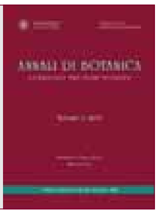
ANNALI DI BOTANICA
Ann. Bot. (Roma), 2011, 1: 9–18



BETA DIVERSITY AND COMMUNITY DIFFERENTIATION IN DRY PERENNIAL SAND GRASSLANDS

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(RECEIVED 16 OCTOBER 2010; RECEIVED IN REVISED FORM 19 DECEMBER 2010; ACCEPTED 22 DECEMBER 2010)

ABSTRACT: The spatial variability of species composition was studied in perennial sand grasslands in Hungary at multiple scales. Three sites were compared along an aridity gradient. Existing differences in climate along this ca. 200 km gradient correspond to regional climate changes predicted for the next 20-30 years. Six stands of *Festucetum vaginatae* grasslands were selected at each site within 400 x 1200 m areas for representing the coarse-scale within-site heterogeneity. Fine-scale compositional heterogeneity of vegetation within stands was sampled by recording the presence of species along 52 m long circular belt transects of 1040 units of 5 cm x 5 cm contiguous microquadrats. This sampling design enabled us to study the patterns of species combinations at a wide range of scales. The highest variability of plant species combinations appeared at very fine scales, between 10 cm and 25 cm. Differences in beta diversity along the gradient were scale-dependent. We found a decreasing trend of beta diversity with increasing aridity at fine scale, and on the contrary, an increasing trend at landscape scale. We conclude that the major trend of the vegetation differentiation due to aridity is the decrease of compositional variability at fine-scale accompanied by a coarse-scale diversification.

KEYWORDS: ARIDITY GRADIENT, BETA DIVERSITY, COMPOSITIONAL VARIABILITY, MULTIPLE SCALES, RESILIENCE

INTRODUCTION

In arid and semiarid environments drought is considered to be the most important environmental driver in controlling vegetation patterns and processes. The correlations between diversity and plant productivity on the one hand, and energy and precipitation on the other hand are well documented and robust relationships in ecology (O'Brien et al., 2000; Willing et al., 2003; Kreft & Jeltz, 2007). At broad macroecological scales, species richness, productivity and plant cover are expected to decrease with increasing aridity (Veron et al., 2002; Zhou et al., 2002). Less is known about the compositional heterogeneity along short precipitation gradients. Understanding vegetation differentiation along short precipitation gradients, however, is important for predicting short-term vegetation responses to climatic changes.

Perennial sand grassland is a component of the remnant natural forest-steppe vegetation of the Hungarian Plain (Fekete, 1992). This vegetation type is expected to respond to climate change in a sensitive way (Kovács-Láng et al., 2008). Regional climate change scenarios predict a decrease in growing season precipitation and an increase in growing season temperature for the Carpathian Basin during the next decades (Molnár & Mika, 1997; Bartoly et al., 2007). Existing differences in climate along a ca. 200 km north-west to south-east gradient in Hungary (Borhidi, 1993; Kun, 2001) correspond to regional climate changes predicted for the next 20-30 years. Sand grasslands occur along this gradient. Therefore, assessing their large-scale variability along the current climate gradient may help to forecast future differentiation of this vegetation type in the region. Landuse effects can accelerate vegetation processes driven by climatic changes. Sand grasslands are especially sensitive to disturbance and they are threatened by man-induced desertification (Li et al., 2006; Huang et al., 2007). Therefore, there is an urgent need to develop effective indicators for early warning about desertification processes.

Beta diversity is the variation of species composition among sites. There are many indices used with little consensus about the applicability to particular questions (Anderson et al., 2010). Based on recent reviews on beta diversity measures (Anderson et al., 2010; Tuomisto, 2010a, b) we selected four standard indices representing variation or turnover of species composition and using presence/absence or abundance data. As an alternative measure of the variation of species composition among sites, we propose to use the number of species combinations estimated over a series of a plot sizes. The realized species combinations give details about the fine-scale coexistence relations. This is a well-established, standard method for fine-scale analysis of plant communities (Juhász-Nagy & Podani, 1983; Tóthmérész & Erdei, 1992; Podani, 2006; Ricotta & Anand, 2006). However, it has not been used or interpreted in the context of beta diversity. Beta diversity changes with altitude (Sang, 2009), with succession (Hogeweg et al., 1985; del Moral, 2007) and with vegetation degradation (Chaneton et al., 2002; Kéfi et al., 2007). Consequently, it can be a sensible indicator of climate change and man-induced desertification (Bestelmeyer et al., 2006; Huang et al., 2007; Kéfi et al., 2007).

