

## SPECIES TURNOVER AS A FUNCTION OF VEGETATION PATTERN

K. Virágh and S. Bartha

Virágh, K. and Bartha, S. (2003): Species turnover as a function of vegetation pattern. – *Tiscia* 34, 47-56.

**Abstract.** In Hungary, during the secondary succession after deforestation xeromesophilous *Brachypodium pinnatum* community often develops and gradually turns into xerophilous grassland. This study reports on fine-scale plant species turnover in three types (Forest-type, Forest-steppe- and Steppe-types) of *Brachypodium pinnatum* dominated grassland, representing contrasting stages of steppe formation. Micro-maps of rooting individuals (or ramets) of vascular plant species were recorded in 20×110 grids of contiguous 5×5 cm microquadrats over three subsequent years. We found that local species turnover showed a slightly increasing tendency from forest to steppe types of *Brachypodium* grassland, coinciding with the declining dominance of *Brachypodium pinnatum* and the slightly increasing number of open spaces (gaps) for local plant colonization. Our results indicated that local species turnover patterns were temporally and spatially non-random in all *Brachypodium* grassland types. High and low local species turnovers were dependent on the spatial structure of vegetation. Spatial behaviors of some matrix-forming grass species proved to be important for structuring the fine-scale species turnover patterns. We found contrasting differences according to the abundances of species. Local turnovers were the lowest in the *Brachypodium pinnatum* dominated microquadrats of the Forest-type and similarly, in the *Festuca rupicola* dominated ones, but only in the Steppe-type. The highest turnovers were revealed in the *Bromus erectus* dominated microquadrats. *Brachypodium pinnatum* decelerated fine-scale turnovers in all types, as the relationship between pattern of presences of this species in the microquadrats and the spatial pattern of high local species turnovers was significantly negative. *Festuca rupicola* both accelerated and decelerated local turnovers, dependently from its coenological status. Spatial patterns of *Bromus erectus* and *Festuca rupicola* were not correlated only with the turnover patterns of Forest-steppe - type. It was stated that behaviour of key grass species in controlling the local species turnovers was not strictly specific but rather differed according to the various fine-scale vegetation patterns of grassland types.

**Keywords:** spatial associations, vegetation dependent local species turnover, key grass species, *Brachypodium* grassland

**K. Virágh, S. Bartha**, Institute of Ecology and Botany, Hungarian Academy of Sciences, H-2163 Vácrátót, Hungary. E-mail: viragh@botanika.hu, sanyi@botanika.hu

### Introduction

In current literature of vegetation dynamics, closely linked to the concept of patch dynamics, the studies of fine-scale dynamics, such as local species turnover and species mobility within a vegetation patch (stand) have been received great importance for understanding of both patterns of species

coexistence, internal dynamics of plant communities and their consequences in community dynamics.

Considering the concepts and methods of fine-scale turnover approaches there exists a great variation. Temporal and spatial dynamics of individual species, usually referred to as mobility and species replacement (turnover), have been studied on fine-scale from the scale of 1 cm<sup>2</sup> to 0.25 m<sup>2</sup> on

small permanent sub-plots, as well as on coarser scale from 1 m<sup>2</sup> to 25 m<sup>2</sup> plots within a community. These were measured as 1) year to year changes in species composition (Glenn and Collins 1990, 1992, Stampfli 1995, Hobbs and Mooney 1995, Tamás and Csontos 1998, Zhang and Skarpe 1995) and 2) cumulative species richness or frequencies (Klimes 1995, 1999, van der Maarel and Sykes 1993, 1997, Sykes *et al.* 1994, Partel and Zobel 1995, van der Maarel *et al.* 1995, van der Maarel 1996a,b, GeiBelbrecht-Taferner *et al.* 1997) for assessment of community dynamics and as 3) species turnover on small plots within the community (Huber 1994, Otsus and Zobel 2002) or 4) in the form of species replacement diagrams (Thórhallsdóttir 1990, Herben *et al.* 1993). In the latter case spatial aspect of this mobility was shown in distribution maps of species and species mobility was combined with capacity for long-distance spreading, with phalanx and guerrilla plant strategies (Herben *et al.* 1993). A system of plant mobility types was proposed by van der Maarel (1996) and his carousel model set up in 1993 has been already discussed in various types of plant communities (Fröborg and Eriksson 1997, Maslov and van der Maarel 2000, del Moral 2000). Different measures of species mobility by indirect and direct indices have been recently summarized by Palmer and Rusch (2001).

As to the results on patterns of local species turnover and factors controlling their changes, it is not surprising, that there are various conclusions, depending on the structure and dynamical state of the studied vegetation and the scales of observation. For illustrating some contrasting opinions, few examples are mentioned.

Recently many studies of fine-scale plant mobility, performed in near-equilibrium or stable communities (van der Maarel and Sykes 1993, Rusch and van der Maarel 1992), have shown that the occupation of microhabitats proceeds at random within plots, where there is no dispersal limitation, and the degrees of colonization and extinction processes can be considered near the same in a year and are also consistent from year to year. On the contrary, several studies (Ryser 1993, van der Maarel *et al.* 1995) have concluded that spatio-temporal patterns of turnover within a community are not totally stochastic, mainly due to the great variation of local population densities, the limitation of seed dispersal and the growth forms and propagation strategies of plants. However, in spite of the fact that there have been increasing evidences on that majority of plant communities are spatially and temporally heterogeneous and fine-scale dynamics, such as local species turnover changes are constrained by the

existing vegetation, there is a lack of studies considering the species turnover not only as a phenomenon but as a function of vegetation pattern.

