

Community differentiation in dry perennial sand grasslands along an aridity gradient.

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Abstract

Spatial variability of species composition was studied in perennial sand grasslands in Hungary at multiple (regional, landscape and stand) 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. We found a decreasing trend of beta diversity (which represents the spatial complexity), 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.

Introduction

Theory suggests that ecosystem level adaptation, efficiency and stability depend strongly on the spatial complexity of ecosystems (WALKER et al. 1981, GUNDERSON and PRITCHARD 2002). Spatial complexity is often represented by beta diversity, i.e. by the variation of species composition among sites. Recently increasing attempts have been made to measure beta diversity at landscape or macroecological scales. 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, KÉFI et al. 2007).

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 (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 (FEKETE 1992). Therefore, there is an urgent need to develop effective indicators for early warning about desertification processes.

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-

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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.

Methods

Within the forest steppe biome in Hungary, three study sites: Gönyű (47°43'N, 17°49'E), Csévharaszt (47°17'N, 19°24'E) and Fülöpháza (46°53'N, 19°23'E) have been chosen along an aridity gradient. The climate is temperate. Mean annual precipitation along the gradient varies between 565 mm and 535 mm. The mean annual temperature varies between 10.07 °C in the north-west and 10.33 °C 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. The relative frequency of droughts and the temporal variability of climatic features expressed by the frequency distribution of precipitation curve types show clear trends and a significant increase in aridity from Gönyű to Fülöpháza (KUN 2001, KOVÁCS-LÁNG et al. 2008).

Six stands of *Festucetum vaginatae* grasslands were selected at each site for representing the coarse-scale within-site heterogeneity. For fine-scale heterogeneity sampling, presences of plant species were recorded along 52 m long circular belt transect of 1040 units of 0.05 m x 0.05 m contiguous microquadrats. The sampling was performed in late spring, during the phenological optimum of the vegetation. Beta diversity indices were calculated at two scales: at fine within-stands and at coarse between-stand scales (for more details see BARTHA et al. 2011).

Various beta diversity measures were used (Anderson et al. 2010). 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 smaller sampling units (Beta(1/0)). $\beta_{Shannon} = H_\gamma/H_\alpha$ includes also relative abundance information (Beta (Shannon)). Beta diversity as the spatial turnover of species composition was represented by the mean 1-Sørensen index (for presence-absence data) and by the mean Bray-Curtis index (for abundance data). We calculated also the maximum number of the realized species combinations (NRC) (JUHÁSZ-NAGY and PODANI 1983) to represent beta diversity at fine scales. As an alternative measure of the coarse-scale beta diversity, we calculated the between-stand relative variance (CV%) of max. NRC. Beta diversity indices were calculated by the PRIMPRO (BARTHA et al. 1998) and SYN-TAX 5.0 (PODANI 1993) software packages. Differences between sites were analysed using one-way ANOVA and with post hoc tests using LSD statistics. Overall trend along the gradient was evaluated by Spearman rank correlation. Homogeneity of variance was tested by Levene statistic (Statistica 7.0, StatSoft Inc., Tulsa, OK, USA).

Results

There were significant differences in beta diversity between sites at both scales (**Table 1**). 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 maximum number of realized species combinations (max. NRC) showed decreasing trend along the aridity gradient (**Figure 1a**). 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 , $p<0.01$, $N=18$). Between-stand relative variance of maximum NRC increased from Gönyű to Fülöpháza (Levene statistics, $p<0.02$) (**Figure 1b**).

Beta-diversity descriptors	Mean					Variance					
	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

Table 1. Differences in beta diversity measures along the aridity gradient

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.

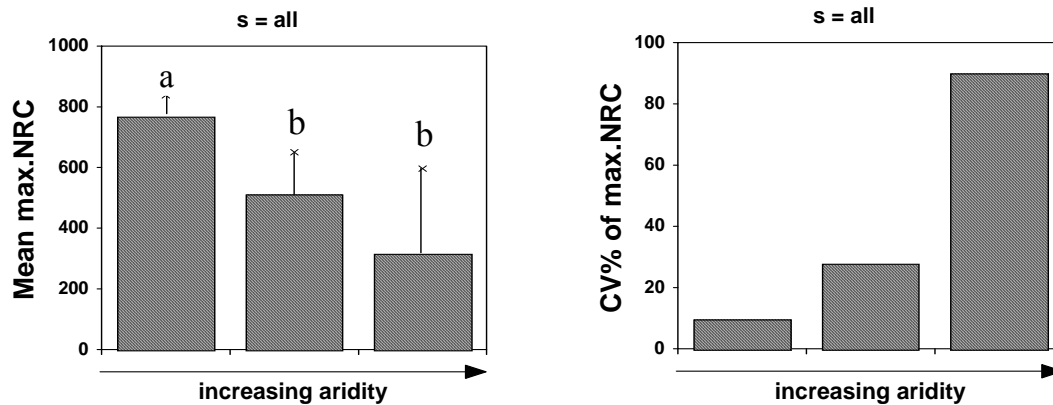


Figure 1.

a, 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 Fülöpháza) represent the gradient from the mesic to the arid direction. At each site, the means (columns) 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 ($p < 0.05$).

b, 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. The columns represent the landscape-scale spatial variability within a site.

Discussion

There is only minor change in mean annual precipitation along the studied 200 km gradient. However, analysing compositional heterogeneity with various beta diversity measures along this gradient, we found a significant decrease of beta diversity at fine within-stand scale, and a significant increase of beta diversity at landscape scale. 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 and PODANI 1983, HOGEWEG et al 1985, BARTHA 1991).

While the dynamical consequences of the spatial differentiation in sand grassland vegetation need experimental approaches and long-term observations, our present study provides direct evidence that “sociological coordination” of vegetation (i.e., the relative structural and compositional invariability of plant communities) decreases with increasing aridity. The term “sociological coordination” was addressed by FEKETE (1992) who compared climatically zonal communities and edaphic communities in the temperate forest steppe zone. He found higher landscape-scale sociological coordination between stands of the climatically zonal communities than between stands of the azonal one. Based on the relative variance (CV%) of NRC, our results demonstrate that “sociological coordination” in sand grasslands decreases with increasing aridity and probably will decrease due to global changes

Decreasing fine-scale compositional heterogeneity involves decreasing resilience (MCNAUGHTON 1988; GUNDERSON and 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 2008). In the present study, CV% of max. NRC showed 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.

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 various vegetation types and to understand the functional aspects of this variability together with the possible consequences on ecosystem services in changing landscapes.

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