Will interannual variability in sand grassland communities increase with climate change?

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Abstract: Decreasing diversity and plant cover, as well as increasing variability of these characteristics with increasing aridity are expected in grasslands due to climate change. These predictions were tested in perennial sand grasslands in Hungary. Two sites were chosen in different positions on an aridity gradient and two stands in each site were monitored for 9 years. Presence of plant species were recorded along 52 m long circular belt transects of 1040 units of 5 cm x 5 cm contiguous microquadrats. This sampling procedure – a version of line-intercept methods – enabled us to monitor diversity and total abundance in a sensitive, precise and non-destructive way. We found no trend but fluctuation in most community level attributes and in species composition. Contrary to fluctuations, between-site differences in diversity did not change and diversity remained lower in the more arid site during our 9-year-study. Compositional diversity performed better than species diversity because allowed us to detect vegetation changes that would have remained hidden if monitoring would be based only on the species richness. Comparing the magnitudes of fluctuations, five times higher relative interannual variability (CV%) was found for compositional diversity at the more arid site, while the relative temporal variability of total abundance and species richness did not show consistent patterns. We conclude that a 9 year-long study was too short to identify trends caused by the changing climate. However, the larger temporal variability of species combinations found in the more arid site suggests larger vulnerability and highlights the importance of non-linear dynamics during climate changes.

Nomenclature: Simon (2000).

Introduction

Space for time substitution has a central role in climate change research (Dunne et al. 2004), but the related predictions were rarely tested over time. Most studies address questions related to large scale biogeographic patterns, e.g., how distribution of species, habitats or biomes change due to the changing climate (Guisan et al. 1998, Zimmermann and Kienast 1999, Walther 2003, Thuiller et al. 2005, Thuiller 2007). Fewer case studies dealt with local transformations at the level of plant communities (Kovács-Láng et al. 2000). Global or regional scale models of vegetation dynamics predict changes over 50-150 years, a temporal extent which is not accessible for short-term field studies (Iverson and Prasad 2001, Fekete and Molnár 2005, Thuiller 2007). However, transformations on the scale of plant communities may

appear within years or decades and they can be directly observed in permanent plots.

Decreasing precipitation and increasing temperature were predicted for many regions in the Temperate Zone together with increasing interannual variability of the environment (Molnár and Mika 1997, Hughes 2000, Thuiller et al. 2005, Bartoly et al. 2007, Thuiller 2007). Regulatory mechanisms in vegetation may dampen the effects of increasing environmental variability (Tuba et al. 1998). By comparing the interannual variability in net primary productivity and precipitation, field studies showed that regulation varies among regions and vegetation types (Paruelo et al. 2000, Veron et al. 2002). Theory suggests that complexity and diversity are key factors in community regulation and functioning (MacNaughton 1988, Tilman 1999, Loreau et al. 2001). However, little is known about how climate change affects community

composition, organization and functioning under natural field conditions. Comparative field studies on the relative interannual variability in key community parameters provide a simple but operational way to approach aspects of community regulation. In order to reveal the temporal variability and pattern of several vegetation attributes long-term studies are needed (Kratz et al. 2003, Kim 2006, Kovács-Láng et al. 2008).

We intend to test the predictions of a former study by Kovács-Láng et al. (2000) on the expected changes in community characteristics due to climate changes in perennial sand grasslands in Hungary. Based on cross-site comparisons, we also evaluate the temporal pattern and the interannual variability of some key community attributes. Perennial sand grassland is a component of the remnant natural forest-steppe vegetation of the Hungarian Plain (Fekete 1992). Since forest-steppe is a transitional biome, and the Hungarian Plain lies at the very edge of the Eastern European forest-steppe zone, this vegetation type is expected to respond in a sensitive way to a climate change. Regional climate change scenarios predict a decrease in growing season precipitation and an increase in growing season temperature for the Carpathian Basin in the next century (Mika 1988, Molnár and Mika 1997, Bartoly et al. 2007, Czúcz 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 with regional climate changes predicted in connection with further global warming over 20-30 years. Therefore, the vegetation of the relatively less arid sites along this gradient is expected to change towards the vegetation types and characteristics of the arid sites. Using space for time substitution, decreasing diversity, plant cover, and changing species composition with an increasing contribution of annuals were predicted by Kovács-Láng et al. (2000) in the perennial sand grasslands due to climate change.

