996, Pollock et al. 1998). The intermediate disturbance hypothesis (IDH) predicts that species richness and species diversity, given a suitable range of environmental disturbance, should peak at intermediate levels of disturbance. The usually recalled mechanism is that, under intermediate disturbance levels, competitive exclusion of faster-colonizers-weaker-competitors is

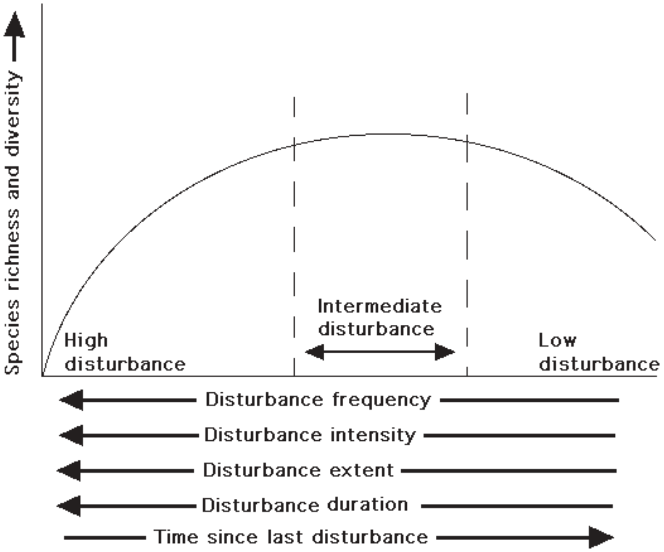

Fig. 1. – The intermediate disturbance hypothesis of the dependence of species richness and diversity on disturbance. Based on Connell (1979), Li et al. (2004), and Shea et al. (2004).

balanced by partial or complete destruction of slower growing competitive dominants (Paine & Vadas 1969, Grime 1973, Horn 1975, Connell 1978, Sousa 1979, Rejmánek 1984, Petraitis et al. 1989, Wilson 1994, Molino & Sabatier 2001, Shea et al. 2004). However, the generality, as well as the correct interpretation of this unimodal diversity-disturbance relationship have been repeatedly questioned (Fox 1981, Schwilk et al. 1997, Mackey & Currie 2001, Arim & Barbosa 2002, Ikeda 2003, Li et al. 2004).

One of the obstacles in completing a simple diversity-disturbance theory is the fact that “disturbance” can be quantified in several meaningful ways (Connell 1978, Malanson 1984, Li et al. 2004, Table 1 in Shea et al. 2004) (Fig. 1):

(a) **Frequency**: The IDH is most commonly interpreted as species coexistence promoted by “intermediate-timescale disturbances”, i.e., disturbances recurring through time at intermediate frequencies.

(b) **Intensity** (the vigour of the disturbing force): Many disturbances exhibit measurable intensities, e.g., fire temperature, salinity of water intrusion, or the amount of biomass grazed.

(c) **Extent** (the area affected by the disturbance): Spatial extent of a disturbance is often consequential for the rate of recolonization (Armstrong 1988). However, where species regenerate from the seedbank or vegetatively, the intensity of disturbance is more important than the area affected by the disturbance.

(d) **Duration**: Duration of a disturbance (e.g., time grazing animals spent in one area, duration of a flood or fire) is often difficult to distinguish from its intensity, but biological consequences may be not always the same.

(e) **Time since last disturbance**: Intervals between disturbances are often too long to allow sufficient number of observations of permanent plots in limited time. Therefore, the

Fig. 2. – Calcareous screes in Hochschwab, Austria. Active stony screes serve as one of the best examples of repeatedly disturbed habitats. Their plant communities should provide suitable systems to study diversity-disturbance relationships.

common practice is that states of plots are described at one point in time and related to the time since the last disturbance. The time is either known or has to be indirectly assessed (for example, as a total vegetation cover or as an age of the oldest trees present). This approach is justified, because the mean time since the last disturbance is a reciprocal function of the mean disturbance frequency. However, it is important to note that the temporary increase of species richness in initial stages of ecological succession ("noninteractive stage") was proposed and tested as a general feature of successional dynamics without any explicit relationship to the IDH (Wilson 1969, Rejmánek & Rejmánková 2002).

Obviously, an environmental disturbance is a multidimensional concept and two-dimensional schema of the IDH (Fig. 1) is inevitably an oversimplification. Outcomes of many disturbances are results of interactions between two or more disturbance attributes (a, b, c, d). Consequently, they represent a major interpretation challenge for ecologists (McCabe & Gotelli 2000, Shea et al. 2004). Separation of individual attributes can be done in properly controlled manipulative experiments, but in the real nature usually two or more of them are linked together to the extent that separate analyzes are unrealistic.

