

# DIVERSITY, REGULATION AND RELIABILITY – FINE-SCALE FUNCTIONAL ORGANIZATION IN VEGETATION

Final report of NKFI (OTKA) K 105608 research grant

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## Introduction

In this project we explored fine-scale spatial and temporal patterns of functional (biomass and soil respiration) and structural (alpha and beta diversity) characteristics in plant communities linking these patterns to potential environmental drivers. Fine-scale approach (with resolution close to the size of plant individuals and with few meters extent) were chosen because we were interested in self-organized emergent community characteristics determined mainly by biotic interactions. We had a special focus on the reliability of community characteristics (i.e the spatial and temporal invariance or consistency of coenostate variables). In our view a plant community stand was considered as a patchwork of interacting meta-communities characterized with convergent or divergent (symmetric/asymmetric) local features due to interactions and similarity of locally self-organized processes.

For exploring biotic drivers of functional patterns, vegetation data were collected at the same scales from the same sampling units (plant cover data and presence/absence data). In some analyses we used plant traits (plant height, plant diameter, specific leaf area (SLA), seed mass (SM), clonal attributes, root architecture). Our study sites were distributed over Hungary at 15 sites (Ásotthalom, Battonya, Bugac, Csévharaszt, Dinnyés, Esztergom, Fülöpháza, Gönyű, Kunpeszér, Magyarszombatfa, Mórahalom, Nagyrákos, Szalafő, Tiszaalpár and Vácrátót). We used alternative sampling designs (transects and grids) and sampled a wide range of natural grasslands including open and closed sand grasslands, mesic loess grasslands and wet meadows. Disturbed or recovering grasslands from the same habitats were sampled as well.

*Abbreviations of measured characteristics:* soil respiration (Rs), soil temperature (Ts), soil moisture (SWC), above ground biomass (AGB), normalized difference vegetation index (NDVI).

## Main Scientific Results

In this report we follow the structure of our original research plan [ publications marked by numbers ].

### **Objective #1** *Developing methods for linking fine-scale functional patterns with vegetation structure*

Alternative sampling designs were tested with different extent (from 1m to 80m), resolution (5x5cm to 1x1m) and spatial arrangement (grids, transects and random plots). Results showed that optimum sample sizes and optimum scaling parameters varied between communities but also within-community [ **2, 3, 11** ]. Final protocols were selected to be applicable in comparative studies at wide range of conditions:

a, At patch scale we used **small circular transects**: 15m long with 75 evenly spaced sampling positions (20cm distance). At each point Rs, Ts, SWC, NDVI, AGB and species cover were detected. The presence/absence patterns of plant species were recorded as well along the same circle (n=300 5x5cm units and n=150 10x10 cm units).

b, At stand scale we used:

b1, **60m biomass transects:** with 31 evenly spaced 50x50cm sampling units (2m distances). AGB was measured together with species cover.

b2, **60x80m grid:** 78 sampling positions (10m distances) used for assessing spatiotemporal patterns. At each point Rs, N<sub>2</sub>O flux, soil organic carbon, total soil nitrogen, Ts, SWC, AGB and species cover were detected.

b3, **large circular transects:** 52m long with contiguous 5x5cm units, presence of species were detected in microquadrats. For assessing spatial invariance (spatial reliability), we developed a new method where these transects were re-sampled with moving windows statistics [ 8, 13 ].

Sampling campaigns were repeated over 5 years and from March to October to represent interannual and seasonal variability.

## **Objective #2** *Evaluating functional, structural and environmental patterns in the context of reliability*

### **2.1. Fine-scale spatial variability of soil respiration - interaction with abiotic drivers**

Using small circular transects we explored the seasonal and interannual variability of fine scale spatial patterns of Rs and its main drivers (Ts and SWC) in a semiarid sandy pasture. Repeated sampling campaigns revealed high variability in the spatial structure of these variables. Ranges of the spatial autocorrelation varied between 0 and 3.6 m for Rs, 0 and 3 m for SWC and 0 and 2.9 m for Ts. Structural variances were larger than 50% in most cases (and even larger than 75% in few cases) indicating moderate to strong spatial dependence for all of the three variables. Spatial dependence between SWC and Rs (analyzed by cross-variograms) was mostly positive with higher strength during periods of water stress. Ts-Rs spatial correlation was mostly negative and it became generally weaker at higher SWC (similarly to SWC-Rs) [ 3 ]. These results show that fine-scale functional patterns are very dynamic and can change within a few days with environmental stresses. Drought conditions led to stronger spatial dependency of the Rs-SWC patterns as well as to larger variability of these variables. In contrast, wet soil conditions led to poor spatial dependency and disappearance of spatial structures. Patch size of Rs depended negatively on transect average SWC. Increasing stress induces more pronounced spatial heterogeneity with increasing grain size (and decreasing spatial reliability).