In a recent study, Kovács-Láng et al. (2000) found decreasing alpha diversity, plant cover and proportion of forest species, and increasing proportion of sand grassland specialists and annuals of continental and submediterranean character along the 200 km north-west to south-east gradient in Hungary. Here, we further explore the vegetation differentiation along this aridity gradient by extending our study to the patterns of beta diversity. We hypothesize that beta diversity will increase along the aridity gradient.

STUDY AREA

Within the forest steppe biome in Hungary, three study sites: Gönyű (47º43'N, 17º49'E), Csévharaszt (47º17'N, 19º24'E) and Fülöpháza (46º53'N, 19º23'E) have been chosen along an aridity gradient (Table 1). The climate is temperate, with continental and submediterranean features; mean annual precipitation along the gradient varies between 565 mm and 535 mm, with maximum precipitation occurring in May and November. The mean annual temperature varies between 10.07 ºC in the north-west and 10.33 ºC in the south-east. There are strong seasonal and daily fluctuations in temperature and air humidity and uneven temporal distribution in precipitation. The climate at Fülöpháza is slightly more arid. Despite of the minor changes in mean climatic attributes, previous studies revealed significant between-site differences in vegetation characteristics (Kovács-Láng et al., 2000). The relative frequency of droughts (Pálfai drought index, Table 1) and the temporal variability of climatic features expressed by the frequency distribution of precipitation curve types show clearer trends and a significant increase in aridity from Gönyű to Fülöpháza (Kun, 2001). The relative cover of the forest component of the forest steppe vegetation changes along the gradient. At Gönyű, at the mesic end of the gradient, forest patches cover 60%. The landscape is more open at Fülöpháza, where sparse juniper-poplar woodland are scattered in the matrix of dry sand grasslands (Kovács-Láng et al., 2000).

The soils belong to the coarse sand soil group (Calcaric arenosol). They are characterized by weakly developed soil profile, alkaline reaction, medium carbonate-content, low colloid, clay and organic matter content, and deep groundwater-table (Várallyay, 1993). Humus content decreases and the $CaCO_3$ content increases from Gönyű to Fülöpháza (Kovács-Láng et al., 2000). All sites are located in nature conservation areas: the Gönyű site has been protected since 1977, whereas the Csévharaszt site since 1939, and Fülöpháza site since 1974. Before protection, all sites experienced some disturbances (grazing and military trainings) in the past.

Table 1. Sites characteristics

	Gönyü	**Csévharaszt**	**Fülöpháza**
Geographical characteristics			
Longitude (East/West) E (°)	17,49	19,24	19,23
Latitude (North/South) N (°)	47,43	47,17	46,53
Elevation (m)	130	140	130
Climatic characteristics (30 years 1951-1980)			
Mean annual precipitation (mm)	565	545	535
Mean annual temperature (°C)	10,07	10,23	10,33
Sunshine duration (hours)	1880	1922	2093
Pálfai drougth index (1931-1998)			
% of years without drought	81	62	54
% of years with moderate drought	14	26	28
% of years with heavy drought	5	12	18
Vegetation characteristics			
Mean cover (%) (16 m^2)	71	55	36
species density (16 m^2)	27	19	16
species pool (1/2 km^2)	125	108	60
Hemicryptophytes (%)	60	61,3	43,8
Geophytes (%)	13,8	4	2
Therophytes (%)	16	26,8	41,7
Other Raunkier's life forms (%)	10,2	7,9	12,5
Sand grassland specialist (%)	5,5	7,3	10,9
Continental species (%)	43,2	44,6	51,6