Another complication is the role of spatial heterogeneity. Wilson (1994), Sheil & Burslem (2003), and Roxburgh et al. (2004) distinguish between "between-patch" and "within-patch" species coexistence mechanisms. The first one, operating via spatially patchy disturbance, is usually associated with the IDH. The terms "between-patch mechanism" (Wilson 1994) and "successional mosaic hypothesis" (Chesson & Huntly 1997) have been used in this connection. However, both mathematical models and empirical data suggest that intermediate levels of disturbance frequencies can promote species coexistence even without the creation of spatial heterogeneity (Bonnis et al. 1995, Chesson & Huntly 1997, Roxburgh et al. 2004).

As active stony screes (talus heaps), with their unstable surfaces, are one of the best examples of repeatedly disturbed habitats, their plant communities should provide suitable systems to study diversity-disturbance relationships (Fig. 2). This is true especially for European calcareous screes with their species-rich floras (Jenny-Lips 1930, Zollitsch 1968, Hadač et al. 1969, Herter 1990, Valachovič et al. 1997). We studied the structure and composition of plant communities on limestone screes in the Northern Calcareous Alps, Austria, with the goal to answer the following questions: (1) Is there a significant unimodal response of species richness and species diversity to disturbance in plant communities on calcareous screes? (2) Are the results the same if plots of different sizes are used for analyses? (3) Do the species richness-disturbance and species diversity-disturbance curves follow the same pattern? (4) Does the level of spatial heterogeneity, expressed as a mean stone diameter, affect the richness-disturbance and diversity-disturbance relationships?

## Methods

### *Study sites*

The study sites were situated in the Northern Calcareous Alps, Austria, at elevations of 760–1200 m (Table 1). The aspects of all plots were similar, generally ranging from SE to SSW. The mean slope of screes varied from 17° to 34°. Stones forming studied screes were Triassic limestones of the Juvavian Unit (Oberhauser, 1980). The general vegetation

Table 1. – Locations and characteristics of the screes studied in the Austrian Alps.

| Location | Coordinates | Elevation (m) | Code | No. of plots (1 m$^2$) | Stone diameter (cm, mean ± s.d.) |
|---|---|---|---|---|---|
| Rax, area of Jacobskögel, Lammelbrünnel, Gsolhirn | 47° 43' N<br>14° 45' W | 1100–1180 | A | 12 | 1.9±1.7 |
| | | | B | 19 | 9.8±5.9 |
| | | | C | 17 | 11.7±6.8 |
| Hochschwab, Bodenbauer-Trawies | 47° 36' N<br>14° 45' W | 950–1200 | D | 12 | 1.5±1.4 |
| | | | E | 12 | 6.6±4.8 |
| | | | F | 21 | 6.0±4.3 |
| | | | G | 12 | 7.7±5.1 |
| Salza, Weichselboden | 47° 41' N<br>15° 11' W | 760 | H | 27 | 1.8±1.6 |

description of this area is provided by Wendelberger (1971), Pachernegg (1973), Hübel & Holzner (1975), Dirnböck & Greimler (1997) and Dirnböck et al. (1999). The studied scree vegetation represents, depending on the degree of perturbation and successional maturity, several communities belonging to the alliance *Stipion calamagrostidis* Jenny-Lips 1930 and mostly to the association *Vincetoxicetum hirundinariae* Kaiser 1926. Stabilized patches dominated with *Brachypodium pinnatum* (L.) P. B.*,* *Calamagrostis varia* (Schrader) Host.*,* *Carex sempervirens* Vill., *Molinia caerulea* (L.) Moench, or *Vincetoxicum hirundinaria* Medicus can be classified as facies of this association. *Vincetoxicetum hirundinariae* is known from Germany (Schwickerath 1944), Switzerland (Herter 1990), Austria (Mertz 2000), and Slovakia (Valachovič & Hadač 1986, Valachovič et al. 1995). We limited our plots to herbaceous vegetation only. Both the shifting of unstable substrata and falling stones from the upper parts of the screes create the natural disturbances on the screes. Both processes are accelerated by full-depth snow avalanches and by frequent chamois trampling.

### *Sampling*

To cover all available levels of disturbance, sampling plots (1 × 1 m quadrats) were located proportionally but randomly within four vegetation cover categories that were defined roughly as < 25%, 25–50%, 50–75%, and > 75%. All plots were located close to one contour line, therefore elevation differences among plots were usually < 5 m. Each plot was subdivided into 25 × 25 cm quadrats, which enabled us to express the results on 0.25 m$^2$, 0.5 m$^2$, and 1 m$^2$ bases. Total cover and covers of individual species were calculated as a mean of visual estimates in four, eight and sixteen 25 × 25 cm quadrats in 0.25 m$^2$, 0.5 m$^2$ and 1 m$^2$ plots, respectively (see Table 2 as an example of resulting cover values for four 1 m$^2$ plots with contrasting vegetation covers). To avoid pseudoreplications, only one 0.25 m$^2$ plot and one 0.5 m$^2$ plot were chosen randomly from each 1 m$^2$ plot for statistical analyses. Twenty random points were located on a tape at the center of each 1 m$^2$ sampling plot, and the diameter of the stone nearest to each point was measured. Mean stone diame-