In such cases, if space for time substitution is used for predicting future vegetation scenarios, a shorter distance in space implies a shorter period in time. In the present study two sites situated along the above described aridity gradient, located at 50 km distance to each other were chosen and monitored for 9 years. Our objective was to test the predictions created on the basis of the space for time substitution and to assess the relative interannual variation in some community attributes. The following questions were addressed: (1) Are there any shifts in the vegetation attributes of the less arid site into the direction of the more arid site? (2) Considering fluctuations, are there any between-site differences in the magnitude of temporal variability in the community attributes?

Materials and methods

Study sites

Two sites, Csévharaszt (47°17'N, 19°24'E) and Fülöpháza (46°53'N, 19°23'E) situated along an aridity gradient in the Kiskunság area (Hungary) were monitored be-

tween 1999 and 2007. Both sites have forest-steppe vegetation. The climate is temperate, with continental and submediterranean features; mean annual precipitation is 568 mm at Csévharaszt, and 522 mm at Fülöpháza (based on data collected from nearby meteorological stations with 70 years records, cf. Kun 2001), maximum precipitation occurring in May and November. The mean annual temperature is 10.3 °C at Csévharaszt and 10.2 °C at Fülöpháza. The climate at Fülöpháza is slightly more arid. There are strong seasonal and daily fluctuations in temperature and air humidity and uneven temporal distribution in precipitation at both sites. Despite of the minor changes in mean climatic attributes, previous studies revealed significant between-site differences in vegetation characteristics (Kovács-Láng et al. 2000, 2008), e.g., average species richness and canopy cover were lower at Fülöpháza than at Csévharaszt. The density of dominant grasses was also lower at Fülöpháza, with larger size of individuals and increasing proportion of belowground and standing dead phytomass fractions. Considering the geographic range types, a larger proportion of species with continental and submediterranean distribution was found for Fülöpháza (Kovács-Láng et al. 2000, 2008). The temporal variability of climatic features expressed by the frequency distribution of precipitation curve types shows clearer trends and a more significant increase of aridity from Csévharaszt to Fülöpháza (Kun 2001). These patterns of temporal variability in climatic conditions correspond well with the biogeographic gradients demonstrated for the vegetation (Fekete et al. 1999).

The soil at Csévharaszt and Fülöpháza developed on calcareous sand. The fixed blown-sand is characterized by weakly developed soil profile, alkaline reaction, medium carbonate-content, extremely low colloid, fine fraction, clay and organic matter content, and deep groundwater-table (Várallyay 1993). No significant between-site differences have been found in soil characteristics of the open perennial grassland communities (Kovács-Láng et al. 2000). Both sites are located in nature conservation areas: the Csévharaszt site has been protected since 1939, whereas the Fülöpháza site since 1974. Before protection, both sites were used as grazing land and after that abandoned. On a landscape scale, Fülöpháza is a more open forest-steppe with less tree cover than in Csévharaszt, and this site experienced stronger disturbances (overgrazing and military trainings) in the past.

Vegetation sampling

Two stands (uniform vegetation patches) of open sand grassland (*Festucetum vaginatae*) were selected randomly and monitored at both sites for 9 years. In each stand presence 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. The size of microquadrats (the finest resolution) was chosen to correspond to the average size of plant individuals or ramets. To avoid soil disturbances, we did not use permanently fixed microquadrats. However, transects were put approximately into the same trace every year, there-

Table 1. Mean value and standard deviation of six vegetation characteristics at Csévharaszt and Fülöpháza over the monitoring period (1999, 2002, 2004-2007). Results of Mann-Whitney U tests are indicated; bold means significant difference between Csévharaszt and Fülöpháza.

Variables	Csévharaszt		Fülöpháza		Mann-Whitney U-test
	mean	st. dev.	mean	st. dev.	(p) sig. 2-tailed
Total Abundance	252.12	± 52.97	176.68	± 27.27	**0.000**
All species number	29.16	± 4.89	20.41	± 3.70	**0.010**
Frequent species number maximum Compositional Diversity	14,75	± 1.91	7.83	± 2.44	**0.000**
	8.26	± 0.54	4.84	± 1.31	**0.000**
Cryptogam Abundance	103.67	± 36.59	90.15	± 8.46	0.111
Vascular Abundance	148.46	± 45.16	86.51	± 20.38	**0.000**