In this paper, we present an analysis of fine-scale patterns of local plant species turnover in connection with spatial vegetation patterns of successional communities. We examine what differences appear in the fine-scale plant species turnovers of three stages of *Brachypodium* grassland and how they are influenced by the gap structure and vegetation canopy height and closure of a stand. In analyzing patterns of local species turnover in connection with spatial vegetation patterns, we only consider the patterns of high and low species turnovers. As previous fine-scale studies (Virágh and Bartha 1998a,c) revealed the differentiation of a characteristic species coalition for each of three patches of *Brachypodium* grassland and found three grass species, such as the mesic, shade-tolerant *Brachypodium pinnatum*, the shade-intolerant *Bromus erectus* and the light-demanding xeric *Festuca rupicola*, playing central roles in spatial organization and forming species coalitions, we expect that spatial patterns of these key grass species can control the patterns of local turnover. Thus, as a first step, we deduced vegetation pattern of a stand into patterns of these three matrix-forming species and to the patterns of turnover of subordinates.

The main objectives of this study are:

- to analyze how local species turnover change in *Brachypodium* types with different species composition and spatial organization of species,

- to compare the relative roles of some key grass species in controlling the patterns of local species turnover.

The following questions are examined:

- are local species turnovers spatially and temporally dependent,

- are local species turnover changes influenced by the species dominance structure and the canopy closure, and

- are there any differences between the relative role of three key grass species according to controlling patterns of fine-scale species turnover and how are these differences related to the various fine-scale vegetation patterns of grassland types and the abundances and growth forms of these species.

## Material and methods

### *Study site*

Field studies were carried out in a landscape protection area in the central part of Hungary, 25 km east of Budapest, within a hilly landscape at 200-300

m a.s.l. Mean annual temperature of the site is 9 °C, mean January temperature is -1.5 °C, mean July temperature is +20.1 °C. Mean annual precipitation is about 600 mm distributed unevenly throughout the year. The most rainy seasons are late spring and early autumn with monthly precipitation maximum in May or June and the second lower maximum in October. Transitional soil types between brown forest soil and chernozem on loess substrate are typical here. The area was formerly covered by dry *Quercus pubescens* oakwood, which was clear-cut in the early 1900s (Anon. 1883, 1943). However, deforestation was incomplete and resulted in a heterogeneous mosaic of secondary successional habitats. The forest management activity stopped and the site had only occasionally been grazed since then. During a landscape-scale survey of the vegetation (Fekete *et al.* 1998) some remnants of oakwood, shrubland, and a patchwork of various xero-mesophilous grasslands on the northeast slopes were found.

*Brachypodium pinnatum* was the dominant component of the sparse undergrowth layer of the former dry oak woodland. Clones of *Brachypodium pinnatum* survived forest clear-felled and they developed into species rich xeromesophilous *Brachypodium* communities. These grasslands can persist for a long time and in certain conditions slowly change into a more xeric type of *Festuca rupicola* dominated grasslands. During these long-term changes many mesic, forest and forest-steppe species disappear, parallel with the colonization of several xeric loess steppe species.

Three typical vegetation types (Forest-type, Forest-steppe-, and Steppe-types) of *Brachypodium pinnatum* dominated grassland were selected for the present study. Most of the species are clonal perennials in these patches and annuals are scarce. The physiognomically uniform stands chosen are floristically and coenologically different from each other (Fekete *et al.* 1998) and each patch-type is spatially well-organized with complex multispecies coalition structures (Virágh and Bartha 1998a, Virágh *et al.* 2000).

Some textural attributes of three *Brachypodium* types are presented in Table 1. It is remarkable that few dominant and frequent (freq.: > 10%) and codominant and less frequent species (freq.: < 5%) occur in all patches, but the proportion of rare species (freq.: < 1%) is very high. Most of the species appear in the Forest-steppe type, but many codominant species are apparent in the Steppe-type.

Forest-type stands are dense and closed, where the average height of the sward is about 60-70 cm. A litter thickness is 10-15 cm. Numerous shade-tolerant species, remnants of the original forest vegetation

live in a dense uniform canopy of *Brachypodium* clones, surviving under the shadow of scattered oak trees and *Crataegus monogyna* shrubs.

Table 1. Characteristics of three types of *Brachypodium pinnatum* grassland, 1993 (2200 microquadrats of 0.0025 m<sup>2</sup>)

	Forest-type	Forest-steppe-type	Steppe-type
Total cover [%]	120	155	130
Average height of the sward [cm]	50-60	30-45	30-35
Litter thickness [cm]	10-15	5-10	2-6
Number of frequent species			
Frequency % > 10	3	5	6
Frequency % > 5	7	8	11
Frequency % > 1	16	26	22
Frequency % < 1	34	31	24
Number of abundant species			
Relative cover % > 1	9	13	16
Relative cover % < 1	41	44	30
Frequency %			
<i>Brachypodium pinnatum</i>	79.5	63.1	52.4
<i>Festuca rupicola</i>	23.7	17.6	20.3
<i>Bromus erectus</i>	5.9	24.7	25.8
Relative cover %			
<i>Brachypodium pinnatum</i>	74.9	35	22
<i>Festuca rupicola</i>	3.6	7.7	15.4
<i>Bromus erectus</i>	2.3	17.6	20

Forest-steppe-type is an intermediate stage from mesic communities to xeric ones. It contains a mixture of mesic and xeric species with many codominant dicots and broad-leaved grasses. The height of sward is 30-45 cm, the litter thickness is 5-10 cm.

