Banska Bystrica (Slovakia)の人工草地・追播草地・半自然草地における植物群落の空間分布と種の多様性

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Spatial Patterns and Species Diversity of Plant Communities in Sown, Oversown, and Semi-Natural Grasslands in Banská Bystrica, Slovakia

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Synopsis

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We analyzed the frequency of occurrence and the spatial patterns of plant species in grassland communities of Banská Bystrica, Slovakia. We established 5×5-m quadrats in three different sites: (1) a grassland established by seeding improved herbage plants after plowing in 1991 ("sown"), (2) a semi-natural grassland oversown with improved herbaceous species in 1991 ("oversown"), and (3) a semi-natural grassland that received no treatment. No fertilizers have been applied for these grasslands. Each quadrat was divided into 100 cells (50 \times 50 cm), and 50 cells were selected in a checkerboard pattern. Each cell was subdivided into four smaller cells (25×25 cm), and each species found in each of the four smaller cells was recorded. We applied the beta-binomial distribution to the analysis of spatial patterns of individual species. The greatest spatial heterogeneity was found in the sown grassland where species with stolons, rhizomes and large tillers dominated. For the dominant species in the grasslands, we obtained a good fit to the beta-binomial distribution. On average, the greatest species richness and diversity were found in the sown grassland where improved plant species and native plants co-existed under the non-fertilized condition, although cell-to-cell variation was very large; in contrast, species richness and diversity were lowest in the semi-natural grassland. This result indicates that an understanding that sown grasslands are poorer in the species diversity than natural/ semi-natural grasslands is not always adequate.

Key words: Beta-binomial distribution, Semi-natural grassland, Slovakia, Spatial heterogeneity, Spatial pattern, Species diversity.

Introduction

Many herbaceous species that grow in temperate grasslands and pastures have their origins in Europe and western Asia. These native plants or old immigrants which can be found in both natural and sown grasslands throughout Europe (Lihan *et al.* 1988). Such plants include *Dactylis glomerata*, *Lolium perenne*, *Trifolium pratense* and *Trifolium repens*. How do these native European and West Asian species affect the spatial patterns and diversity of plants composing natural and sown grassland communities in central Europe?

The following four measures of spatial patterns have been evaluated in past vegetation studies: (1) "individual species" (e.g., Shiyomi et al. 2000; Tsutsumi et al. 2001), (2) "botanical composition" (e.g., Olsong-Whittaker et al. 1985; Shiyomi et al. 2000), (3) "species diversity" (e.g., Olsong-Whittaker et al. 1985), and (4) "biomass" (e.g., Shiyomi et al. 1984; Hirata 1994; Shiyomi et al. 1998; Tsutsumi et al. 2000). Although individual plant species and plant communities in grasslands have their own spatial patterns, each pattern is influenced by management practices, such as cutting, grazing, fertilizing, weeding, etc., and by environmental conditions, such as soil fertility, water availability, micro-geology, and organism activity (e.g., Olsong-Whittaker et al. 1985; Bonham et al. 1995).

In this study, the spatial pattern of each species in a community refers to the frequency of occurrence of individual species in the community and their spatial heterogeneity. Plants that disperse by airborne seeds, such as Compositae, may form a random spatial pattern, while plants that propagate clonally such as *Trifolium repens* may form much more heterogeneous patches (Shiyomi *et al.* 2000). A grassland community is a mixture of plant species that have

different spatial patterns. Therefore, the spatial patterns of such a mixture are based on the botanical composition and species diversity.

We used a statistical model to describe the spatial patterns exhibited by individual plant species per quadrat (Pielou 1977; Shiyomi 1981). The vegetation of natural and semi-natural grasslands forms an inherent landscape in mountainous areas in Slovakia. Therefore, it is important that agricultural use and management practices are designed to maintain current species diversity and species-to-species associations (Ruzickova 1987; Rychnovska 1987). Grasslands, including semi-natural grasslands, form species-rich floras in this area, and fertilized and non-fertilized semi-natural grasslands are commonly used for forage production (Regal and Vesela 1985; Ruzickova 1987; Jancovic and Hoiubek 1992).