fore the performed sampling is considered to be permanent and representative at the scale of vegetation patches. The large number and small size of microquadrats ensure the precise estimation of the abundance of species (cf. line-intercept sampling, Stampfli 1991, Murphy and Lodge 2002, Kercher et al. 2003). All stands were sampled in 1999, 2002, and annually between 2004 and 2007, each year in mid-May.
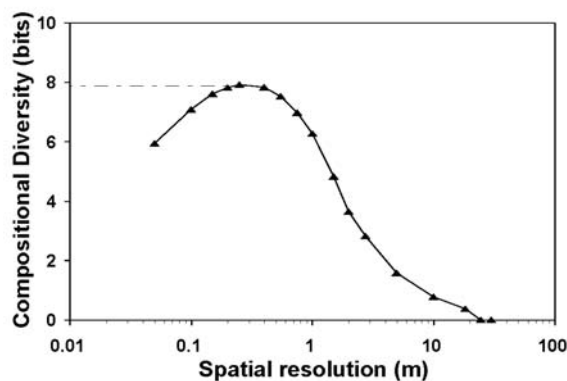
Data analysis

From each transect, total abundance (by summing up the total number of presence of each plant individual along the transect), the total number of species, and the number of frequent species (above the frequency threshold of 2%, cf. Tóthmérész and Erdei 1992) were assessed. Within-stand variability of vegetation was measured by Compositional diversity (Juhász-Nagy and Podani 1983), an entropy measure based on the calculation of Shannon-diversity of the frequency distribution of species combinations at increasing plot sizes: $H_j = \sum f_{kj} \log_2 f_{kj}$, where f_{kj} is the frequency of the k-th species combination detected at plot size j. For comparison, only the maximum values of this function were used in this study. Compositional diversity was calculated across a

Figure 1. Compositional diversity as a function of sampling scale. At each resolution the diversity of species combinations was calculated in 1040 overlapping sampling units for each transect position. We used the maximum of this function for further comparisons in this study.

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 (Podani 1987). Principal coordinate analyses (PCoA) were used for analysing temporal changes in species composition in each site. Bray-Curtis index was used for abundance data and Sorensen index for binary data. The SYN-TAX 5.0 software package (Podani 1993) was used for the ordinations. For the computerized sampling in spatial series and for the calculation of compositional diversity we used the PRIMPRO program (Bartha et al. 1998). Differences between sites were analysed by Mann-Whitney U tests (Sokal and Rohlf 1995). Temporal changes were tested by Friedman's test (a non-parametric alternative to the one-way repeated measures analysis of variance) (Campbell 1974). Non-parametric tests were performed with Statistica 7.0 (StatSoft Inc., Tulsa, OK, USA).

Results

Significant differences in total abundance, total species richness, number of frequent species and maximum compositional diversity were found between Csévharaszt and Fülöpháza (Table 1). Except the abundance of cryptogamic species, all vegetation characteristics showed higher values at Csévharaszt. However, when the sites were analysed separately no significant temporal differences over the 9 years of monitoring have been revealed by the Friedman's test (Table 2). The multivariate analyses showed similar results (Fig. 2). Compositional changes did not indicate the convergence of sites over time since stands from Csévharaszt did not change into the direction of the more arid stands from Fülöpháza. Trajectories were distinct and fluctuated individualistically without any trend. Multivariate analyses based on abundances (Fig. 2 a,c) and on binary data (Fig. 2 b,d) showed similar patterns. Relative abundance of plant functional types fluctuated over time (Fig. 3), while the diversity of functional types was lower at Fülöpháza (Fig. 3). Variability without any trend was detected as well for total abundance and for the diversity estimates (Fig. 4). All estimates of diversity were larger at Csévharaszt than at Fülöpháza. However, differences were the greatest if measured by compositional diversity.

Table 2. Temporal change in six vegetation characteristics (mean and standard deviation) at Csévharaszt and Fülöpháza. Differences over time were analysed by Friedman's test.