Table 2. – Examples of species composition and individual species cover (%) in 1 $m^2$ plots with low (6%), medium (43% and 69%) and high (99%) total vegetation cover on the scree B.

| Species | Total cover (%)<br>6 | 43 | 69 | 99 |
|---|---|---|---|---|
| *Minuartia austriaca* (Jacq.) Hayek | 1 | – | – | – |
| *Gymnocarpium robertianum* (Hoffm.) Newman | 2 | – | – | – |
| *Geranium robertianum* L. | < 1 | – | – | – |
| *Rumex scutatus* L. | 3 | – | < 1 | – |
| *Carlina acaulis* L. | – | 2 | – | – |
| *Helleborus niger* L. | – | 14 | 5 | – |
| *Buphthalmum salicifolium* L. | – | 3 | 9 | – |
| *Vincetoxicum hirundinaria* Medicus | – | 12 | 7 | – |
| *Carduus defloratus* L. | – | 3 | 16 | – |
| *Cuscuta epithymum* (L.) Murray | – | < 1 | 1 | – |
| *Falcaria vulgaris* Bernh. | – | 2 | 2 | – |
| *Teucrium montanum* L. | – | 2 | 3 | 1 |
| *Acinos alpinus* (L.) Moench | – | < 1 | 5 | 1 |
| *Brachypodium pinnatum* (L.) P.B. | – | 11 | 9 | 31 |
| *Galium lucidum* All. | – | 3 | 1 | 1 |
| *Ranunculus montanus* Willd. agg. | – | < 1 | < 1 | 2 |
| *Stachys alopecuros* (L.) Benth. | – | 2 | 1 | 7 |
| *Cirsium erisithales* (Jacq.) Scop. | – | < 1 | 1 | 4 |
| *Polygala chamaebuxus* L. | – | < 1 | 1 | 4 |
| *Cyclamen purpurascens* Miller | – | < 1 | – | 1 |
| *Euphorbia austriaca* Kern. | – | 2 | – | 1 |
| *Campanula cochleariifolia* Lam. | – | < 1 | – | < 1 |
| *Aconitum napellus* L. agg. | – | – | 1 | – |
| *Gentianella austriaca* Kern. | – | – | 1 | – |
| *Pimpinella saxifraga* L. | – | – | 2 | – |
| *Viola collina* Besser | – | – | < 1 | – |
| *Bupleurum falcatum* L. | – | – | 2 | – |
| *Carex mucronata* All. | – | – | 3 | – |
| *Erica carnea* L. | – | – | 1 | – |
| *Achillea* sp. | – | – | < 1 | – |
| *Thesium alpinum* L. | – | – | < 1 | – |
| *Anthyllis vulneraria* subsp. *alpestris* (Schult.) A. et G. | – | – | 1 | – |
| *Sesleria caerulea* (L.) Ard. | – | – | 1 | – |
| *Trifolium* sp. | – | – | < 1 | – |
| *Thymus pulegioides* L. | – | – | 1 | – |
| *Orobanche alba* Willd. | – | – | < 1 | – |
| *Helictotrichon parlatorei* (Woods) Pilger | – | – | 5 | 2 |
| *Rhinanthus aristatus* Personn. | – | – | 2 | 1 |
| *Carex sempervirens* Vill. | – | – | 5 | 62 |
| *Leontodon montanus* Lam. | – | – | – | 2 |
| *Potentilla aurea* L. | – | – | – | 3 |
| *Lotus corniculatus* L. agg. | – | – | – | < 1 |
| *Thalictrum minus* L. | – | – | – | 2 |

ter for each scree was calculated as the mean of diameters of all stones measured in all plots located within the scree. Sampling was conducted during the months of September and October 1983.

The amount of disturbance was estimated as the area without vegetation cover, i.e., as the proportion of area without vegetation or litter apparently produced during the current growing season [100 – vegetation cover (%)]. The relevance of this indirect measure of disturbance level was supported by qualitative examination of ground stability, by short-term observations of those sites that were more or less continuously affected by rolling stones, and by published observations from similar habitats (Cannone & Gerold 2003). Moreover, to verify the estimate of disturbance level as an area without vegetation cover, we painted all the stones hitting 20 two meters long contour lines and counted them. These lines were established within patches with different vegetation cover on D, E, and H screes in 1988. In 1990 we counted the numbers of painted stones left and quantified the disturbance as the percentage of stones missing or buried.