The objectives of this study were to answer the following four questions about spatial heterogeneity and species diversity within grasslands in Banská Bystrica, Slovakia, central Europe: (1) What are the frequency of occurrence and degree of spatial heterogeneity of dominant species? (2) How do spatial patterns change with grassland management or history? (3) Can the statistical model proposed by Shiyomi *et al.* (2000) be applied to vegetation in Slovakia? (4) Which are more spatially heterogeneous and have a more diverse species composition: semi-natural or sown grasslands? This paper discussed the relationships between species diversity and spatial pattern, too.

Materials and Methods

We surveyed three types of grasslands, located at three adjacent sites, at the Grassland and Mountain Agriculture Research Institute, Banská Bystrica, Slovakia (48°44′N, 19°09′E, 460 m a.s.l.). These three grasslands were established in 1991 by the following methods: (1) the "sown" grassland was established on an old semi-natural grassland by artificial sowing of improved herbaceous plants after plowing; (2) the "oversown" grassland was established by artificial oversowing of improved herbaceous plants after scouring the soil surface with a rake dozer, and (3) the "semi-natural" grassland was not subjected to artificial treatment. The plant species sown at the establishment of the first two grasslands were varieties of Dactylis glomerata, Lolium perenne, Festlolium (Festuca arundinacea $\times L$. perenne), Trifolium repens (tetraploid), and Trifolium pratense. Each grassland was harvested three times every year (1 June, mid-July, and late August or early September).

At the study site, the measured precipitation was $441\,\mathrm{mm}$, and the mean air-temperature was $13.6\,^{\circ}\mathrm{C}$ during the growing season. The sites were oriented

north-east to north-west with a gentle slope, and the soil pH was around 4.0. No fertilizer has been applied and no grazing has been carried out in the three grasslands since the establishment. The completely same management has been practiced for the three grasslands. The productivity of the sown, oversown, and semi-natural grasslands (means for 1992 to 1995) was 4.0, 4.5, and 3.8 DM ton ha ¹ yr⁻¹, respectively.

A 5×5 -m square was established within each of the three grasslands. Each of these quadrats was subdivided into 100 cells ($50\times50\,\mathrm{cm}$; referred to as L-quadrats hereafter), and 50 cells were selected in a checkerboard pattern within each square. The total surveyed area for each grassland was $0.25\,\mathrm{m}^2\times50=12.5\,\mathrm{m}^2$. Each L-quadrat was divided into four smaller quadrats ($25\times25\,\mathrm{cm}$; referred to as S-quadrats). For each S-quadrat, we visually observed and recorded the occurrence of all species forming the grassland communities. The survey was conducted in August, 1998.

Model and Analysis

Although the vegetation of a given grassland is composed of s species, we will concentrate on only one species. If the vegetation is not highly heterogeneous over the grassland, the distribution of species i may follow a random pattern. "Random pattern" implies that the number of S-quadrats containing species i per L-quadrat follows a binomial distribution. In general, we let each L-quadrat be divided into n S-quadrats of equal area and let the probability that species i occurs in an S-quadrat be π , which remains constant throughout the grassland ($n \ge 2$). The probability that species i occurs in j of the n S-quadrats within an L-quadrat, P(j), is expressed by the equation : $P(j) = {}_{n}C_{j} \pi^{i}(1-\pi)^{n-j}$ for $j=0, 1, 2, \cdots, n$.

In a grassland that has experienced substantial disturbance, such as grazing or invasion of plants from surrounding areas, the vegetation may have a much more heterogeneous distribution than expected randomly. Then, we assumed that π changes continuously in the grassland, from site to site, according to a beta-distribution (e.g., Wilks 1962). The distribution that is derived based on this assumption, i.e., the beta-binomial (BB) distribution, is given by the following equation (Skellam 1948; Irwin 1954; Kemp and Kemp 1956; Shiyomi 1981; Hughes and Madden 1993; Shiyomi *et al.* 2000):

$$P(0) = \beta_i(\beta_i+1)\cdots(\beta_i+n-1)/\{(\alpha_i+\beta_i)(\alpha_i+\beta_i+1) \cdots (\alpha_i+\beta_i+n-1)\},$$

$$P(j) = P(j-1)(n-j+1)(\alpha_i+j-1)/\{(\beta_i+n-j)j\}$$
 for $j = 1, 2, \dots, n$, (1)

where
$$\alpha_i = p_i(\rho_i^{-1} - 1)$$
, $\beta_i = q_i(\rho_i^{-1} - 1)$, $0 \le p_i \le 1$, $(n-1)^{-1}$