Based on Kovács-Láng et al., (2000; 2005; 2008) and Kun, 2001

MATERIAL AND METHODS

We used a nested design with three levels. First, we had three study sites: Gönyű, Csévharaszt and Fülöpháza, respresenting the changing landscapes along the aridity gradient. Each site had the same size of 400 x 1200 m area representing the site-specific mosaic of woodlands, open sand grasslands, and dried out remnant of wetlands (Kovács-Láng et al., 2000; 2008). Second, we used a stratified random design selecting relatively large (minimum 30 m in diameter) uniform vegetation patches of open sand grassland (*Festucetum vaginatae*) from the heterogeneous vegetation mosaic. Six stands of *Festucetum vaginatae* grasslands were selected at each site for representing the coarse-scale within-site heterogeneity. Third, we sampled the fine-scale heterogeneity within-stands. For this fine-scale sampling, we used a standard pattern analysis design (cf. Juhász-Nagy & Podani, 1983; Bartha, 1991; Bartha & Kertész 1998; Campetella et al., 2004; Bartha et al., 2004, 2008b; Virágh et al., 2008). Presences of plant species were recorded along a 52 m long circular belt transect of 1040 units of 0.05 m x 0.05 m contiguous microquadrats. Circular transect is preferred to avoid edge effects during secondary computerized sampling (Podani, 1987) and to allow various types of permutation tests (not shown in this paper) (Bartha & Kertész, 1998). The large number and small size of microquadrats ensure the precise estimation of frequency of species and species combinations (Bartha et al., 2004; 2008; Virágh et al., 2008). Species abundances were estimated by the frequency of species in the microquadrats. The sampling was performed between mid-May and mid-June, 1996, during the phenological optimum of this community.

Five beta diversity measures were calculated. 1, Whittaker $\beta_W = \gamma/\alpha$, where γ is the total number of species in the sampled vegetation patch and α is the average number of species recorded in the sampling units (Whittaker, 1960). 2, $\beta_{Shannon} = H_\gamma/H_\alpha$ includes also relative abundance information based on the exponential form of the Shannon-Wiener index for the pooled γ level and for the average of α level sampling units (Jost, 2007). 3, Spatial turnover of species composition, represented by the mean 1-Sørensen index (for presence-absence data), where 1-Sørensen index is calculated between all pairs of the sampling units. 4, Spatial turnover represented by the mean Bray-Curtis index that is the corresponding dissimilarity index with abundance data (Anderson et al., 2010).

Beta diversity indices were calculated at two scales. At coarse scale, between transects: γ diversity was the pooled richness and pooled diversity at site scale, and α diversity was represented by the average richness and diversity of transects (N=6). Multivariate dissimilarity measures were calculated between transects (N=15 pairs). At fine scale, within transect α diversity was the average of richness and diversity in 20 cm long subtransects (N=20), and the related mean dissimilarity measures were also calculated between the 20 cm long subtransects (N=190 pairs).

5, For representing fine-scale beta diversity, we estimated also the maximum number of the realized species combinations (NRC) (Juhász-Nagy & Podani, 1983). NRC was calculated across a range of scales (Fig. 1) from 5 cm x 5 cm to 5 cm x 25 m by merging two, then three, then four, …etc. consecutive microquadrats by subsequent computerised samplings from the baseline transect data sets (spatial series analysis; Podani, 1987). For this computerized sampling in spatial series and for the calculation of the number of species combinations and the richness and diversity at each scale, we used the PRIMPRO and the SVAR programs (Bartha et al., 1998; Mucina & Bartha, 1999). The number of species combinations changes with scales and it shows a unimodal curve (Fig. 1). The maximum of this curve (max. NRC) was used to represent beta diversity at fine scales, i.e. within a particular vegetation patch. The spatial scale (resolution) where the curve reaches its maximum is characteristics for the vegetation patterns (Bartha et al., 1998). Therefore, these maximum scales (scale of max. NRC) were also recorded and their patterns were tested along the aridity gradient. Other studies of fine-scale beta diversity used arbitrary chosen spatial scales. Our method enables us to determine the natural characteristic scales of plant communities (for details see Juhász-Nagy & Podani, 1983; Bartha et al., 1998). As an alternative measure of the coarse-scale beta diversity, we calculated the relative variance (CV%) of the max. NRC of the six transects for each site.

Multivariate dissimilarity indices were calculated by the SYN-TAX 5.0 software package (Podani, 1993). Differences between sites were analysed using one-way ANOVA (with the three sites as levels) and with post hoc tests using LSD statistics (Sokal & Rohlf, 1995). Overall trend of vegetation characteristics along the gradient was evaluated by Spearman rank correlation. A rank value was assigned to each site (ordered as Gönyű i=1, Csévharaszt i=2, Fülöpháza i=3) and the correlation between these ranks and the vegetation characteristics was tested (N=18, degree of freedom=17). In order to evaluate difference in variance and possible trends among sites, the homogeneity of variance was tested by Levene statistic for each pair of sites (Campbell, 1974). Tests were performed with Statistica 7.0 (StatSoft Inc., Tulsa, OK, USA).