### *Data analysis*

Species richness (SR) was expressed as the total number of vascular plant species present in a plot. Species diversity (SD) was expressed by the Simpson's index of diversity, $SD = 1/(\Sigma p^2_i)$, where $p_i$ is the proportion of total vascular plant cover contributed by species i. This is equivalent to Hill's $N_2$ index of diversity (Hill 1973). The significance of unimodal SR- and SD-disturbance relations was tested using analysis of covariance (ANCOVA). Ascending (to the left of the maximum) and descending (to the right of the maximum) SR and SD data were analyzed separately. When both analyses revealed significant (positive and negative, respectively) effects of vegetation cover, the overall unimodal response was pronounced as significant. The position of the peak (maximum) was determined by polynomials of the third order. Those were also used to estimate the vegetation cover at maxima of species richness and diversity. The third order polynomials were used because they are more flexible functions and fitted positions of maxima more accurately than second order polynomials. All statistical analyses were carried out in StatView 5.0.1 (SAS Institute Inc. 1998). The Min/Max Analyzer procedure in Hubbard & West (1993) was used for identification of the maxima of polynomial functions.

## Results

The relationship between disturbance (expressed as percentage of stones moved or buried in two years) and visual estimates of vegetation cover on screes D, E, and H are presented in Fig. 3. The relationship is negative and significant for screes from two areas where marked contour lines were established: Hochschwab (D and E) and Salza (H). This justifies the use of [100 – vegetation cover (%)] as a surrogate for actual measurements of disturbance.

Examples of the unimodal SR and SD relations to disturbance based on plots of different sizes are presented in Fig. 4. However, only a few screes exhibited such symmetrical unimodal responses. Maxima on some screes were reached at cover values substantially different from 50% (Fig. 5). The analysis of covariance revealed that unimodality was

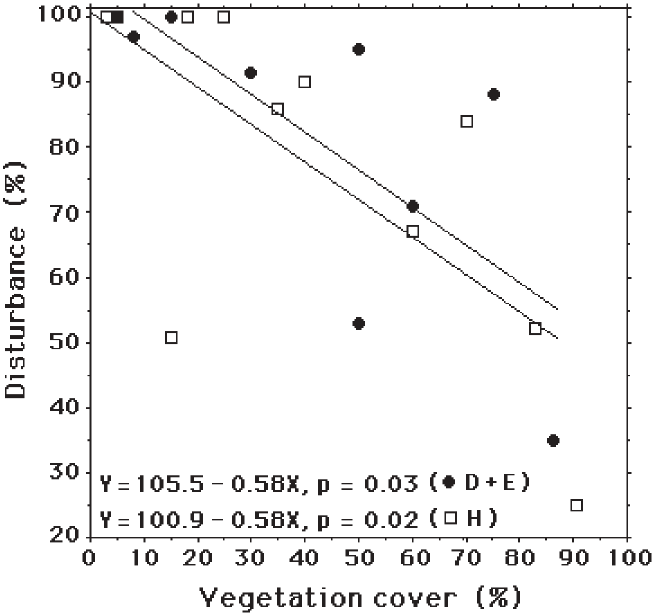

Fig. 3. – Relationship between disturbance (expressed as percentage of stones moved or buried in two years – see the text for details) and visual estimates of vegetation cover on screes D, E (Hochschwab), and H (Salza). As the two regression lines are not significantly different, the data can be fitted just by one regression line: Y = 102.9–0.58X, P < 0.001.

Table 3. – Summary statistics for ANCOVA used to assess the unimodality of species richness and species diversity data from $1m^2$ plots on eight screes. Relevant significance levels are in bold.

| | Ascending portion of the data (to the left from maxima) | | | Descending portion of the data (to the right from maxima) | | |
|---|---|---|---|---|---|---|
| Source | df | F | P | df | F | P |
| Species richness | | | | | | |
| Scree | 7 | 0.41 | 0.893 | 7 | 2.73 | 0.020 |
| Cover | 1 | 153.46 | **<0.0001** | 1 | 32.21 | **<0.0001** |
| Scree × cover | 7 | 1.84 | 0.097 | 7 | 1.63 | 0.155 |
| Residual | 58 | | | 42 | | |
| Species diversity | | | | | | |
| Scree | 7 | 0.52 | 0.813 | 7 | 3.41 | 0.004 |
| Cover | 1 | 59.71 | **<0.0001** | 1 | 10.97 | **0.002** |
| Scree × cover | 7 | 2.48 | 0.031 | 7 | 1.87 | 0.094 |
| Residual | 47 | | | 53 | | |

highly significant for both SR and SD and for all three plot sizes. Significance levels for the effect of cover, both positive and negative with respect to the maximum, were never > 0.01. An example of the complete analysis for SR and SD in $1m^2$ plots is in Table 3. In-