 $\leq \rho_i \leq 1, q_i = 1-p_i$, and n is the number of S-quadrats within an L-quadrat (n=4 in our case). The proportion of S-quadrats containing species i is given by p_i . The correlation coefficient of the number of occurrences between n S-quadrats within each L-quadrat over the given number of L-quadrats is denoted by ρ_i . This parameter ρ can be used as an index to describe the spatial heterogeneity of a species (Hughes and Madden 1993; Shiyomi $et\ al.\ 2000$). A high ρ -value indicates high heterogeneity in the number of occurrences between N L-quadrats (in our case N=50); $\rho=0$ indicates a random pattern, i.e., the occurrence follows a binomial distribution.

The mean μ_i and variance σ_i^2 of the beta-binomial distribution can be expressed by the following formulae (Shiyomi 1981):

$$\mu_i = p_i n$$
, and $\sigma_i^2 = n p_i q_i \{1 + \rho_i (n-1)\}.$ (2)

The actual values of the parameters p_i and ρ_i are estimated by the moment method using estimated values for μ_i and σ_i^2 in equation 2, where $p_i+q_i=1$, as follows:

$$p_i = m_i/n$$
, and $\rho_i = s_i^2 / \{n(n-1)p_iq_i\} - 1/(n-1)$,

where m_i and s_i^2 are the estimated mean and variance of the observed frequency distribution, respectively.

The community average of ρ_c is given by the following formula for s species (Shiyomi *et al.* 2000):

$$\rho_{c} = \sum_{i=1}^{S} p_{i} \rho_{i} / \sum_{i=1}^{S} p_{i}.$$
 (3)

A large ρ_c -value indicates that the community typically forms large patches, while a small value

indicates that individual species mix with each other. As a measure of species diversity, we used the Shannon-Wiener index, H' (e.g., Pielou 1977):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i, \tag{4}$$

where p_i is the proportion of the number of S-quadrats containing species i.

Results

1. Overview

Table 1 shows the dominant species, the total number of species present, the species diversity for the whole area, and the community heterogeneity in the three grasslands. The sown grassland had a greater species diversity and a greater community heterogeneity than the semi-natural grassland. Although the sown grassland was re-established in 1991 by plowing, species diversity had increased relative to the other grasslands during the seven-year period as a result of the restored native plants and the invasion of plants from surrounding areas. The oversown grassland, which had a mixture of native and improved herbage, had a high species richness. The same native species as the improved herbage plants were also observed in the semi-natural grassland because these native plants had been naturally maintained in the field.

2. Occurrence

Figure 1 compares the occurrence, p, among the three grasslands. Of the 51 species observed in all the surveys, Taraxacum officinale (To), Trifolium repens (Tr; diploid, native), Dactylis glomerata (Dg), and Poa pratensis (Pp) were dominant at each of the three sites. By contrast, we found specialized species with an advantage in the sown grassland, including Lolium perenne (Lp), Festlolium (Fest), Glechoma

Table 1. Overview of the three grasslands surveyed.

Grassland type	Sown	Oversown	Semi-natural	
Dominant species	T. officinale, $p=1$	T. officinale, $p=1$	T. officinale, $p=1$	
	G. hederacea, $p=0.96$	T. repens, $p=1$	T. repens, $p=1$	
	Festlolium, $p = 0.965$	P. pratensis, $p = 0.99$	P. pratensis, $p=0.9$	
	D. glomerata, $p = 0.905$	D. glomerata, $p=0.81$	T. flavescens, $p = 0.875$	
	D. carota, $p = 0.785$	T. flavescens, $p = 0.79$	D. glomerata, $p = 0.865$	
	T. repens, $p=0.75$	C. holosteoides, $p = 0.5$	C. holosteoides, $p = 0.58$	
	P. pratensis, $p = 0.635$	A. millefolium, $p = 0.465$		
	A. millefolium, $p=0.685$			
	L. perenne, $p=0.445$			
Number of species	37	37	31	
Species diversity, H'	1.15	0.93	0.76	
Community spatial heterogeneity, ρ_c	0.30	0.21	0.19	

See legend of Fig. 1 for full genus names. H' is calculated based on natural logarithms.

p denotes the proportion of S-quadrats containing each species, e.g., p=1 indicates that all S-quadrats contained the species. See text for details.