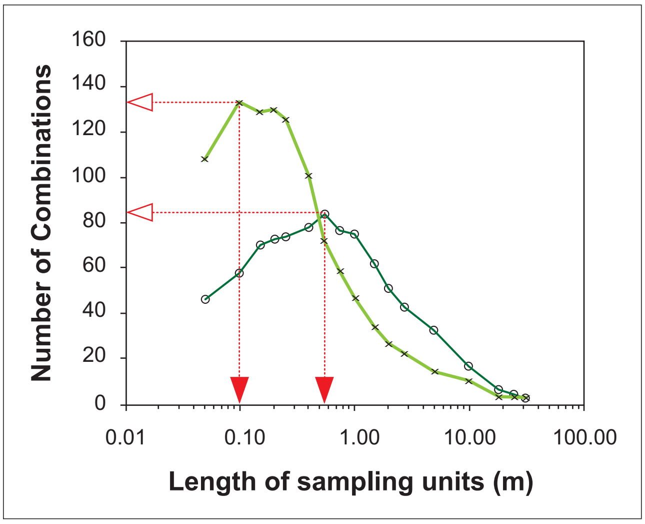

Figure 1. The number of realized species combinations (NRC) as a function of sampling scale (resolution). At each resolution (i.e., at each sampling unit size) the number of species combinations was calculated in 1040 overlapping sampling units for each transect position along the circular transect. We used the maximum of this function (max. NRC) and the related scale (Scale of max. NRC) for further comparisons in this study. The max. NRC refers to the intensity of vegetation pattern, while the related scale (Scale of max. NRC) refers to the grain of vegetation pattern. Two examples are shown from the sand grasslands in Fülöpháza.

Results

The pattern of rank order of the most abundant species (Table 2) showed high variability and a clear trend with increasing aridity in *Festucetum vaginatae* communities. At the more mesic site (at Gönyű) *Stipa borysthenica* and *Festuca vaginata* often appeared together (i.e. they were codominants) accompanied by some perennial forbs (*Aster linosyris*, *Dianthus serotinus*, *Gypsophila fastigiata ssp. arenaria* and *Helianthemum ovatum*). This pattern was similar in all sampled stands with occasional contributions of the lichen *Cladonia convoluta* and some graminoids: *Carex liparicarpos*, *Koeleria glauca* or *Poa bulbosa*. The cryptogams formed the most abundant group at Csévharaszt (with *Cladonia furcata*, *Cladonia magyarica*, *Cladonia convoluta* and *Tortula ruralis*). Perennial grasses, *Stipa borythenica* and *Poa bulbosa,* appeared here only in the 3rd rank. *Festuca vaginata* still occurred together with *Stipa borysthenica*, however with lower rank in the abundance hierarchy. Cryptogams (*Tortula ruralis*, *Tortella inclinata* and *Cladonia convoluta*) were most abundant also at Fülöpháza, at the arid end of the gradient. At Fülöpháza *Festuca vaginata* and *Stipa borysthenica* often appeared separately, and the abundance of annuals (*Cerastium semidecandrum*, *Arenaria serpyllifolia*, and *Erophila verna*) became apparent. In some patches *Fumana procumbens* was dominant. *Poa bulbosa* also appeared among the most abundant species. The heterogeneity of rank patterns was the highest at the most arid site.

Table 2. The rank order of the first most abundant species in dry perennial sand grasslands along an aridity gradient (six stands sampled at each sites).

Ranks/Stands	1	2	3	4	5	6	
1	S	S	S	S	S	S	**Gönyü**
2	PF	F	F	F	oPGr	F	**(more mesic)**
3	PF	PF	oPGr	C	PF	oPGr	
1	C	C	C	C	C	C	**Csévharaszt**
2	C	C	C	C	C	C	**(intermediate)**
3	C	S	oPGr	S	C	S	
1	PF	C	C	C	C	F	**Fülöpháza**
2	C	S	oPGr	S	F	oPGr	**(more arid)**
3	S	Ann	Ann	C	Ann	C	

Ann=Annuals, C=Cryptogams, F=Festuca vaginata,
S=Stipa borysthenica
PF=Perennial forbs, oPGr=other Perennial graminoids

Standard beta diversity measures (with one exception: Whittaker's classic β_W) confirmed the qualitative picture of differentiation given by the pattern of the rank orders of abundant species. There were significant differences in beta diversity between sites at both scales (Table 3). At coarse scale, the highest beta diversity appeared at Fülöpháza. The opposite trend was found at fine spatial scales with the highest beta diversity at Gönyű and the lowest at Fülöpháza. The detected number of species combinations was clearly scale-dependent (Fig. 1), with the highest values between 10 cm and 25 cm. Above 25 cm the number of species combinations gradually decreased.