Variables	Sites\Dates	1999	2002	2004	2005	2006	2007	Friedman Asymp. Sig.
Total Abundance	Csévharaszt	195.1 (± 18.2)	206.0 (± 19.7)	258.3 (± 26.2)	336.2 (± 25.6)	272.0 (± 19.8)	245.0 (± 6.5)	0.093
	Fülöpháza	177.2 (± 9.9)	170.7 (± 43.2)	156.4 (± 4.9)	211.9 (± 13.9)	178.0 (± 9.6)	165.8 (± 2)	0.210
All species number	Csévharaszt	31.5 (± 1.5)	26.5 (± 5.5)	31.0 (± 4.0)	30.0 (± 3.0)	28.5 (± 3.5)	27.5 (± 6.5)	0.272
	Fülöpháza	17.0 (± 2.0)	16.5 (± 0.5)	23.5 (± 3.5)	23.0 (± 1.0)	22.5 (± 2.5)	20.0 (± 2)	0.119
Freq. species number	Csévharaszt	13.5 (± 0.5)	12.5 (± 1.5)	16.5 (± 1.5)	16.5 (± 0.5)	15.5 (± 0.5)	14.0 (± 1)	0.105
	Fülöpháza	6.5 (± 0.5)	8.5 (± 2.5)	7.0 (± 2.0)	11.5 (± 1.5)	6.0 (± 0.0)	7.5 (± 0.5)	0.475
max Comp. Diversity	Csévharaszt	8.2 (± 0.08)	7.6 (± 0.3)	8.6 (± 0.2)	9.0 (± 0.2)	8.3 (± 0.2)	7.8 (± 0.4)	0.093
	Fülöpháza	3.9 (± 0.02)	5.3 (± 1.1)	4.6 (± 1.3)	6.6 (± 0.7)	3.6 (± 0.2)	4.9 (± 0.5)	0.306
Cryptogam Abundance	Csévharaszt	68.4 (± 44.5)	90.2 (± 29.7)	103.9 (± 18.8)	136.5 (± 29.1)	118.1 (± 11)	104.8 (± 21.4)	0.084
	Fülöpháza	89.1 (± 2.65)	83.8 (± 14.6)	89.5 (± 1.8)	98.2 (± 1.7)	93.8 (± 2.25)	86.4 (± 5.35)	0.291
Vascular Abundance	Csévharaszt	126.7 (± 26.3)	115.8 (± 49.5)	154.4 (± 45)	199.7 (± 3.45)	153.9 (± 30.8)	140.2 (± 8.05)	0.115
	Fülöpháza	88.1 (± 7.3)	86.9 (± 28.6)	66.9 (± 3.1)	113.7 (± 12.3)	84.1 (± 7.4)	79.3 (± 3.3)	0.279
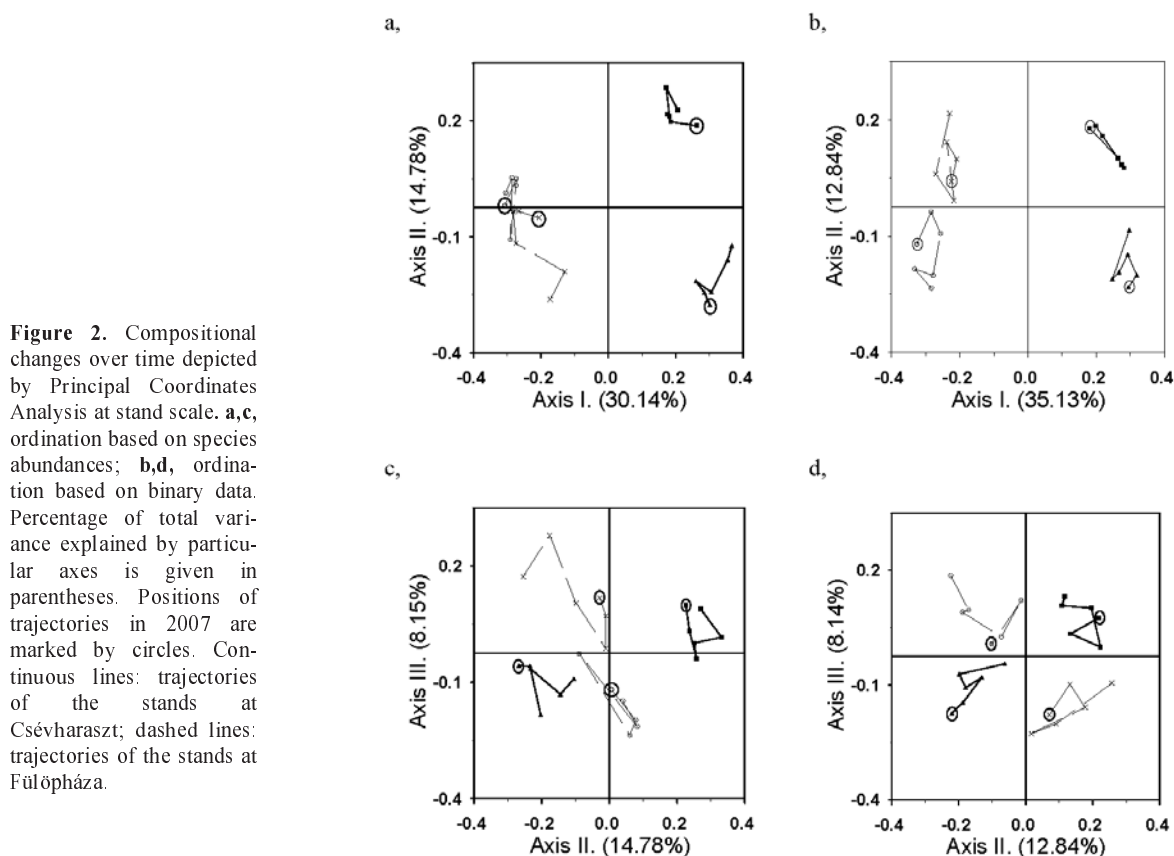
Figure 2. Compositional changes over time depicted by Principal Coordinates Analysis at stand scale. **a,c,** ordination based on species abundances; **b,d,** ordination based on binary data. Percentage of total variance explained by particular axes is given in parentheses. Positions of trajectories in 2007 are marked by circles. Continuous lines: trajectories of the stands at Csévharaszt; dashed lines: trajectories of the stands at Fülöpháza.