Steppe-type develops after a long exposure to light and drought, as the result of invasion of xerophilous species. The viability and density of *Brachypodium* ramets are lower. The height of sward is 30-35 cm, and the litter thickness is only 2-6 cm here. The canopy is rather open, and the number of gaps is the highest in this patch.

These vegetation types also represent a light gradient associated with the declining dominance of *Brachypodium pinnatum* (Virágh and Bartha 1998a,b, Fekete *et al.* 2000, Fóti *et al.* 2002, Mojzes *et al.* 2003). There are three matrix grass species with different growth forms, such as the shade-tolerant *Brachypodium pinnatum* (a clone with sparsely distributed tillers), the shade-intolerant *Bromus erectus* of dense tussock and the drought tolerant, light demanding *Festuca rupicola* of sparse clump, which play important roles in coenological

differentiation at stand-scale and in spatial organization of species while forming characteristic multispecies coalitions at fine-scale. Their segregation in space is obvious in our communities, where they are generally significantly associated to the subordinated dicots and other grass species, but rare to each other (Virágh and Bartha 1998c).

#### Field sampling

Micro-maps of rooting individuals (or ramets) of vascular plant species were recorded in 20×110 grids of contiguous 5×5 cm micro-quadrats at the end of June, 1993, 1994 and 1995 in each vegetation type. Seedlings were not included, since they strongly differ in their resource use and competitive dynamics from the more established plants (Herben *et al.* 1993). Because of the heterogeneity and the limited size of the study area and the very laborious and time-consuming sampling, we could not sample many independent replicates of each vegetation type. However, when we studied the multispecies spatial patterns and interspecific associations in these three *Brachypodium* types (Virágh and Bartha 1998) and for a validation of the trends found we divided the 20×110 grids into two 10×110 subgrids and repeated the whole analyses with the pairs of subgrids, all trends remained the same showing the robustness of our results and indicating some stationarity of the studied vegetation patterns. Therefore, the analyses here concerned the whole 20×110 grids which could be also accept as representative for the *Brachypodium* stands.

#### Statistical methods

Species richness was measured at two different scales: microquadrat scale (the mean value per microquadrat) and stand scale (the total number of species found across all microquadrats within a stand, study area was 5.5 m<sup>2</sup>). Colonization was expressed by the number of species appearing in all microquadrats (2200) of a stand in a year (*t*) but being absent in the previous (*t*-1) year. Similarly, extinction was calculated as the number of species disappearing from the microquadrats between two consecutive years. Relative colonization % was the ratio of the number of species appearing in all microquadrats in a year (*t*) and the total number of species present in that year (*t*). Relative extinction % was calculated as the number of species disappearing from all microquadrats of a stand between year (*t*-1) and year (*t*), divided by the number of species present in year (*t*-1) (cf. Gibson and Brown 1991, Bartha *et al.* 2003).

Fine-scale local species turnover (TO) was defined as the sum of the local (5×5 cm microquadrat

scale) colonization and extinction between subsequent years. Note that the estimation of local turnover here was based on the numbers of newly appearing species and disappearing ones from each microquadrat between two consecutive years but could not consider the disappeared ramets which were replaced with new ones in the same microplots within a year. It means that in this sense local turnovers in our data may be underestimated. Percentage local relative turnover (*RTO*%) was calculated as  $RTO\% = 100 \times TO / ST2$  where *ST2* is the number of species in the micro-quadrats in the second year. Average local turnover and average local colonization and extinction were estimated at microquadrat-scale (the mean value per microquadrat). Because we were interested in the effect of dominant grasses (*Brachypodium pinnatum*, *Bromus erectus*, *Festuca rupicola*) on the turnover of all other (subordinate species), during the calculations of turnover values the three dominant grasses were omitted.

Percentage relative turnover data were transformed into binary data: *BRT0* = 1 if *RTO*% > the mean, and *BRT0* = 0 if *RTO*% < the mean, producing micro-maps with patterns of high and low local turnovers.

Micro-maps of species turnovers were analyzed by contagion indices, modified from indices used in landscape ecology (O'Neill *et al.* 1988, Li and Reynolds 1993).

$$\text{Temporal contagion} = \frac{1}{N} \sum_{i=1}^N (BRT0_{ij} - BRT0_{ik})^2$$

that expresses the average temporal dependence of local species turnovers between subsequent years *j* and *k*. *N* is the number of micro-quadrats.

$$\text{Spatial contagion} = \frac{1}{N} \sum_{i=1}^N \left( \frac{1}{M_i} \sum_{n=1}^{M_i} (BRT0_i - BRT0_n)^2 \right)$$

(*M<sub>i</sub>* the number of proximate quadrats around microquadrat *i*, *N* is the number of micro-quadrats)

Because high and low turnovers could similarly appear in the adjacent quadrats by chance as well, we applied a null model, where the same local turnover values were used as in the field, however they were randomly assigned to the positions in the micro-maps (complete randomization from Diggle 1983). The observed values of contagion indices were compared with the values obtained from the null model. The significance was expressed as the relative frequency of the randomizations resulted in higher values than the observed one. 5000 randomizations were applied in each test. A significant result indicated the

tendency that the (spatially or temporally) adjacent micro-quadrats had similarly higher or lower species turnovers, i.e. the local species turnovers were not independent.