### **2.2. Cross-site comparative analyses of grassland soil CO<sub>2</sub> efflux - context dependent effects of biotic and abiotic drivers**

Based on the same standard sampling protocol we further explored these relationships by 77 measurement campaigns at 8 contrasting grassland sites. We sampled open sandy grasslands with low soil carbon and water content, closed sandy grasslands with high soil carbon content, closed sandy grasslands with high soil water content and closed loess grasslands with high biomass. We found that spatial pattern of Rs was dependent on SWC, but in a highly complex way [ 2 ]. Relationship between the autocorrelation length of Rs and soil moisture varied and was conditioned by the combination of other factors (average Ts, spatially structured variability of Ts and total sample variance of Rs). For example, negative correlation between SWC and range of Rs did not exist at low Ts when Ts became the main limiting and driving factor of the spatial structure of Rs [ 2 ]. Our results suggest the existence of specific types of emergent functional patterns related to some threshold values of driving variables (mainly soil moisture, soil temperature and structural vegetation characteristics). The

contrasting soil conditions and vegetation structures of these grasslands enabled us to put our results into the context of land use and climate change. Relationships found between Rs, SWC and Ts suggest that grasslands with good soil and proper management have substantial acclimation capacity to climatic variability. However, if drying process occurs with simultaneous loss of soil organic matter due to inappropriate management, the coupling of these variables may diminish or cease completely. This aspect needs further verification comparing successional (regenerating), degraded and natural communities.

### 2.3. Changing spatial reliability of vegetation structure during degradation and succession.

Our cross-site studies suggested the potential importance of vegetation structures in controlling functional patterns. Therefore, we performed an independent study exploring how vegetation structure change during succession and degradation. Abandoned agricultural fields of various ages and mature natural grasslands were analyzed (three series, sampled by large circular transects in Hungary, Romania and Slovenia). For quantifying spatial reliability, we calculated the relative variance (CV%) of repeated estimates of alpha and beta diversity (from moving window statistics). Our results suggest increasing fine-scale coexistence of species and convergence of metacommunities to similar local assemblages in succession [ 10, 12, 18 ]. We performed similar analyses for exploring degradation series. One data set represented a grazing gradient in cattle pastures at Transylvanian Lowland, Romania. Another data set was collected in Western Hungary, in 6 wet meadows colonized by different amount of the invasive *Solidago gigantea*. Using the same sampling protocol and the same analyses, in degradation we found divergence of metacommunities (i.e. decreasing reliability) with increasing level of grazing pressure and with increasing abundance of invasive plant species [ 9, 10, 18, 19 ]. The increasing spatial stability (convergence) in regenerating communities and the decreasing spatial stability (divergence) due to degradation seem to be general and robust trends (Fig. 1). In contrast, there are grasslands adapted to natural disturbances (e.g. to small mammal disturbances) with no detectable degradation [ 7 ].

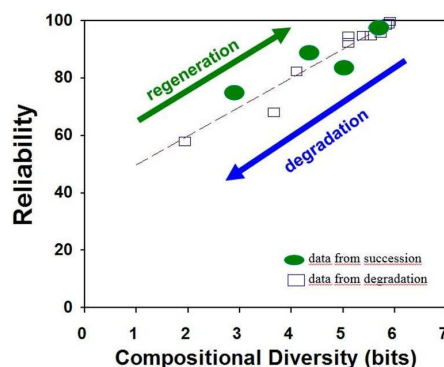


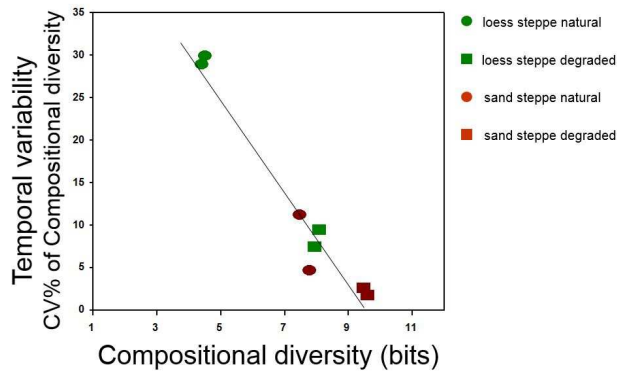
Figure 1. Reliability trends in succession and degradation (each point represent a vegetation stand).  
(Publications: 9, 10, 12, 18, 19)

### 2.4. Can grassland stability be inferred from fine-scale spatial patterns? - Relationship between spatial and temporal reliability