As fluctuation was the typical pattern revealed over the 9 years for all the vegetation attributes, we compared the magnitude of interannual variabilities expressed by the coefficient of variation (CV%) (Fig. 5). The CV%s of total abundances were slightly smaller at Fülöpháza, while no clear differences were found in case of total species richness. Interannual variability of diversity had been found to be considerably larger at Fülöpháza when diversity was measured by the compositional diversity or by the number of frequent species.

Discussion

### Trends in community attributes

The two stands along the climatic gradient expressed distinct, individualistic behaviour. Contrary to our predictions
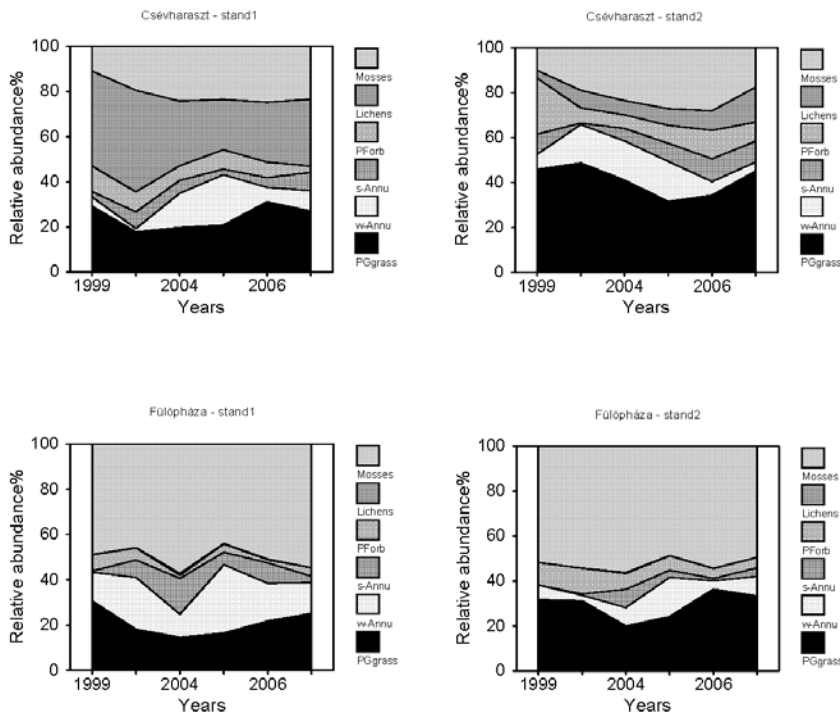
Figure 3. Temporal changes in the relative abundance of plant functional types at Csévharaszt and Fülöpháza. (PForb = perennial forbs, PGrass = perennial grasses, w-Annu = winter annuals, s-Annu = summer annuals.)
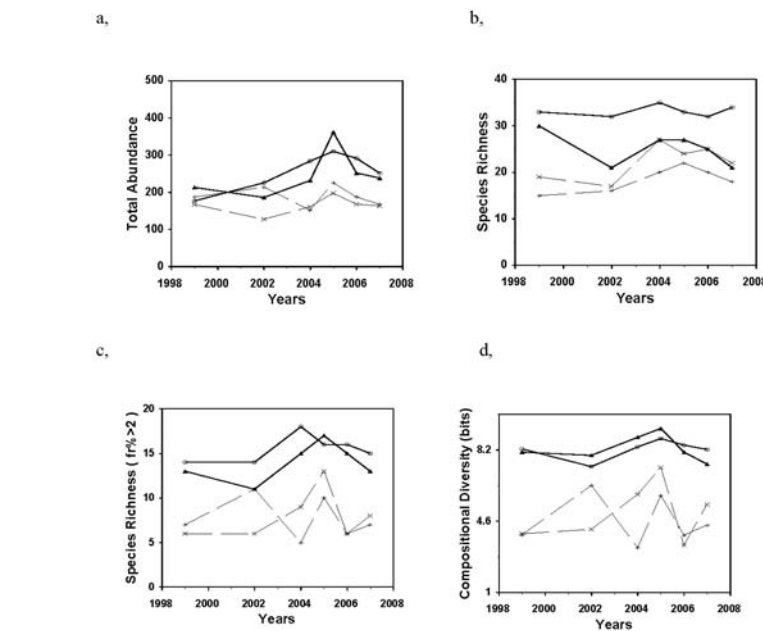
Figure 4. Temporal changes in the total abundance **(a)** and diversity **(b-d)** in four perennial sand grassland stands. (Diversity is expressed **b,** by the number of all species; **c,** by the number of frequent species (fr% > 2); and **d,** by the maximum of compositional diversity.) Continuous lines: two stands at Csévharaszt; dashed lines: two stands at Fülöpháza.
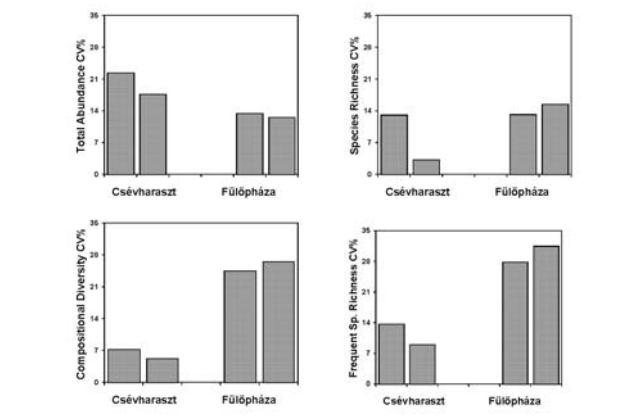
Figure 5. Interannual relative variability (coefficient of variation) in abundance and diversity in perennial sand grassland communities measured at Csévharaszt and at the more arid Fülöpháza. The two columns represent the temporal variability in the two stands monitored in each site over 9 years.