Table 3. Differences in beta diversity measures along the aridity gradient

	MEAN							**VARIANCE**			
Beta-diversity descriptors	**N**	**Gönyü**	**Csévharaszt**	**Fülöpháza**	**F**	**One-Way ANOVA Sig.**	**All Sites Spearman correlation Sig.**	**Gönyü**	**Csévharaszt**	**Fülöpháza**	**Levene statistic (homog. of var.) Sig.**
Fine scale (20 cm)											
Beta(1/0)	18	6.803a	6.230a	5.950a	0,501	0,616	-0,376	0,782	1,608	4,411	0,406
Beta(Shannon)	18	**5.850a**	3.399b	2.891b	20,496	**0,000**	**-0.787(**)**	0,412	1,169	0,618	0,276
Sorensen	18	**0.607a**	0.509b	0.438b	6,539	**0,009**	**-0.669(**)**	0,002	0,008	0,010	0,080
Bray-Curtis	18	**0.676a**	0.571ab	**0.497b**	4,187	**0,036**	**-0.616(**)**	0,002	0,012	0,020	0,079
Coarse scale (stands)											
Beta(1/0)	18	2.010a	2.208a	2.373a	1,050	0,374	0,236	0,067	0,087	0,413	0,051
Beta(Shannon)	18	1.505a	1.421a	**3.014b**	3,653	**0,048**	0,275	0.064a	0.209a	**3.683b**	**0,000**
Sorensen	45	0.327a	0.357a	**0.484b**	22,564	**0,000**	**0.645(**)**	0,003	0,003	0,009	0,145
Bray-Curtis	45	0.347a	0.368a	**0.566b**	21,911	**0,000**	**0.595(**)**	0.004a	0.002a	**0.023b**	**0,000**

Gönyü n=6, Csévharaszt n=6, Fülöpháza n=6. Not significant differences at P=0.05 based on One-Way ANOVA, post hoc tests were accomplished according to LSD statistic.
Means followed by the same letters within a row mean that means are not significantly different.
Homogeneity of variance was tested by Levene statistic for each pairs of stations. Significant different values are marked in bold.
Spearman correlation of each variable respect to the type of station (following such order: Gönyü n=1, Csévharaszt n=2, Fülöpháza n=3) are reported.
P < 0.05 (*); P < 0.01 (**). Significant different values are marked in bold.

The maximum number of realized species combinations (max. NRC) showed a decreasing trend along the aridity gradient (Fig. 2a). We found the highest max. NRC at Gönyű (one-way ANOVA, F=8.844, $p<0.003$) and an overall decreasing trend with increasing aridity (the Spearman rank correlation was -0.734, $p<0.01$, N=18). Because the total species richness showed a similar decreasing trend along the gradient (cf. Table 1) we made and additional test using constant numbers of species (the 10 most abundant species) from each stand. The patterns with constant number of species were similar to the results with all species: the max. NRC was significantly higher at Gönyű than at Fülöpháza (one-way ANOVA, F=3.877, $p<0.05$), and the overall trend was also significant (the Spearman rank correlation was -0.531, $p<0.05$, N=18) (Fig. 2b). The spatial scale where the maximum number of combinations appeared varied between sites (Fig. 1). However, by testing the pattern of these maximum scales (the grain of the patterns) we found no significant differences between sites (Fig. 2c).