Relationship between species turnover and vegetation was investigated by calculating the spatial associations between the patterns of dominant grass species and the micro-maps of high/low local species turnovers.

From the basic grid data computerized sampling was performed with three different, increasing sampling unit sizes (5×5 cm, 5×10 cm, and 5×15 cm), and pairwise associations were calculated from 2×2 contingency tables:

$$mI(A,B) = m \log m + a \log a + b \log b + c \log c + d \log d - (a+c) \log(a+c) - (b+d) \log(b+d) - (a+b) \log(a+b) - (c+d) \log(c+d)$$

(Symbols *a*, *b*, *c*, and *d* correspond to the notation of the 2×2 contingency table. ‘*a*’ is the number of sampling units where both variables, *A* and *B* are present, ‘*d*’ is the number of empty quadrats. ‘*b*’ and ‘*c*’ note the number of quadrats, where only one variable is present, *A* or *B* respectively.  $m = a + b + c + d$  is the sample size.)

Significance of any observed *mI(A,B)* value was calculated by comparing it with the values obtained by Monte-Carlo randomizations, i.e. representations of the null hypotheses. We used a null model where the presences of a variable were randomly redistributed among the quadrats, by using Monte-Carlo simulation (Site-model, Watkins and Wilson 1992). The significance was expressed as the relative frequency of the randomizations resulted in higher values than the observed one. 5000 randomizations were applied in each test. The trend of the association, i.e. whether the association was positive or negative, was given by a comparison of the expected and observed values of the joint occurrence

of variables *A* and *B*. Calculations were repeated at three sampling unit sizes (5×5 cm, 5×10 cm, and 5×15 cm) at fine scales.

## Results

### *Species turnover*

The total number of species recorded in the 2200 microquadrats (5.5 m<sup>2</sup>) ranged between 50 and 67 in the *Brachypodium* grassland types over 3 years (Table 2). Species richness was the lowest in the Forest-type and the highest in the Forest-steppe - type. Most of the newly detected species appeared in each vegetation type in 1994 and 1995. The average number of species of 0.0025 m<sup>2</sup> microquadrats ranged between 1.07 and 2.05 with a minimum of 0 and maximum of 8 species (Table 2). The percentage number of 5×5 cm vegetation-free gaps (species number is nil) varied between 4%-10% within a stand over 3 years, showing higher values in all grassland types in 1993 and lower values in two subsequent years. The number of gaps was slightly increasing from the mesic Forest-type to the xeric Steppe-type in each year (Table 2).

Percent relative colonization was much higher than percent relative extinction at stand scale in all *Brachypodium* types from 1993 to 1994, but relative colonization and extinction balanced from 1994 to 1995, except the Forest-steppe type. Similar tendency was apparent at microquadrat scale, as well.

Stand-scale relative turnovers (Table 3A) varied between 31% and 58%, while average relative local turnovers (Table 3B) were much higher ranging between 85% and 102% at microquadrat-scale, indicating intensive fine-scale dynamics from year to year. Although the changes of relative turnover showed rather fluctuation at stand-scale, but local species turnover changed at micro-scale showed a slightly increasing tendency from forest to steppe types of *Brachypodium* grassland (Tables 3A and 3B).

Table 2. Species richness at stand-scale and average species number and percent number of 5 cm x 5 cm gaps estimated at microquadrat-scale

	1993			1994			1995		
	Forest-type	Forest-steppe-type	Steppe-type	Forest-type	Forest-steppe-type	Steppe-type	Forest-type	Forest-steppe-type	Steppe-type
Total number of species / 5.5 m <sup>2</sup>	50	57	46	61	67	61	62	63	59
Average number of species / 0.0025 m <sup>2</sup>	1.72	2.13	1.07	2.09	2.38	1.31	2.08	2.50	1.34
Percent number of 25cm <sup>2</sup> gaps/5.5 m <sup>2</sup>	7.7	8.6	10.5	3.8	4.8	6	4	4.8	5.5

Table 3. Plant colonization and turnover changes in three *Brachypodium* types over three years

A: Colonization is the number of newly appearing species between subsequent years and extinction is the number of disappeared species between subsequent years within a stand (study area is 5.5 m<sup>2</sup>). Relative colonization % is the ratio of the number of species appearing in the microquadrats (2200) in a year (t) and the total number of species present in that year (t). relative extinction % is expressed as the number of species disappearing from all microquadrats of a stand between year (t-1) and year (t), divided by the total number of species present in the year (t-1).

B: Average local turnover and average local colonization and extinction estimated at microquadrat-scale. Average relative local turnover is calculated as local species turnover per number of species of the microquadrats in the second year.

A)

Stand-scale (5.5 m <sup>2</sup> )	1993-1994			1994-1995		
	Forest-type	Forest-steppe-type	Steppe-type	Forest-type	Forest-steppe-type	Steppe-type
Turnover	19	30	29	27	24	34
Relative turnover (%)	31	44	47	44	38	58
Colonization	15	20	22	14	10	16
Extinction	4	10	7	13	14	18
Relative colonization (%)	25	30	36	23	16	27
Relative extinction (%)	8	20	15	21	21	30

B)

Microquadrat-scale (0.0025 m <sup>2</sup> )	1993-1994			1994-1995		
	Forest-type	Forest-steppe-type	Steppe-type	Forest-type	Forest-steppe-type	Steppe-type
Average local turnover	1.8	2.1	2.04	1.83	2.20	2.21
Average relative local turnover (%)	85.9	90.59	90.88	88.43	91.36	101.79
Average local colonization	1.08	1.17	1.17	0.91	1.16	1.08
Average local extinction	0.72	0.92	0.87	0.92	1.04	1.12

*Within-stand patterns of local species turnovers (significance of contagion indices)*

*Local temporal dependence*

Significant temporal contagion indices obtained for all *Brachypodium* types indicated that the local species turnovers between subsequent years were not independent from each other. It meant that e.g. the micro-quadrats of slow species exchanges were relatively constant in time.