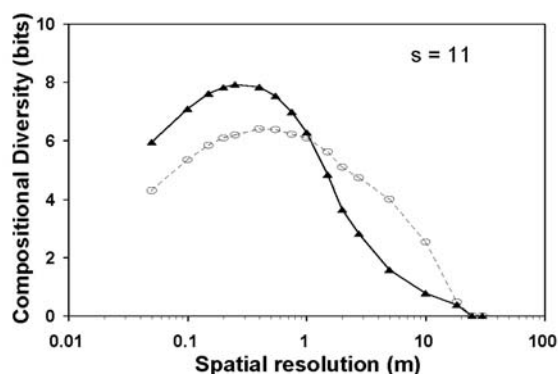
which were based on a single extensive survey made in 1996 (Kovács-Láng et al. 2000), neither a decrease in abundance and diversity nor a shift in species composition in the direction of the more arid site was found within the study period. Although the temporal changes predicted have not been found, other results of this previous study were confirmed, i.e., between-site differences in vegetation characteristics and their trends along the aridity gradient remained valid when measured repeatedly over 9 years. Differences in the relative abundance of functional types did not change within the study period and diversity remained lower in the more arid site. However, there were remarkable differences in the effectiveness of diversity measures for detecting temporal patterns. Although all diversity measures showed similar pat-
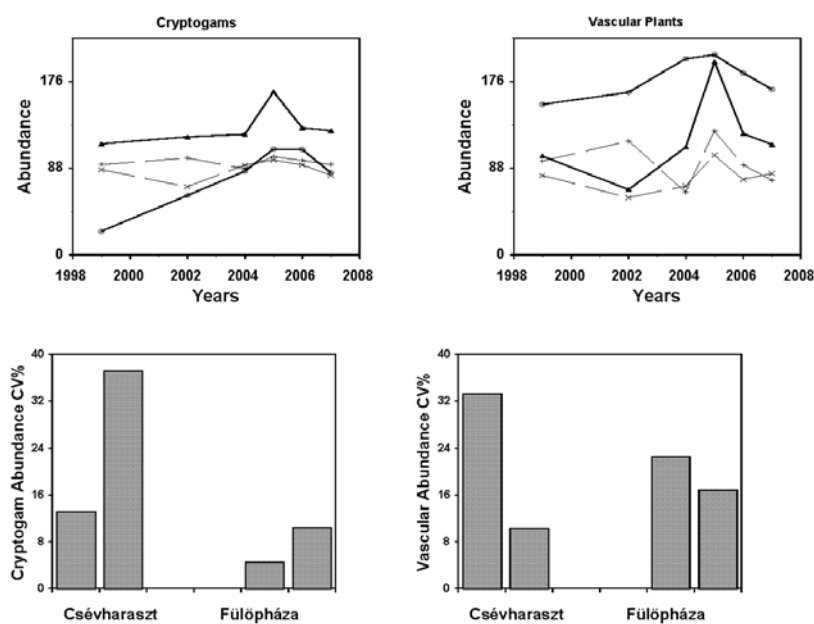
terns, relationships were more distinct and more strongly significant if compositional diversity was used. For example in 2002 the number of frequent species was the same in two stands (one stand from Fülöpháza and the other one from Csévharaszt), while the compositional diversity, as well as its maxima differed between the two sites (Fig. 6). Our results present an additional support for other studies emphasizing the advantages of compositional diversity over other diversity measures (Podani et al. 1993, Csillag et al. 2001, Canullo and Campetella 2005, 2006, Podani 2006, Ricotta 2006, Ricotta and Anand 2006), but the present study is the first application of this methodology in climate change research.