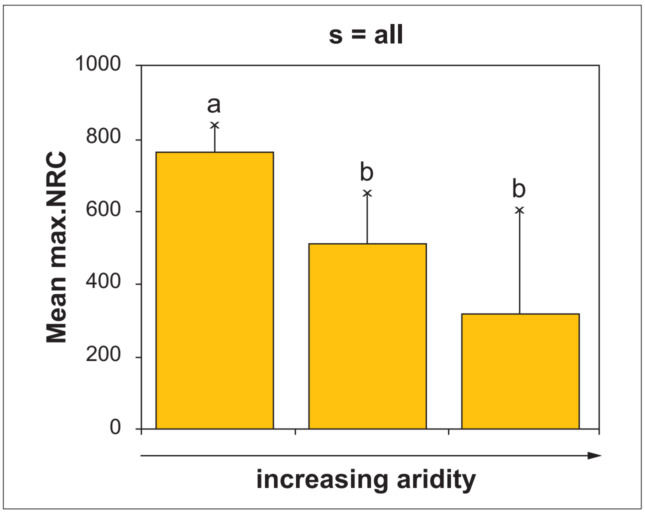

Fig. 2a

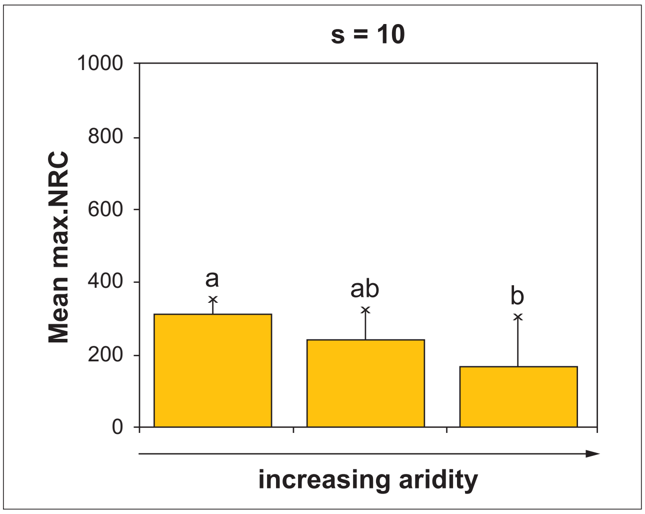

Fig. 2b

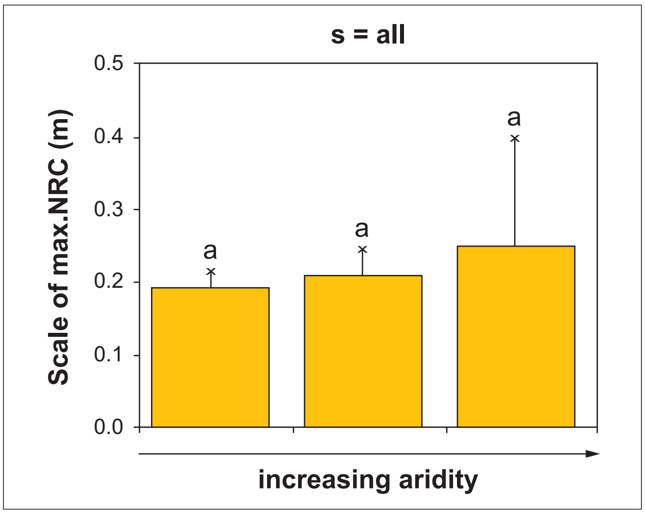

Fig. 2c

Figure 2. The number of realized species combinations (NRC) representing beta diversity (spatial variability) in the sand grassland vegetation along an aridity gradient. Data from three sites (Gönyű, Csévharaszt, and Fülöháza) represent the gradient from the mesic to the arid direction. **a,** all species considered; **b,** constant number of species (s=10); **c,** maximum scales calculated for all species. At each site, the means (colums) represent the spatial variability at patch scale, and the standard deviations (small bars) represent the spatial variability at landscape scale. Mean values marked by different letters mean significant differences ($p < 0.05$).

As an alternative to the coarse-scale analysis with standard beta diversity indices, the between-stand variance of maximum NRC was also tested. This variance increased from Gönyű to Fülöpháza (Levene statistics, p<0.02) for both versions of data (1, when all species were considered; 2, with constant number of species, s=10). Because the mean and variance of max. NRC changed simultaneously the coefficient of variation was also calculated. This measure showed a consistent increase in relative variability for max. NRC and the corresponding maximum scales (Fig. 3a-c) from Gönyű to Fülöpháza.