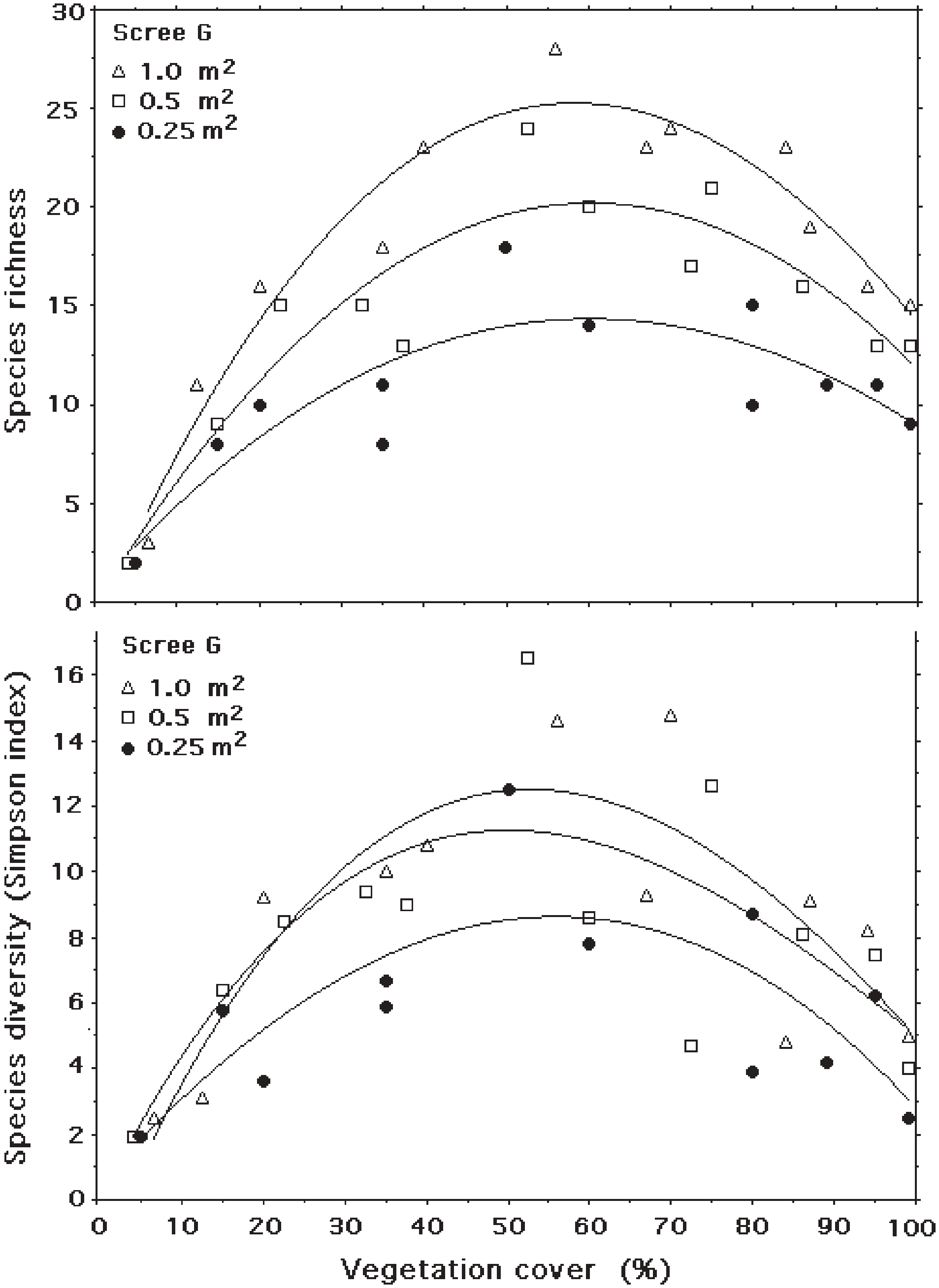

Fig. 4. – Dependence of species richness and diversity on total vegetation cover in plots of 0.25, 0.5, and 1.0 $m^2$ in plant communities on scree G. The relationships were fitted by polynomials of the third order.