*Local spatial dependence*

Significant spatial dependence of local species turnovers between spatially adjacent micro-quadrats was revealed in the Forest- and Forest-steppe types in each year: small localities with similarly low or high species turnover occurred close to each other. On the contrary, a non-significant spatial contagion was found in the Steppe-type, which showed a decreasing spatial dependence in this type.

*Vegetation pattern vs. local species turnover*

Plexus diagrams (Fig. 1) depicted the significant spatial associations between spatial patterns of 3 grasses and patterns of localities with high/low local species turnovers.

Significant positive spatial associations between species turnovers of the subsequent years showed that the patterns of local turnovers were not independent in time (cf. local temporal contagion indices). Many significant spatial associations between spatial patterns of particular species and turnover patterns indicated that the local species exchanges were influenced by the spatial pattern of existing vegetation as well, and inversely the spatial vegetation patterns were generated by the patterns of turnovers. Although, the significant associations did not appear in every year, we do not think that the revealed correlations would change considerably during a short time interval (3 years), but rather, the lack of significant associations could be induced by the changes of species abundances and interspecies competition. Therefore, in the interpretation of

results we accepted a significant value if there was at least one year with significant value.

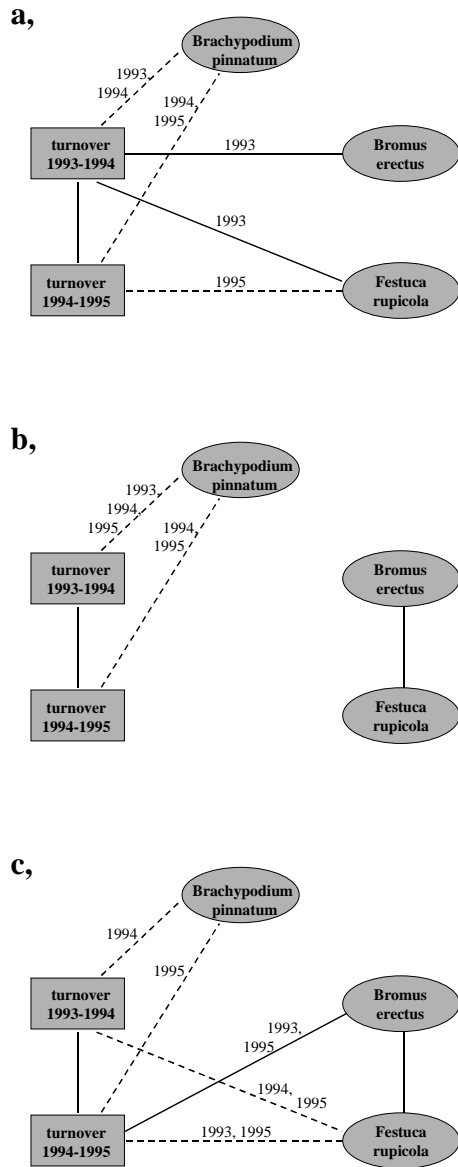


Figure 1. Plexus diagrams depicting the spatial associations between the patterns of three grasses and the patterns of high/low local species turnovers. a: Forest-type, b: Forest-steppe type, c: Steppe-type. \_\_\_\_\_ significant positive associations, - - - - - significant negative associations

In the Forest-type (Fig. 1a) significant spatial associations were found between the spatial patterns of three dominant grasses and the spatial patterns of local species turnovers. Our results suggested that

*Brachypodium pinnatum* “decelerated”, while the subordinate—rare *Festuca rupicola* and *Bromus erectus* “accelerated” the turnovers in this vegetation type.

Spatial patterns of *Bromus erectus* and *Festuca rupicola* were not correlated with the turnover patterns in the Forest-steppe-type (Fig. 1b). Here numerous dicots might also be responsible for the degree of turnovers (see Virágh and Bartha 1998c). *Brachypodium pinnatum* showed negative associations with the temporal species turnovers.

In the Steppe-type (Fig. 1c) both *Brachypodium pinnatum* and *Festuca rupicola* revealed negative relationships with the turnover patterns. Only the spatial pattern of *Bromus erectus* was correlated positively with the relative species exchanges. There was a positive significant association between spatial patterns of *Bromus erectus* and *Festuca rupicola*, indicating that these species could co-occur in this patch and also in the Forest-steppe type. However, these species could not coexist with *Brachypodium pinnatum* in any of the patches.