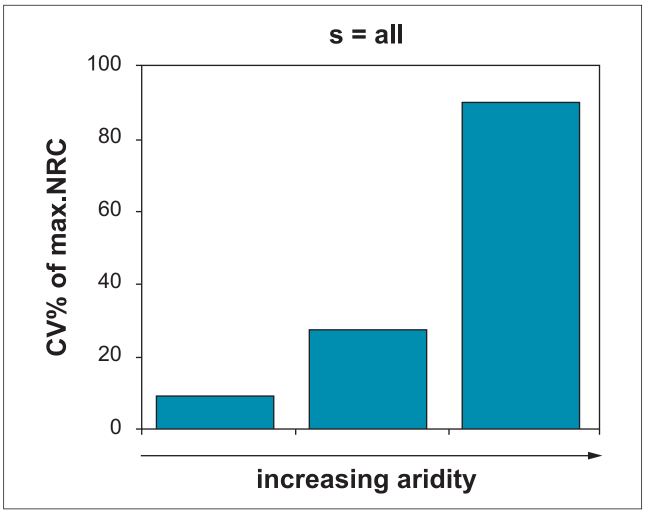

Fig. 3a

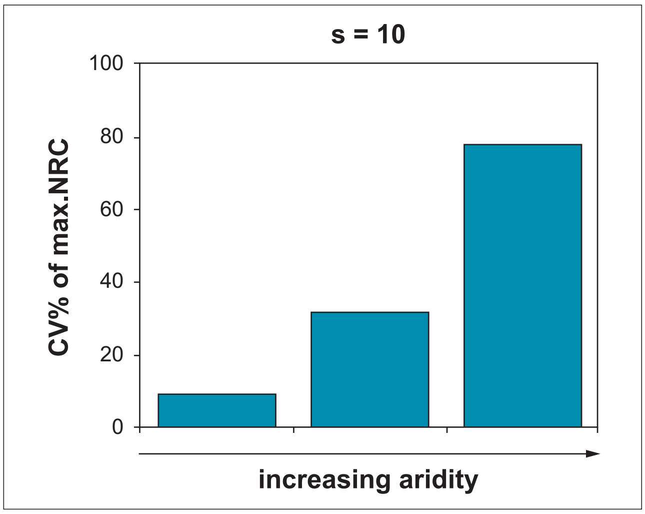

Fig. 3b

DISCUSSION

The high between-stand variability in rank orders of the most abundant species supports the results of earlier studies that reported high compositional variability in the *Festucetum vaginatae* community (Fekete, 1992). In addition, our study revealed a trend of differentiation with increasing aridity. At relatively mesic conditions, *Festuca vaginata* and *Stipa borysthenica* are codominants with high contribution of perennial forbs. As aridity increases, the mosses and lichens become prevalent and the contribution of annuals increases. At the arid end, there are stands where *Festuca* and *Stipa*

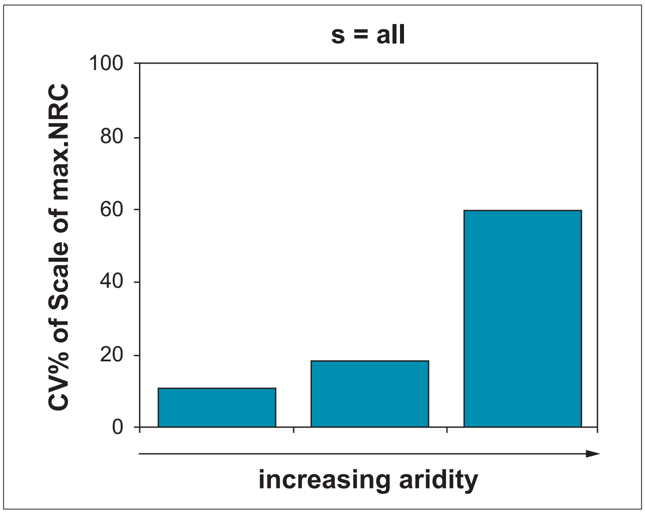

Fig. 3c

Figure 3. Relative variability (coefficient of variation) of beta diversity of the sand grassland vegetation along an aridity gradient, expressed by the CV% of maximum number of realized species combinations and by the CV% of maximum scales. **a,** all species considered; **b,** constant number of species (s=10); **c,** maximum scales calculated for all species. The columns represent the landscape-scale spatial variability within a site.

remain codominants, however, more often only one of them is present at patch scale. At the same time, there is a general decrease in species richness at patch-scale.

Analysing compositional heterogeneity with various beta diversity measures along the aridity gradient, we found a general decrease of beta diversity at fine-scale, and a general increase of beta diversity at landscape scale. We can conclude that the major trend of the community differentiation in dry perennial sand grasslands (*Festucetum vaginatae*) due to increasing aridity is the decrease of within community heterogeneity of species combinations at fine-scale accompanied by a coarse-scale diversification. These changes are similar to the trends found during community degradation in other systems (Bartha et al., 2004) and opposite to the patterns reported from successional communities (Juhász-Nagy & Podani, 1983; Hogeweg et al., 1985; Bartha, 1991). It is important to note that the pattern of beta diversity along the aridity gradient was scale-dependent. Beta diversity increased at coarse scale but it decreased at fine scale.