Figure 6. Compositional diversity as a function of sampling scale in 2002. Continuous lines: one stand at Csévharaszt; dashed lines: one stand at Fülöpháza. The number of frequent species (fr% > 2) was equal in the two stands (s=11) in this year.

Between-site relative interannual variability in community attributes

With increasing aridity lower mean biomass (lower total abundance in our case) and higher relative variability is expected (Jobbágy et al. 2002, Veron et al. 2002). Contrary to this expectation, we found lower relative interannual variability (coefficient of variation) in the total abundance at the more arid Fülöpháza site than at Csévharaszt. A more detailed analysis revealed that this pattern was due to the higher contribution of cryptogams at Fülöpháza (Fig 3.) and the lower temporal variability of this functional group (Fig 7.). Lepš (2004) reported negative relationship between mean abundance of plant species and the interannual variability of their abundances in an experimental community. There are few cryptogam species at Fülöpháza, but one of them, *Syntrichia ruralis* is extremely abundant and covers more than 80 % of the soil surface. This species plays an important role also in the functioning of this system (Csintalan et al. 2000, Hamerlynck et al. 2000, Lhotsky et al. 2008). In line with the relationship found by Lepš (2004), we interpret the lower variability of total abundance found at Fülöpháza by the high

Figure 7. Temporal changes in total abundance divided into cryptogams and vascular plants in perennial sand grasslands and the related coefficients of variation of abundances. Continuous lines: two stands at Csévharaszt; dashed lines: two stands at Fülöpháza.

contribution and relatively constant abundance of *Syntrichia ruralis*.