Using monitoring data sampled by large circular transects from 8 grassland sites (natural and slightly degraded sand and loess grasslands) we compared spatial and temporal patterns. Spatial reliability was estimated by moving windows statistics as in the previous paragraph. Temporal reliability was

expressed by the temporal CV% of diversity sampled over time in the sample windows. Five times higher relative interannual variability was found in more arid and more degraded sites (**Fig. 2a**). Spatial reliability in the initial year showed positive correlation with temporal reliability during the next 5-6 years period (**Fig. 2b**). Our results imply that diversity and structural complexity are important sources of adaptive behaviour of vegetation and future dynamic behaviour of grasslands can be predicted from snapshot assessments [ 10, 18, 19, 20 ].

a,



b,

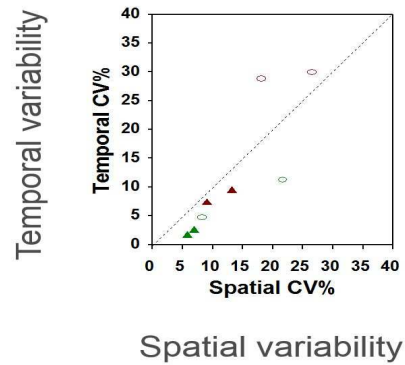


Figure 2. Relationship between spatial and temporal variability of diversity in grasslands (each point represent a vegetation stand). (Publications: 10, 18, 19, 20)

### 2.5. Within-stand variability of above ground biomass

Stand scale homogeneity (spatial reliability) of above ground productivity of vegetation was assessed by 60m biomass transects in various grasslands (58 transects sampled in open and closed sand grasslands, mesic steppe meadows on loess, wet meadows and ruderal assemblages from abandoned agricultural fields). Spatial variability of biomass was expressed by the coefficient of variation of spatial replicates sampled along the transect. Considering the spatial variability of biomass in natural grasslands, negative relationship was found between spatial CV% and the mean values of biomass (**Fig. 3**). Similar trend appeared in regenerating transitional communities (old fields) but the biomass was spatially more variable [ 14, 17 ].

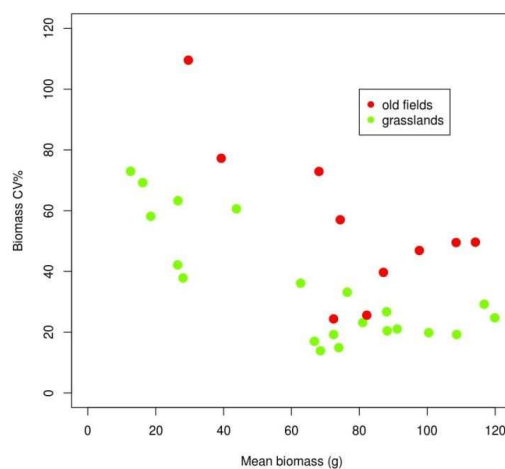


Figure 3. Relationship between biomass CV% and mean biomass. (Publications: 14, 17)

### **Objective #3** *Assessing mechanisms from functional patterns – a deductive approach*

#### **3.1. Evidence of unimodal relationship between productivity and species richness – global versus local scale patterns**

We had the opportunity to join to an international collaboration (30 sites in 19 countries and 6 continents) for testing the classic humped-back model (HBM) between productivity and species richness. Based on a worldwide coordinated survey, using extremely large local sample sizes (n=64, 1x1m plots,) and careful consideration of sampling conditions, our data supported the HBM model [4]. This study offered some important conclusions that were relevant to our OTKA project. First: the consistency of results depends on the range of site productivities sampled and the classic HBM appears only at broad productivity range. Second: the relationship was a „constraint type” suggesting multiple additional factors limiting species richness at given productivity levels. Furthermore, we learnt that these global and regional scale relationships reflect some overall near-equilibrium patterns more relevant for evolutionary interpretation. Therefore, we decided to change our methodology focusing on regulation instead of regressions. For exploring regulatory relationships we extended our spatial analyses with temporal replicates.

#### **3.2. Assessing temporal variability of spatial functional patterns – pattern regulation**

We studied the temporal variability of grassland CO<sub>2</sub> flux and biomass spatial patterns over 4 years under varying environmental conditions in a semiarid grassland near Bugac. Soil respiration and biomass were monitored 9 times (representing also seasonal variability). The sampling scheme was the 60x80m grid sampled at two sites with contrasting management (grazed vs. mowed). Data analysis was based on variography and kriging. Altitude (slightly undulating micro-relief, with 1-2 m differences) showed strong spatial correlation to the abiotic co-variables, soil moisture and temperature, with a consequent correlation with soil respiration and above-ground biomass [ 1 ]. We concluded that in grasslands minor topographical differences are important in the formation and regeneration of functional patterns at stand scale. The temporal variability of the signs (positive or negative) of the autocorrelations found between these spatial patterns suggest a complex interaction network of studied variables regulating these patterns. The patterns were more variable in drought years, while under well-watered conditions we detected higher stability (higher reliability) and also homogeneity. Grazing potentially created increased heterogeneity and regulation of the patterns, while mowing appeared to have had a homogenizing effect resulting in a lesser degree of pattern regulation [ 1 ].