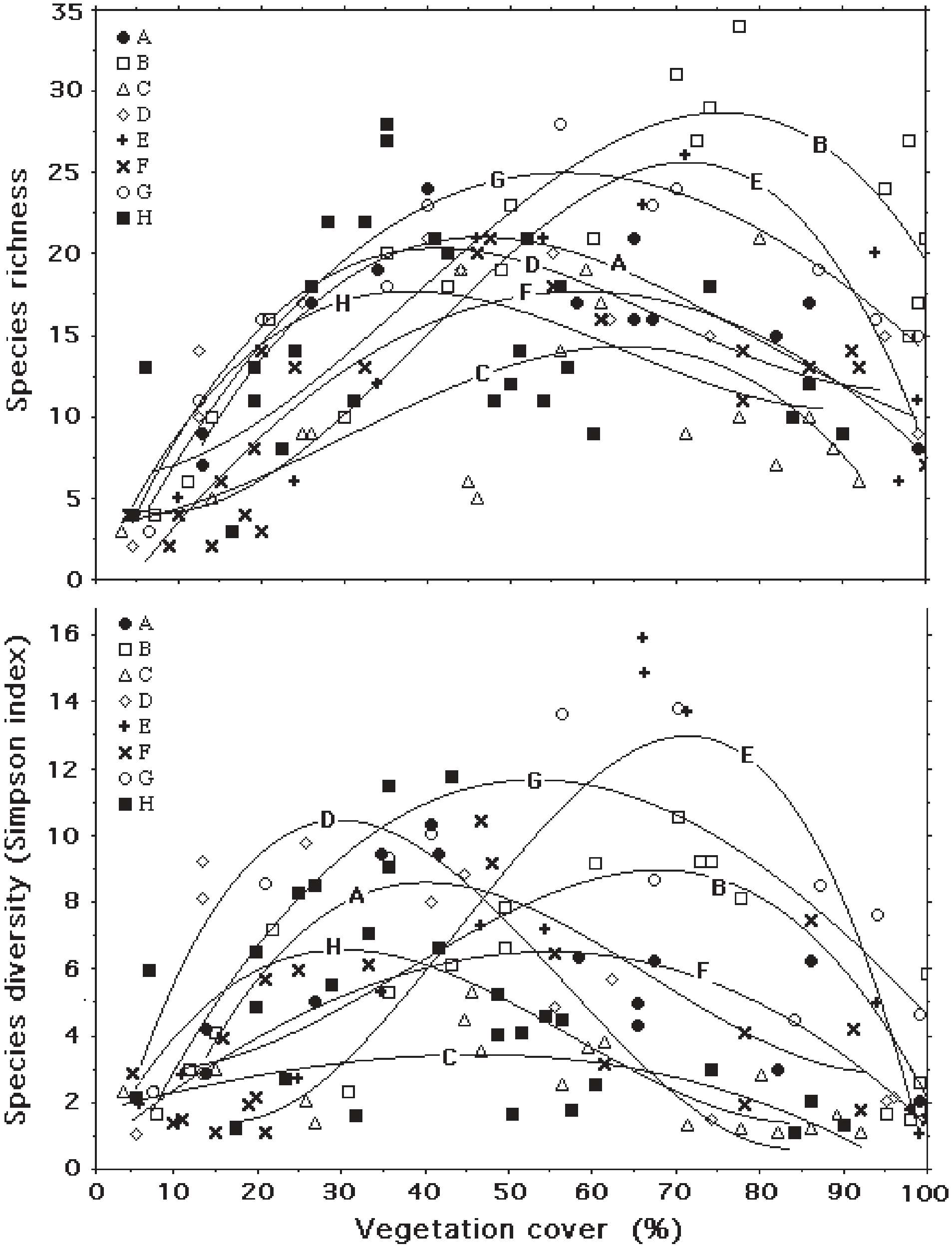

Fig. 5. – Dependence of species richness and diversity on total vegetation cover in plots of 1.0 m$^2$ in plant communities on all eight screes. The relationships were fitted by polynomials of the third order.