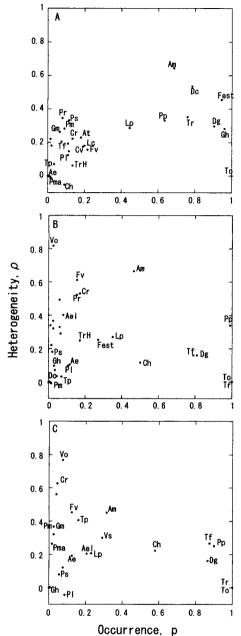


Fig. 1. Occurrence and spatial heterogeneity of species observed in a sown (A), oversown (B), and semi-natural grassland (C) in Banská Bystrica, Slovakia. Species are listed in alphabetical order: Achillea millefolium (Am), Agrimonia eupatoria (Ae), Agrostis tenuis (At), Arrhenatherum elatius (Ael), Campanula rapunculoides (Cr), Cerastium holosteoides (Ch), Chrysanthemum vulgare (Cv), Dactylis glomerata (Dg), Daucus carota (Dc), Falcaria vulgaris (Fv), Festulolium (Fest), Galium mollugo (Gm), Glechoma hederacea (Gh), Lolium perenne (Lp), Lotus corniculatus (Lc), Pimpinella saxifraga (Ps), Plantago lanceolata (Pl), Plantago major (Pma), Plantago media (Pm), Poa pratensis (Pp), Potentilla reptans (Pr), Taraxacum officinale (To), Trifolium pratense (Tp), Trifolium repens (diploid, native, Tr), Trifolium repens (tetraploid, TrH), Trisetum flavescens (Tf), Veronica officinalis (Vo), and Veronica serpyllifolia (Vs).

hederacea (Gh), Daucus carota (Dc), and Achillea millefolium (Am). Cerastium holosteoides (Ch), Trisetum flavescens (Tf), Trifolium pratense (Tp), Agrimonia eupatoria (Ae), and Arrhenatherum elatius (Ael) which occurred more frequently in the semi-natural grassland than in the other two types of grassland.

3. Beta-binomial (BB) distribution

One of the objectives of this study was to determine whether the beta-binomial distribution, which has a theoretical base in this type of survey (Shiyomi et al. 2000), could be applied to Slovakian grasslands. Table 2 shows the results of the goodness-of-fit test to the BB and binomial distributions using the chisquare statistics. Eleven observed frequency distributions sufficed to test the BB distribution, and ten of these 11 cases (including A. millefolium and L. perenne in all three grasslands) were not significant at the 5% level. Of these ten cases, two that had a small ρ -value (L. perenne in the sown and seminatural grasslands) were also not significant for the binomial distribution at the 5% level (the binomial distribution is mathematically included in the BB distribution family; Skellam 1948). These results show that the BB distribution fitted very well to the obtained data. From the derivation of the model, we concluded that these plant species were distributed heterogeneously, not randomly (i.e., they were patchily distributed).

4. Spatial heterogeneity

Figure 1 illustrates the degree of heterogeneity (p) for each species in the three grasslands. The ρ-values for A. millefolium (Am), G. hederacea (Gh), Festlolium (Fest), Daucus carota (Dc), and Pimpinella saxifraga (Ps) in the semi-natural grassland tended to be smaller than in the sown grassland. At a scale of 50 $\times 50$ cm, these species formed clearer patches in the sown grassland than in the semi-natural grassland. By contrast, the ρ -values of *Campanula rapunculoides* (Cr), C. holosteoides (Ch), and Falcaria vulgaris (Fv) were greater in the semi-natural grassland than in the sown grassland; in other words, these species formed more defined patches in the semi-natural grassland than in the sown grassland. The ρ -values for D. glomerata (Dg), L. perenne (Lp), and T. flavescens (Tf) did not differ substantially among the three grasslands.

Figure 1 shows the relationships between the p-and ρ -values for each species in the three grasslands. The ρ -value was zero for T. officinale (To), which occurred in all S-quadrats in each grassland, and for T. repens (Tr; 2n), which occurred in all S-quadrats in the oversown and semi-natural grasslands. In general, A. millefolium (Am) had a very high ρ -value, i.e., it formed stable patches; P. pratensis (Pp) also tended to exhibit high heterogeneity regardless of its

Table 2. Goodness-of-fit to the beta-binomial (BB) distribution using chi-square statistics.