## Discussion

### *Species turnover in different types of Brachypodium pinnatum grassland*

The changes of species richness and relative turnover % showed rather fluctuation at stand-scale in each *Brachypodium* type over three years. Average relative local species turnover was very high at microquadrat-scale, indicating a slightly increasing tendency from forest to steppe types of *Brachypodium* grassland. Closed canopy vegetation gradually opened and microheterogeneity increased, all induced increasing intensity of local species turnover towards more xeric *Brachypodium* types. This may indicate that multilayered *Brachypodium pinnatum* stand canopy involved a highly competitive environment with high relative local species exchanges and spatial differentiation at microquadrat-scale (cf. Bartha *et al.* 2003, Virágh and Bartha 1998a). Strong fine-scale spatial differentiation among species into contrasting species coalitions according to *Brachypodium* types had been pronounced by previous studies (Virágh and Bartha 1998a, Virágh *et al.* 2000). We also suggest that more intensive fine-scale turnover dynamics from Forest-type to Steppe-type may be principally influenced by a gradual decline of abundance—dominance of *Brachypodium pinnatum*, associated with changes of abundance shift among species and spatial organization of individuals, as well as coincided with varying light conditions and decreasing canopy height and litter thickness.

#### *Plant colonization changes over three years*

It was clear that colonization and average local colonization were the highest between 1993 and 1994, while extinction and average local extinction were between 1994 and 1995, in all *Brachypodium* types. The number of gaps decreased over three years. If we inspected the annual total precipitation (341 mm in 1992, 493 mm in 1993, 482 mm in 1994 and 637 mm in 1995) and considered the years 1993 and 1994 as extreme dry and the year 1995 as strongly wet according to the 13-year precipitation average (554.6 mm) in the study site, we could take some speculation on the role of climatic feature for vegetation dynamics. We thought that as our investigation was started in an exceptionally dry year (1992), thus the decreasing speed of species colonization, increase in extinction from 1993 to 1995, as well as decrease in gap availability during following years could be interpreted as a post-drought dynamics. The drought caused damage to the vegetation, created the openings, so the current study showed how during 1993 and 1995 the vegetation recovered.

#### *Within-stand patterns of vegetation and local species turnover*

Our results showed that local species turnover patterns were temporally and spatially non-random in our spatially heterogeneous *Brachypodium* grassland types. High and low local species turnovers were dependent on the spatial structure of vegetation. Spatial behaviours of some matrix-forming grass species controlled the fine-scale species turnover patterns.

Recently many papers (Rusch and van der Maarel 1992, van der Maarel and Sykes 1993, Herben *et al.* 1993, 1994, Fröborg and Eriksson 1997, Klimes 1999, Palmer and Rusch 2001) had focused on spatial mobility of particular species at different scales and its underlying mechanisms (Otsus and Zobel 2002, Tamm *et al.* 2002, Sammul *et al.* 2003). Most of them emphasized that species mobility was shown to vary individualistically (e.g. van der Maarel and Sykes 1993), however, few studies had already pointed to the importance of spatial dynamics of whole community for influencing strategies of spatial exploitation of particular species or turnover rates of all constituent species (e.g. Otsus and Zobel 2002).

#### *Relative role of matrix-forming grass species in controlling local species turnover patterns*

Comparing the relative role of three key grass species we can state that the species differed from

structuring the patterns of local turnovers in *Brachypodium* patches.

The dominant clonal *Brachypodium pinnatum* decelerated fine-scale turnovers in all types, as the relationships between patterns of occurrences of this species in the microquadrats and the spatial patterns of high local species turnovers were significantly negative.

On the contrary, the local species exchanges of microquadrats including *Bromus erectus* were always high. Spatial behaviour of this species, however, differed in *Brachypodium* types of contrasting coenological structure and spatial microheterogeneity. *Bromus erectus*, as a rare species with low cover in the Forest-type, most frequently occurred in the gaps within the dense clonal architecture of predominant *Brachypodium pinnatum*, where in the gaps there were always the highest species mobility due to some gap-exploiter species mainly propagating by seeds and where the vegetative appearances of *Brachypodium pinnatum* also accounted for increasing the rate of local temporal turnovers. Seeds of *Bromus erectus* only dispersed from the species pool of near neighbours into this vegetation type, as the individuals never reached their mature phase with producing seeds within this community. In the Forest-steppe and Steppe-type this species was codominant due to spreading successfully both by vegetatively and generatively. It showed significant positive spatial associations with many graminoids and dicots (see Virágh and Bartha 1998), but its well-developed individuals (clumps) did not prevent newly appearances of other species, either. In the Steppe-type where the key grasses were spatially segregated in the open canopy of vegetation, *Bromus erectus* had a great success in exploiting open spaces by vegetatively or mainly by generatively, as well as it also allowed local colonization of many other dicots into microquadrats dominated by itself.

*Festuca rupicola* both accelerated and decelerated local turnovers. *Festuca rupicola* also appeared in the small openings of the dense stand predominated by *Brachypodium pinnatum* in the Forest-type, and as a low-frequent species accelerated local species turnovers, similarly to *Bromus erectus*. Nevertheless, when frequency of *Festuca rupicola* increased by 20 - 30 % in this patch (1995), it could decelerate local species exchanges, as well. Fine-scale spatial patterns of *Festuca rupicola* could be considered relatively stable in Steppe-type, where it frequently occupied the same places from year to year and limited appearances of other species. Hence, *Festuca* decelerated local species dynamics, such as *Brachypodium pinnatum* did.