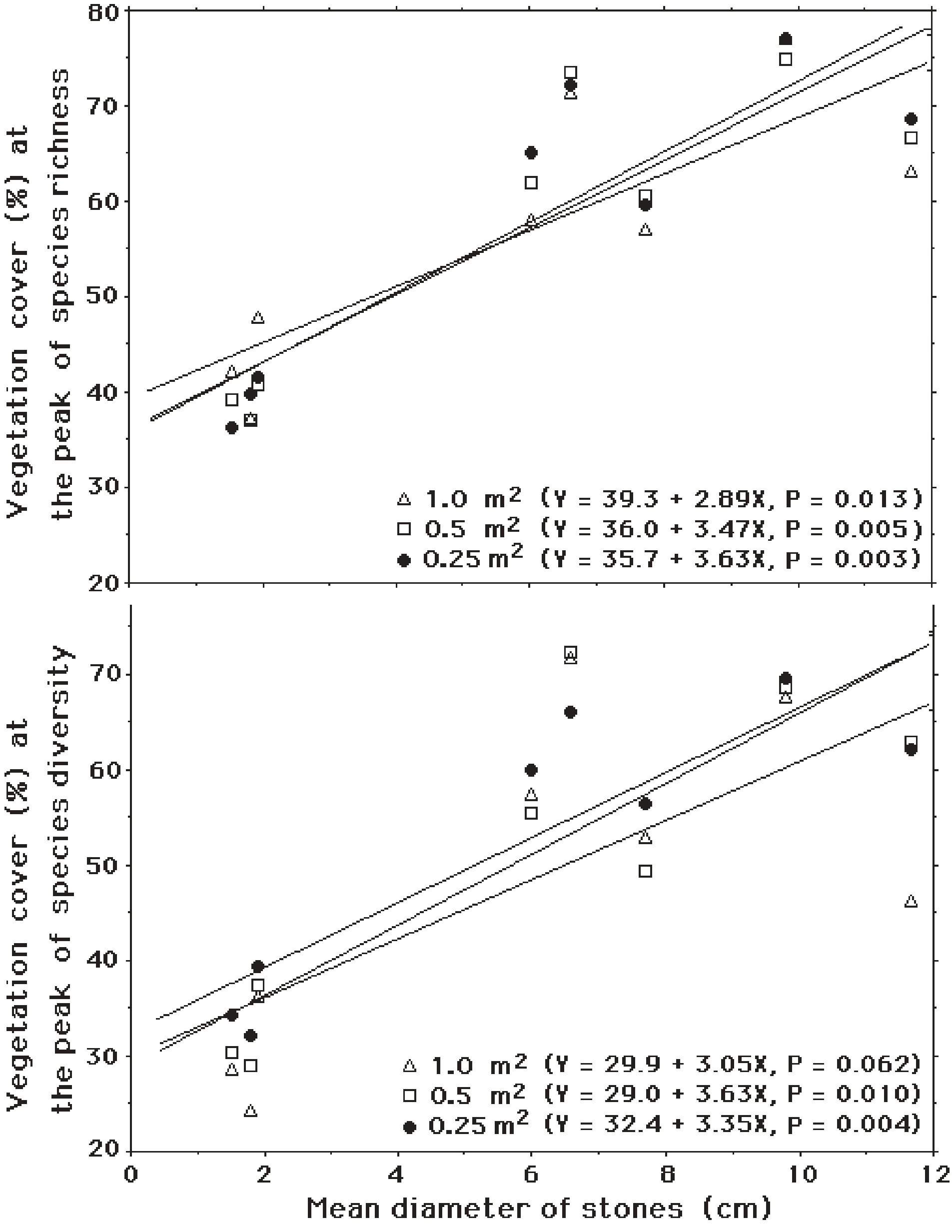

Fig. 6. – Dependence of vegetation cover at the maximum species richness and at the maximum diversity on the degree of environmental heterogeneity of individual screes expressed as the mean stone diameter.

terestingly, unimodality tested this way was highly significant even when ANCOVA analyses were performed on two data sets arbitrarily defined by cover < 50% and > 50%. As square-root transformation is often recommended for discrete dependent variables, all analyses were repeated with square-root transformed species richness. The results were essentially the same.

The maxima of richness- and diversity-disturbance curves, calculated on the basis of third-degree polynomials, are shifted to the higher cover (lower disturbance) with increasing mean stone diameter. This shift is significant for all plot sizes (Fig. 6). For screes with the mean stone diameters ~ 2 cm, the maxima lie between 24 and 47% cover (screes A, D and H), while for stone diameter > 5 cm, the maxima move towards 50–76%. Differences in the position of the species richness and diversity maxima can be demonstrated even within the same scree: in the upper part where stones are generally small, the maximum is at covers < 50%, while in the lower part with larger boulders the maximum corresponds to covers > 50% (data not shown). No relationship between cover and actual values at maxima was found ($R^2$ values between 0.001 and 0.08).

## Discussion

Several recent reviews and original studies questioned the universality of the IDH (Schwilk et al. 1997, Mackey & Currie, 2001, Ikeda 2003, Li et al. 2004). Regardless of this, our study documents unimodal species richness and diversity responses with respect to different levels of disturbance and, therefore, the validity of the IDH for plant communities on calcareous screes (Fig. 5, Table 3). The intermediate-disturbance hypothesis seems to be supported by our data for both species richness and species diversity.

Our data do not allow us to specify which of the disturbance attributes mentioned earlier (frequency, intensity, extent, duration) are critical for this system. However, based on our observations, frequency seems most likely to be the dominant attribute. On the other hand, there must be some effects of intensity and/or extent because rocks very often do not move individually and independently of each other, and they do not have the same size. Duration seems to be the least relevant disturbance attribute in scree systems. It is conceivable, however, that some vegetated spots can be covered only temporarily with stones that are later moved away.

Only individuals with sufficient belowground resources can recover from frequent, intensive, and/or extensive disturbances on screes. As noted already by others (Hess 1909, Somson 1984, Fahrig et al. 1994), these kinds of disturbances can be tolerated more easily by clonal perennials with root resprouting abilities than by annual plants. Indeed, among annuals, only *Geranium robertianum* L., *Gypsophila muralis* L., and *Linum catharticum* L. were somewhat frequent in our plots.