Probability*	>0.5	0.5-0.25	0.25-0.1	0.1-0.05	0.05-0.01	0.01-0.001	< 0.001
Beta-binomial	0	2 (1)	4 (1)	4	1	0	0

Eleven observed frequency distributions were sufficient for testing distribution. The BB distribution was not significant at the 5% level in 10 cases. The two cases in parentheses were not significant for the binomial distribution. *Probability that the null hypothesis is true, i.e., that the frequency of occurrence follows the BB distribution.

degree of occurrence. In contrast, T. flavescens (Tf) and D. glomerata (Dg), which both occurred frequently, had low ρ -values. Several plant species, including A. millefolium (Am) and C. rapunculoides (Cr), had a greater heterogeneity than the others regardless of their habitats, and several other species, including the three plantains (Pl, Pm, Pma), had low heterogeneity compared to other species regardless of their habitats. The high value of ρ_c (Table 1) in the sown grassland might be ascribed to the large number of introduced herbage species that typically developed large stocks.

5. Species diversity

Figure 2 illustrates the spatial patterns of species richness and diversity per L-quadrat using frequency distributions. The means of species richness and diversity clearly differed among the three grasslands, as did the variances in species richness (Table 3). The sown grassland had the greatest species richness/diversity, while the semi-natural grassland had the lowest.

The spatial heterogeneity in species richness differed among the three grasslands, while spatial heterogeneity in species diversity differed only slightly (these spatial heterogeneities were based on the variances in distribution, Table 3). The sown grassland had the greatest heterogeneity in species richness, while the semi-natural grassland had the smallest.

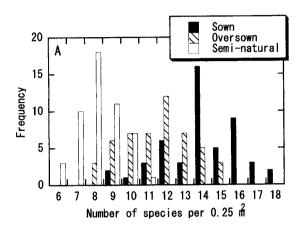
Discussion

1. Is the beta-binomial (BB) model applicable?

Shiyomi *et al.* (2000), Tsutsumi *et al.* (2001) and Wang *et al.* (2002) reported good fits of the BB distribution to plant species grown in Japanese and Chinese grasslands. With the exception of 11 cases, the 50 L-quadrats that we surveyed in this study were not sufficient to test the null hypothesis that each plant population in a grassland community was distributed according to the BB distribution. In ten of these 11 cases, however, it was verified that the BB distribution was a good model to describe the statistical, ecological behavior of plant populations.

2. What factors increases spatial heterogeneity in the sown grassland?

In grasslands used for grazing, spatial heterogeneity is formed by non-uniform plant-animal interac-



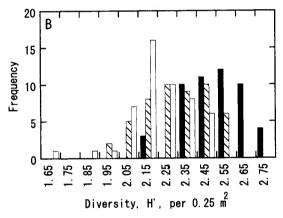


Fig. 2. Frequency distribution of species richness (A) and species diversity (B) in sown, oversown, and seminatural grasslands. The means and variances are shown in Table 3.

tions. These interactions result in site-to-site differences, such as differences in grazing intensity and differences in nutrition concentration (i.e., unequal distribution of dung pads and urine patches), which affect the growth rates of plants (Hakamata and Hirashima 1978; Illius et al. 1987; Hirata 1994; Shiyomi et al. 1998). The results of this study indicate that even in grasslands harvested by cutting, some species had a high degree of spatial heterogeneity. What causes such spatial heterogeneity? Two factors can be considered. First, clonal plants, such as white clover and *Potentilla*, generally develop ramets. These plants form clonal patches or large stocks around the mother plant (Shiyomi et al. 2000). Conversely, plants that propagate mainly via seed dis-

Table 3. Means and variances of species richness and species diversity (H').

Grassland	Species	s richness	Species diversity		
type	Mean	Variance	Mean	Variance	
Sown	14.0ª	4.49ª	2.501 ^a	0.0222a	
Oversown	$11.5^{\rm b}$	3.64^{a}	2.309^{b}	0.0262^{a}	
Semi-natural	8.2^{c}	1.37^{b}	2.208°	0.0244^{a}	

Different letters in the same column indicate a statistically significant difference at the 5% level.

persal, such as Compositae and the plantains, disperse their seeds from the mother plant, and the seeds land at random on the ground. These plants were generally distributed at random (Shiyomi *et al.* 2000). Another factor is the architecture inherent in each plant species. Erect and creeping plants tend to have different spatial heterogeneities. Most grasses are of the erect type; except for some that form large stalks, grasses grow vertically, not horizontally. They do not form highly heterogeneous patterns.