An often debated methodological problem is the hidden dependence between beta and alpha diversity (Wilson & Shmida, 1984; Jost, 2007; 2010; Veech & Crist, 2010; Baselga, 2010). This hidden dependence can lead to misinterpretation of the results when beta diversity values are compared between areas with different alpha diversity (Jost, 2007). In this paper, we used multiplicative beta diversity measures to minimize this problem (Baselga, 2010). This problem was recognized also in case of the number of realized species combinations (Juhász-Nagy & Podani, 1983; Bartha, 2008). We used a very simple solution when NRC was calculated with constant number of species. Results show that significant difference between sites remained. NRC varies at constant alpha diversity if there are changes in the abundance hierarchy or in the spatial pattern. Our results calculated with constant numbers of species clearly indicate these other aspects of changing community organization.

There is only minor change in mean annual precipitation along the studied 200 km gradient. However, interannual variability of precipitation, especially the frequency of droughts varies considerably (Table 1). This macroclimatic variability is modified by land-use. In Hungary, sand grasslands are components of the transitional forest-steppe biome. Forest cover modifies the local microclimate (Prach, 1982). As the actual forest cover changes, the related microclimatic effects vary as well. Forest cover is more than 60% at Gönyű and less than 5 % at Fülöpháza. Macroclimatic differences are magnified by differences in forest cover and sand grasslands near Fülöpháza experience higher frequency of droughts.

Although sand grassland species are known to be well-adapted to harsh environmental conditions (Fekete et al., 1995; Kalapos et al., 2008), local mass dieback can appear in the populations of dominant species during serious drought periods. Mass dieback of dominant grasses was recorded at the patch scale during the serious droughts in 2003 at Fülöpháza (Kovács-Láng et al., 2008). The stress-induced disturbance imposed by synchronized dieback of dominant grasses generates patch-scale micro-successions that results in vegetation mosaic at landscape level (Bartha et al., 2008a). The identity of dominant species, diversity, and dominance structure can differ considerably among patches. Although differentiation can be strong at patch scale, these vegetation states are dynamically related. Micro-successions are driven by the regeneration cycles of dominant grasses (Bartha et al., 2008a).

Our analyses showed that the spatial variability of plant species coexistence (expressed by the number of the realized species combinations in the sample) is highest between 10 cm and 25 cm. This fine-scale maximum beta diversity might be constrained by the morphology of dominant grasses. The lower beta diversity values detected at the arid end of the gradient might be a result of larger average plant (or clone) size. This interpretation is supported by Lhotsky et al., (2000) who measured larger diameters of dominant grasses at Fülöpháza than at Gönyű.

We argue that the dynamical character of micro-successions typical for perennial sand grasslands depends on the compositional complexity and variability of vegetation. Permanent plot studies have provided evidence that high spatiotemporal variability at the fine within-stand scale results in high stability at stand scale (Herben et al., 1993; Virágh & Bartha, 1996; 2003). Decreasing fine-scale compositional heterogeneity involves decreasing resilience (McNaughton, 1988; Gunderson & Pritchard, 2002). In a previous permanent plot study, we found considerably (5 times) higher relative interannual variability of fine-scale structural complexity at Fülöpháza than at Csévharaszt (Bartha et al., 2008b). In our present study CV% of the max. NRC showed a consistent increase from Gönyű to Fülöpháza. We suppose that this increase of the coarse-scale spatial heterogeneity is related to the temporal heterogeneity of vegetation. The increasing interannual variability in vegetation induced by climatic or land-use changes at fine scale, finally result in increased spatial heterogeneity at landscape scale.

Quantifying vegetation states and transformations in this dynamic landscape is a major methodological challenge. The processes of vegetation differentiation induced by climatic and land-use changes require long-term monitoring. According to our experiences, the sampling design we used in this study provides a relatively simple and effective method for monitoring various aspects of vegetation patterns at multiple scales (Juhász-Nagy & Podani, 1983; Bartha, 1991; Campetella et al., 2004; Bartha et al., 2004; 2008b; Virágh et al., 2008).

Our present study provides evidence of scale-dependent changes of beta diversity in sand grassland communities with increasing aridity. More comparative studies are needed to explore the fine-scale and coarse-scale structural variability in syntaxa and to understand the functional aspects of this variability together with the possible consequences on ecosystem services in changing landscapes.

ACKNOWLEDGEMENTS

This study is part of the KISKUN Long Term Ecological Research Programme. We thank Edit Molnár, Barbara Lhotsky, Szilárd Bokros, Réka Aszalós, Péter Ittzés, and Wylie Harris for assistance during the field work. We acknowledge the general support of the Kiskunság National Park and the Duna-Ipoly National Park. The research was supported by the Hungarian National Science Foundation (OTKA K 72561, K 62338 and T 21166).

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