Are unimodal richness/diversity response phenomena described above products of "between-patch" or "within-patch" processes? While results from plots of all three sizes are, in qualitative terms, identical, this still does not mean that species coexistence is promoted by the "within-patch" mechanisms. This uniformity of results is more likely a consequence of the nested sampling design (see Methods) and of a strong spatial autocorrelation in this system (vegetation in neighbouring plots has likely similar cover and diversity). Even a casual observer would conclude that plant communities on screes form a mosaic of patches representing communities at different stages of successional process. The patches themselves may be of very different sizes from $10^{-2}$ to $10^2$ $m^2$. Undoubtedly, a between-patch mechanism involving the recolonization of species by dispersal from distant patches is an important part of the story. However, post-disturbance survival of many “scree specialists” in below-ground organs and their subsequent species/environment specific vigour of regeneration can be classified as a form of the “storage effect” (Chesson & Huntly 1997, Chesson 2000). This may be the mechanism promoting species coexistence in temporarily varying but spatially homogeneous environments – within patches in our case.

Like in many other ecosystems, there are three sets of environmental factors playing a central role in the organization of scree communities (Jenny-Lips 1930, Krammer & Möhl 2002): disturbance, stress, and spatial heterogeneity. Their interplay can produce an enormous variety of habitats. In contrast to many other systems, disturbance-created habitats on screes are not necessarily those with a plentitude of critical resources such as nutrients and moisture. Therefore, low vegetation cover may also be an indication of high levels of stress in these habitats. In fact, permanently mobile non-vegetated screes represent one of the best examples of habitats for which viable strategies of plants do not exist (see Table 1 in Grime 1979). It is even possible to argue that cover is partly a surrogate for productivity and that the horizontal axes in Figs. 4 & 5 could be labelled “Decreasing severity of stress and/or disturbance” (see Fig. 46 in Grime 1979). However, Zöttl (1952, sec. Ellenberg 1988) found that a shortage of nutrients in calcareous screes is not really critical and moisture conditions are not as extreme as one would expect. Unfortunately, it seems that no other studies on the quantification of conditions on limestone screes have been published since 1952.

Only a rough quantification of disturbance and heterogeneity was attempted in this study. The maxima of species richness- and species diversity-disturbance curves were shifted towards higher vegetation cover (i.e. lower disturbance) with increasing mean diameters of the scree-building stones (Fig. 6). One possible interpretation is a synergistic effect of disturbance frequency and disturbance intensity/extent. The other option is that an increase in spatial heterogeneity promoting species coexistence in successionally advanced plots caused this shift. In the first case it would be the size of rocks representing intensity/extent of disturbance that would be responsible for slower rates of recolonization by some of the species. In other words, higher intensity/extent of disturbances would result in higher diversity only at longer intervals between disturbances (Malanson 1984). This would assume, however, that lower frequency of disturbance is reflected in higher vegetation cover regardless of disturbance intensity/extent. The second explanation seems to be more plausible. Large stones may cause below-ground habitat partitioning, segregation of the root systems of neighbouring individuals, and promotion of species coexistence in plots that would otherwise be dominated by strong competitors (Hölscher et al. 2002).

An interesting property of the scree ecosystems is a feedback between disturbance and vegetation. Less disturbance results in higher vegetation cover and higher vegetation cover often decreases disturbance, i.e. prevents stone movement. As nearly always, there are no shortcuts from observed patterns to understanding of underlying mechanisms. Only long-term observations of vegetation in permanent plots, intimate knowledge of life histories of individual species, and experimental manipulations can provide deeper insights into the organization of such extremely variable plant communities that are typical for calcareous screes. Interestingly, all three approaches were initiated a long time ago (Hess 1909, Jenny-Lips 1930, Zöttl 1951). Unfortunately, it seems that there has not been any serious continuation. Obviously, adequate quantification of individual attributes of disturbance and stress in scree systems will be a serious challenge for plant ecologists for many years to come.

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## Souhrn

Hypotéza intermediární disturbance (IDH) předpovídá, že druhové bohatství a druhová diverzita biologických společenstev dosahují nejvyšších hodnot při intermediárních hladinách disturbance. Tuto hypotézu jsme testovali na osmi vápencovych sutích v rakouských Alpách. Údaje o celkové pokryvnosti vegetace a o pokryvnosti jednotlivých druhů jsme získali z ploch 0,25 m$^2$, 0,5 m$^2$ a 1,0 m$^2$. Pro přibližné hodnocení disturbance (pohyb kamenů a destrukce biomasy) jsme použili index [100 – pokryvnost vegetace (%)]. Oprávněnost tohoto indexu jsme potvrdili pozorováním pohybu označených kamenů po dvou letech. Jednovrcholová závislost druhového bohatství a druhové diverzity na disturbanci byla zjištěna pro plochy všech tří velikostí v souladu s IDH. Nejvyšší hodnoty druhového bohatství a druhové diverzity byly posunuty k vyšším hodnotám celkové pokryvnosti vegetace (= nižší disturbance) se vzrůstající průměrnou velikostí kamenů ve studovaných sutích. Tento posun je možno interpretovat buď jako synergistický vliv frekvence disturbance v kombinaci s její intenzitou a rozsahem, nebo jako důsledek zvýšení prostorové heterogenity podporující koexistenci druhů na sukcesně pokročilých plochách.

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