We also emphasized here that the same species had different fine-scale spatial behaviours according to their abundances and hence they could have different roles in generating local species turnovers in vegetation types of contrasting spatial organizations and fine-scale coexistence structures. Role of species with similar propagating strategies, such as *Bromus erectus* and *Festuca rupicola* with limited clonal growth, was different in influencing fine-scale turnovers, or inversely, other species of different growth forms and propagating strategies, such as *Brachypodium pinnatum* with extensive clonal growth and *Bromus erectus*, behaved similarly in generating slow local species turnovers in certain coenological conditions. Such like conclusions merged from the studies by Herben *et al.* (1993) and also Klimes (1999), when fine-scale spatial dynamics of individual species and its correlation with plant growth form were investigated.

Thus, answering our first questions posed in the introduction, we can say, that in the *Brachypodium* grassland types developing after clear-felled oakwoods, local species turnovers were principally constrained by the abundance and dominance relationships among species and also influenced by the canopy height and closure. Referring to the second question we can conclude that the fine-scale species turnover patterns were temporally and spatially non-random. High and low local species turnovers depended on spatial structure of vegetation. As to the third question, we suggest that some matrix grass species had important roles in structuring the local species turnover patterns, according to their abundances. Their spatio-temporal behaviours were not specific but influenced by the microcoenological structure and spatial organization of the whole community.

As our study revealed close relationships between spatio-temporal changes of local species turnover and spatial patterns of three matrix-forming grass species, therefore we suggest that fine-scale species turnover is not only a phenomenon but is a function of vegetation pattern and it is also a mechanism which generates spatial structure of vegetation. Still, we also think that much more similar analyses may be necessary to make comparisons between many types of communities, which can also promote a further synthesis on vegetation dynamics characterized by species turnover as a working mechanism, dependent on vegetation pattern.

## Acknowledgements

We thank Marek Sammul and one anonymous referees for comments and criticism on a previous version of this paper which markedly improved the manuscript. The authors are grateful to András Kun, András Horváth and Zoltán Botta-Dukát for their useful suggestions. This study was supported by the Hungarian Scientific Research Fund OTKA, No T-030459.

## References

- Anon. (1883): Military Survey Map. II. Institute of War History, Budapest.
- Anon. (1943): Military Survey Map. III. Institute of War History, Budapest.
- Bartha, S., Meiners, S. J., Pickett, S. T. A. and Cadenasso, M. L. (2003): Plant colonization windows in a mesic old field succession. - *Appl. Veg. Science* 6, 205-212.
- del Moral, R. (2000): Local species turnover on Mount St. Helens, Washington. - *Proceedings IAVS Symposium, 2000*. Opulus Press Uppsala, 195-197 pp.
- Diggle, P. J. (1983): *Statistical analysis of spatial point patterns*. Academic Press, London.
- Fekete, G., Virágh, K., Aszalós, R. and Orlóci, L. (1998): Landscape and coenological differentiation in *Brachypodium pinnatum* grassland. - *Coenoses* 13, 39-53.
- Fekete G., Virágh K., Aszalós R. and Précsényi I. (2000): Static and dynamic approaches to landscape heterogeneity in the Hungarian forest-steppe zone. - *J. Veg. Sci.* 11, 375-382.
- Fóti, Sz., Virágh, K., Balogh, J., Nagy, Z. and Tuba, Z. (2002): Comparative synphysiological studies on *Brachypodium pinnatum* dominated forest and steppe-type grasslands. - *Acta Biologica Szegediensis* 46, 227-229. <http://www.sci.u-szeged.hu/ABS>
- Fröberg, H. and Eriksson, O. (1997): Local colonization and extinction of field layer plants in a deciduous forest and their dependence upon life history textures. - *J. Veg. Sci.* 8, 395-400.
- GeiBelbrecht-Tafener, L., GeiBelbrecht, J. and Mucina, L. (1997): Fine-scale spatial population patterns and mobility of winter-annual herbs in a dry grassland. - *J. Veg. Sci.* 8, 209-216.
- Gibson, C. W. D. and Brown, V. K. (1991): The effects of grazing on local colonization and extinction during early succession. - *J. Veg. Sci.* 2, 291-300.
- Glenn, S. M. and Collins, S. L. (1990): Patch structure in tallgrass prairies: dynamics of satellite species. - *Oikos* 57, 229-236.
- Glenn, S. M. and Collins, S. L. (1992): Effects of scale and disturbance on rates of immigrations and extinction of species in prairies. - *Oikos* 63, 272-280.
- Herben, T., Krahulec, F., Hadincová, V. and Kovárová, M. (1993): Small-scale spatial dynamics of plant species in a grassland community over six years. - *J. Veg. Sci.* 4, 171-178.
- Herben, T., Krahulec, F., Hadincová, V. and Pechácková, S. (1994): Is a grassland community composed of coexisting species with low and high spatial mobility? - *Folia Geobot. Phytotax.* 29, 459-468.
- Hobbs, R. J. and Mooney, H. A. (1995): Spatial and temporal variability in California annual grassland: results from a long-term study. - *J. Veg. Sci.* 6, 43-56.