In the sown grassland, Glechoma hederacea (Gh), and tetraploid white clover (TrH) forming clonal patches and creeping architecture, and Daucus carota (Dc) and Festlolium (Fest) forming large stocks dominate (Table 1 and Fig. 1). These plant species with high values of p and p were seeded, or invaded from the surrounding area at and after the grassland establishment with plowing, and these species produced the high spatial heterogeneity. In the seminatural grassland, Trisetum flavescens (Tf) with an erect type and Cerastium holosteoides (Ch) forming non-clonal, small-sized individuals dominate. These plant species have high p-values but low p-values, and produced the low spatial heterogeneity (Table 1 and Fig. 1).

For p-values < 0.2, the ρ -values varied over a wide range, especially in the oversown and semi-natural grasslands (Fig. 1), for two reasons. First, species such as V. officinalis (Vo), F. vulgaris (Fv), and C. rapunculoides (Cr) had consistently high ρ-values in the two grasslands. Since these plants tended to form large clonal stocks or plant bodies, they naturally had the opportunity to occupy three or four S-quadrats in an L-quadrat even when their occurrence was very low. By contrast, P. lanceolata (Pl), P. media (Pm), P. major (Pma), C. holosteoides (Ch), Galium mollugo (Gm), and A. eupatoria (Ae) had low ρ -values, indicating low heterogeneity or a nearly random distribution. Since these species generally do not form large clonal stocks, the probability that they will occupy three or four S-quadrats in an Lquadrat is low when their occurrence is low. Most of these species propagate by seeds. The second reason is that species with a low p-value may have a contingent ρ -value by chance. That is, species with a low p-value sometimes have a large ρ -value and sometimes have a small ρ -value. For example, suppose that two plants of one species are found throughout an area. If by chance the two plants occur in the same L-quadrat, their ρ -value is very high, but if the two plants occur in two different L-quadrats, the ρ -value is very low.

According to published reports, spatial heterogeneity was very high in fertilized sown grasslands in Japan (ρ_c =0.24 to 0.59, Tsutsumi et al. 2001), low in non-fertilized natural grasslands exposed to heavy grazing in northern China (ρ_c =0.22 to 0.23, Wang et al. 2002) and medium in non-fertilized semi-natural grasslands exposed to heavy to low grazing in central Japan (ρ_c =0.32 to 0.36, Yasuda et al. 2003). The heterogeneity seen in our study of grasslands in Slovakia (ρ_c =0.19 to 0.30, Table 1) was near that of the Chinese grasslands or intermediate between the values for the Chinese and Japanese semi-natural grasslands. The reason for these differences among the three grasslands of Slovakia, China and Japan may be that the clump sizes and architectures of the plant species making up the communities differed. Plant species in sown grasslands in Japan, which tolerate heavy application of fertilizers, grew vigorously and formed large clumps, while plant species in degraded natural grasslands in China, which tolerate the severe environmental conditions, were generally small and only formed small clumps. Plant species in Slovakian grasslands that were not fertilized and not grazed were of intermediate size, because grasslands in this area are composed of a mixture of natural species and man-made species.

3. What factors increase species diversity in sown grasslands?

Agricultural pastures like the sown grassland in this case are usually characterized by a few dominant species with low frequency and ground cover of associated plant species. On the other hand, seminatural or natural grasslands are characterized by an even distribution of relative abundances among many plant species compared with agricultural pastures (Mitchley 2001). Although this is the general knowledge in European grasslands, the Slovakian data showed an opposite result. One of the purposes of this study is to point out this inconsistency (Table 1 and Fig. 2).

A high H'-value indicates a spatially intricate mixture of many species. The sown grassland with the highest H'-value consisted of a larger mixture of species than the semi-natural grassland. The oversown grassland was intermediate between the other two. The variances shown in Table 3 indicate that the sown grassland had the greatest spatial heteroge-

neity in species richness, i.e., the spatial pattern in the sown grassland tended to be patchy with very low to very high species richness, compared to the semi-natural grassland. High species richness/diversity, despite large site-to-site variation, can be maintained in artificial sown grasslands in this experimental site.