It is generally accepted that complexity and diversity have important roles in regulating community functions (MacNaughton 1988, Tilman and Downing 1994, Loreau et al. 2001, Bai et al. 2004). Less is known about how diversity regulates its own dynamics. We found considerably (5 times) lower relative interannual variability in compositional diversity at Csévharaszt, at the less arid and more diverse site. The coefficient of variation in the number of frequent species showed a similar pattern while no difference was found if all species considered. Higher compositional diversity reflects higher fine-scale structural complexity and involves higher fine-scale spatiotemporal variability and resilience (Bartha 2007). All these characteristics provide a higher stability at stand scale (Herben et al. 1993, Virágh and Bartha 1996, 2003). Fekete (1992) compared the stand-scale compositional variability between loess and sand grasslands. He found less compositional variability in loess grassland and concluded that loess grasslands are more 'co-ordinated' (they have higher level of organization and higher structural stability) than sand grasslands. A later study (Gosz et al. 2000) comparing many sand grasslands along an aridity gradient showed that the spatial variation of the compositional diversity (as a measure of 'co-ordinatedness') increases with increasing aridity in sand grasslands. We found increasing relative interannual variability in compositional diversity with increasing aridity, i.e., our results correspond to the finding of Gosz et al. (2000). However, spatial variation may be caused by other factors as well e.g., by the landscape-scale spatial variability in soil characteristics, variability in land-use history and natural disturbances. Our temporal study provides new and more reliable evidence that 'co-ordinatedness' (relative stand-scale structural stability) of vegetation decreases with increasing aridity, thus according to our results 'co-ordinatedness' in sand grassland is expected to decrease due to global changes.

Limitations of the space for time substitution in predicting real processes related to climate changes

Developing predictions is a major aim in climate change related research. However, there is no standard methodology for testing such predictions in the field. The importance of long-term studies has been emphasized by many authors (Pickett 1989, Knapp et al. 1998, Kratz et al. 2003, Kim 2006) without a general agreement about the related temporal scales.

Although the limitations of the deductive approach inferring temporal processes from spatial patterns are well documented (Pickett 1989, Molnár and Botta-Dukát 1998, Csecserits et al. 2007), this approach is predominant in predictive climate change research (Dunne et al. 2004, Guisan et al. 2006). Studying ecological gradients is valuable for surveying statistical correlations of large number of attributes and for exploring their patterns along wide range of scales. However, such descriptive multivariate statistical models do not

prove the causal background and they are unable to reveal the relative importance of particular factors (Graham 2003, Dormann 2007). Contrary to the criticism on methodology, several studies address the question if land-use change or climate change is the most important driver of vegetation changes (Dullinger et al. 2004, Gehrig-Fasel et al. 2007). In a recent review, Fekete and Molnár (2005) concluded that land-use seems to be the dominant driving force in generating compositional and structural changes in the Central European vegetation. In our view, a more important task is revealing how these factors interact in particular cases and how these interactions put additional constraints on vegetation dynamics.

Landscape-scale biotic constraints can maintain such local microclimatic and soil conditions which are not in equilibrium with the regional climate. Present landscape-scale biotic constraints (e.g., the amount and distribution of forests and woodland fragments) are strongly determined by the history of land-use (Biró and Molnár 1998, Molnár 2003, Biró 2006). The longer history of nature conservation and the higher forest cover at Csévharaszt probably buffer the general increase in aridity, provide refugees for species for surviving droughts, and also promote the local regeneration of steppe patches. These conditions explain why this site changed less than expected on the basis of space for time substitution. Fülöpháza can be an opposite example, where the past disturbances accelerated the climate induced trends to the direction of desertification, and the almost treeless landscape was not so effective in promoting the large-scale regeneration after the cessation of intensive grazing around 1970.

We conclude that no simple prediction from space for time is possible for vegetation changes in the Kiskunság area. Models based on slow gradual changes and linear approximations (cf. Dunne et al. 2004, Guisan et al. 2006) may not describe properly the dynamics of this hierarchic mosaic landscape. We suggest the application of concepts and models developed for other semi-arid systems (Walker et al. 1981, Gunderson and Pritchard 2002) in order to be able to predict and understand vegetation changes followed by climate changes. These complex non-linear models assume that biotic interactions may buffer changes in climate and can maintain states far from equilibrium. Close to a threshold, small effects (e.g., disturbances or land-use changes) may cause abrupt changes. Understanding dynamical behaviour and developing predictions in these systems need long-term continuous monitoring of vegetation patterns at multiple scales. Our study is part of a complex long-term research program for understanding the landscape dynamics of the Kiskunság (Kovács-Láng et al. 2008).

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