- Huber, R. (1994): Changes in plant species richness in a calcareous grassland following changes in environmental conditions. *Folia Geobot. Phytotax.* 29, 469-482.
- Klimes, L. (1995): Small-scale distribution of species richness in a grassland (Bílé Karpaty Mts., Czech republic). - *Folia Geobot. Phytotax.* Praha 30, 499-510.
- Klimes, L. (1999): Small-scale plant mobility in a species-rich grassland. - *J. Veg. Sci.* 10, 209-218.
- Li, H. and Reynolds, J. F. (1993): A new contagion index to quantify spatial patterns of landscapes. - *Landscape Ecology* 8, 155-162.
- Maslov, A. A. and van der Maarel, E. (2000): Limitation and extensions of the carousel model in boreal forest communities. *Proceedings IAVS Symposium, 2000.* - Opulus Press Uppsala, 361-364 pp.
- Mojzes, A., Kalapos, T. and Virágh, K. (2003): Plasticity of leaf and shoot morphology and leaf photochemistry for *Brachypodium pinnatum* (L.) Beauv. growing in contrasting microenvironments in a semiarid loess forest-steppe vegetation mosaic. - *Flora* 198, 304-320.
- O'Neill, R. V., Krummel, J. R., Gardner, R. H., Sugihara, G., Jackson, B., DeAngelis, D. L., Milne, B. T., Turner, M. G., Zymunt, B., Christensen, S. W., Dale, V. H. and Graham, R. L. (1988): Indices of landscape pattern. - *Landscape Ecology* 1, 153-162.
- Otsus, M. and Zobel, M. (2002): Small-scale turnover in a calcareous grassland, its pattern and components. - *J. Veg. Sci.* 13, 199-206.
- Palmer, M. W. and Rusch, G. M. (2001): How fast is the carousel? Direct indices of species mobility with examples from an Oklahoma grassland. - *J. Veg. Sci.* 12, 305-318.
- Partel, M. and Zobel, M. (1995): Small-scale dynamics and species richness in successional alvar plant communities. - *Ecography* 18, 83-90.
- Rusch, G. and van der Maarel, E. (1992): Species turnover and seedling recruitment in limestone grassland. - *Oikos* 63, 139-146.
- Ryser, P. (1993): Influences of neighbouring plants on seedling establishment in limestone grassland. - *J. Veg. Sci.* 4, 195-202.
- Sammul, M., Kull, K. and Tamm, A. (2003): Clonal growth in a species-rich grassland: results of a 20-year fertilization experiment. - *Folia Geobotanica* 38, 1-20.
- Stampfli, A. (1995): Species composition and standing crop variation in an unfertilized meadow and its relationship to climatic variability during six years. - *Folia Geobot. Phytotax.* 30, 117-130.
- Sykes, M. T., van der Maarel, E., Peet, R. K. and Williams, J. H. (1994): High species mobility in species-rich plant communities: an intercontinental comparison. - *Folia Geobot. Phytotax.* 29, 439-448.
- Tamás, J. and Csontos, P. (1998): A növényzet tűz utáni regenerálódása dolomitra telepített feketefenyvesek helyén. (Early regeneration of dolomite vegetation after burning of *Pinus nigra* plantations.) In: Csontos, P. (ed.): *Sziklagyepek szünbotanikai kutatása.* (Synbotanical studies of rock grasslands.) - Scientia Kiadó, Budapest. p. 231-267.
- Tamm, A., Kull, K. and Sammul, M. (2002): Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis. - *Evol. Ecol.* 15, 383-401.
- Thórhallsdóttir, T. E. (1990): The dynamics of a grassland community: A simultaneous investigation of spatial and temporal heterogeneity at various scales. - *J. Ecol.* 78, 884-908.
- van der Maarel, E. (1996a): Pattern and process in the plant community: Fifty years after A. S. Watt. - *J. Veg. Sci.* 7, 19-28.
- van der Maarel, E. (1996b): Vegetation dynamics and dynamic vegetation science. - *Acta Bot. Nerdl.* 45, 421-422.
- van der Maarel, E. and Sykes, M. T. (1993): Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. - *J. Veg. Sci.* 4, 179-188.
- van der Maarel, E., Noest, V. and Palmer, M. W. (1995): Variation in species richness on small grassland quadrats: Niche structure or small-scale plant mobility? - *J. Veg. Sci.* 6, 741-752.
- van der Maarel, E. and Sykes, M. T. (1997): Rates of small-scale species mobility in alvar limestone grassland. - *J. Veg. Sci.* 8, 199-208.
- Virágh, K. and Bartha, S. (1998a): Interspecific associations in different successional stages of *Brachypodium pinnatum* grasslands after deforestation in Hungary. - *Tiscia* 31, 3-12.
- Virágh, K. and Bartha, S. (1998b): Koalíciós struktúra átrendeződések a löszsztepprétek kialakulása felé tartó szukcesszió során. (Changes of coalition structure during the secondary succession toward the development of xerophilous loess steppe vegetation.) - *Kitaibelia* 68, 337-338.
- Virágh, K. and Bartha, S. (1998c): Fine-scale spatial differentiation of *Brachypodium* grasslands after deforestation in Hungary, In: Sjögren E., van der Maarel E., Pokarzhevskaya G. (eds.): *Abstracts of the 41st IAVS Symposium on "Vegetation Science I Retrospect and Perspective"*, 26 July - 1 August 1998, Uppsala, Sweden. *Studies in Plant Ecology*, Vol. 20, - Opulus Press, Uppsala, p.102.
- Virágh, K., Bartha, S. and Botta-Dukát, Z. (2000): Fine-scale coalition structure in *Brachypodium* grassland. *Proceedings IAVS Symposium, 2000.* - Opulus Press Uppsala. 366-369 pp.
- Watkins, A. J. and Wilson, J. B. (1992): Fine-scale community structure of lawn. - *J. Ecol.* 80, 15-24.
- Zhang, W. and Skarpe, S. 1995. Small-scale species dynamics in semi-arid steppe vegetation in Inner Mongolia. *J. Veg. Sci.* 6: 583-592.