The native types of the improved herbage plants, e.g., L. perenne, D. glomerata and T. repens, are often found in semi-natural grasslands in central Europe. These plants even invade sown grasslands from surrounding areas especially under non-fertilized, uncultivated condition. The sown grasslands also contained other native species that are frequently observed in oversown and semi-natural grasslands, such as G. hederacea, Lotus corniculatus, Veronica chamaedrys, Vicia cracca, and Agrostis tenuis, some of which are common annual weeds in crop fields. Furthermore, in the sown grassland, improved herbage plants, such as Festlolium, T. repens (3n) and L. perenne, were abundant compared to the seminatural grassland. Even in cutting grasslands, there may be site-to-site differences in soil fertility (Sutherland 1990). The niches containing relatively fertile soil are suitable for seeded herbage plants and their accompanying native weed species, but these niches are not suitable for native plants that do not tolerate fertile soils. Since native plants and seeded plants occupied different micro-sites in the grassland, the sown grassland is be characterized by high species diversity. This result indicates that understanding that sown grasslands are usually poorer in the species diversity than native grasslands in the same area (Mitchley 2001) is not always adequate.

4. Conclusions

What were the relationships between the spatial pattern of the community (ρ_c) and species diversity (H')? Four possible relationships (Categories) can be considered: (1) the community is composed of many species that form large overlapping patches, (2) the community is composed of a few species that form large mutually exclusive patches, (3) the community is composed of a few species that form small mutually exclusive patches, and (4) the community is composed of many species that form small mutually exclusive patches. The sown grassland had high spatial heterogeneity at the community level, as well as high species diversity, while the semi-natural grassland had relatively low heterogeneity and low species diversity. In the sown grassland, the many species forming the community tended to form large multiple patches (Category 1), while the semi-natural grassland had slightly fewer species than the sown grassland and these tended to form small patches (Category 3). Species diversity, as well as spatial patterns including occurrence and heterogeneity, may be important characteristics for assessing grassland quality and grassland environment.

In principle, any spatial index, including p, ρ , and H', measured using quadrat methods is sensitive to quadrat size. The characteristics of the spatial pattern of species may be depicted by measuring spatial patterns using different quadrat sizes. A difference in scaling will quantitatively reveal latent species-to-species characteristics of spatial patterns in a plant community (Tsutsumi *et al.* 2002).

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要 旨

塩見正衛・Gaborcík N*・小泉 博*・Javorková A*・Uhliarová E*・Jezíková O* (2004): Banská Bystrica (Slovakia) の人工草地・追播草地・半自然草地における植物群落の空間分布と種の多様性. 日草誌 50, 1-8. 310-0851 水戸市千波町 168-35, *Technical University in Zvolen, Faculty of Ecology and Environmental Sciences (Kolpasska I. 96900, Banská Stiavnica, Slovakia), **・岐阜大学流域圏科学研究センター (501-1193 岐阜市柳戸 1-1), *** Grassland and Mountain Agriculture Research Institute (Mlàdeznička 36, 97421, Banská Bystrica, Slovakia)

Banská Bystrica (Slovakia) の無施肥で維持されている草地に存 在するそれぞれの植物種の出現頻度と、その空間分布を 1998 年夏 に調査した。次の3つの草地それぞれに、5m四方の区画を設けた: (1) 1991 年に半自然草地を耕起, 改良牧草を播種した人工草地, (2) 半自然草地を 1991 年にレーキ・ドーサーで半耕起し、改良牧草を 追播した追播草地, (3) 処理を施さない半自然草地。それぞれの草 地に, 25 cm×25 cm の枠 4 つを含む 50 cm×50 cm の枠を 50 個ず つ置き、ベータ・二項分布に基づく方法を用いて植生調査を行っ た。空間的不均一性は人工草地で最も高く、半自然草地で最も低 かった。人工草地では、大きな株を作る植物種やクローナル植物種 が多く存在したためである。また、どの草地でも、種の多様性の空 間的不均一性は高かったが、種の多様性自体は人工草地で最も高 く、半自然草地で最も低かった。人玉草地は、改良牧草の他に多く の自生植物が含まれていた。この結果は、人工草地は半自然・自然 草地よりも種の多様性が低いという一般の見解にしたがっていない 草地が存在することを示している。

キーワード:空間的不均一性,空間分布,種の豊富さ,スロバキア, 半自然草地,ベーター二項分布.