#### **3.3. Model fits reflect pattern regulation**

Analyzing the fine-scale functional patterns of soil respiration, soil moisture and soil temperature by geostatistics (77 small circular transects), we found that model fits (i.e. detectability of spatial patterns) depend on specific conditions (vegetation closure in combination with large Rs and SWC values, as well as low variability of Ts and Rs). Our results show a shift from homogeneity and dominance of biotic processes to an increased heterogeneity and abiotic regulation in drought prone ecosystems under decreasing soil moisture [ 2 ].

#### **3.4. Linking functional patterns to vegetation characteristics**

In case of 60m biomass transects, when biomass and diversity were analyzed separately, we found

negative relationships between spatial CV% and mean values at both characteristics. Wet meadows and loess steppe meadows showed the highest spatial reliability of diversity and as well as the highest spatial reliability of biomass. However, we did not find relationships between mean diversity and the spatial reliability of biomass at stand scale (**Fig. 4a**) [ 14 ]. Similar relationships were assessed at patch scale using small circular transects. Data were collected from the same type of grasslands as for the 60m long transects (172 transects sampled at 15 sites from different seasons (March to November) and different years (2013-2017). According to our hypothesis, the highest functional reliability is expected in spatially well-organized plant communities with high structural complexity (high beta diversity) at fine scale. Our results have supported this hypothesis: we found lower CV% of soil respiration in vegetation communities with higher beta diversity (higher structural complexity) at vegetation patch scale (**Fig. 4b**) [ 15, 16 ].

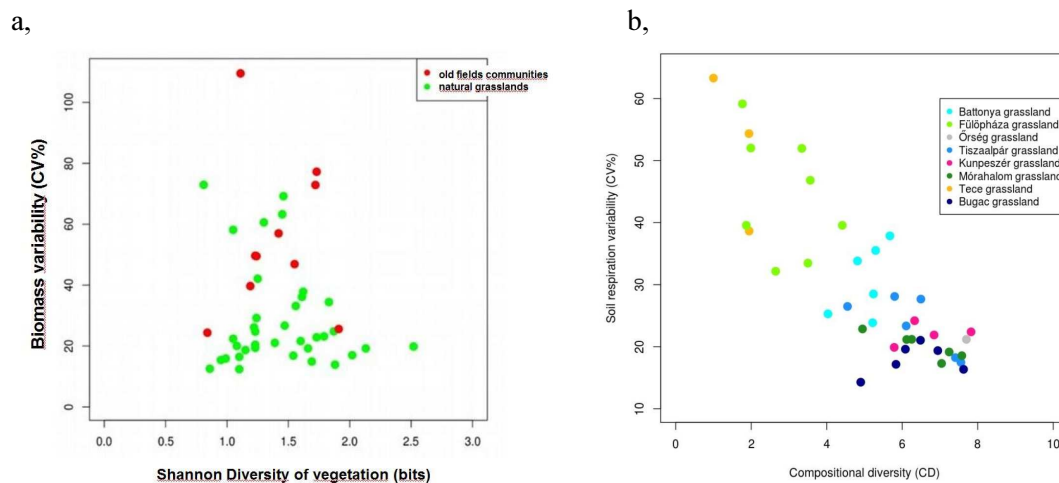


Figure 4. Relationship between functional reliability and vegetation diversity a, Biomass CV% and stand scale diversity b, Patch-scale soil respiration and compositional diversity. (Publications 14, 15, 16)

### 3.5. Exploring mechanisms affecting reliability of vegetation patterns

Dominance and diversity is often negatively related in plant communities. We tested this relationship in a wide range of successional plant communities and found that only a small portion of species acts as strong biotic filter [ 5 ]. Our results showed that spatial patterns and associations between dominants and subordinates vary with dynamical states (stable or transitional) and environmental conditions. Using hierarchical approach, we showed that the spatial functional organization of subordinate species affected by the spatial organization of dominant grass matrix in an abandoned mountain meadow. We found that trait-based assembly rules are consistent within habitats but may vary from community to community indicating that heterogeneous landscapes might support multiple processes of coexistence [ 6 ]. Changing biotic filters due to changing patterns of dominant species modulate the contribution of subordinate species to functional patterns and to the reliability of ecosystem services.

## Problems

Due to unfavorable weather conditions and some technical problems (with our field instruments) we needed an additional field season to finish our field measurements. Therefore we asked and received permission for extending our study period with one additional year until 31 December 2017.

## Publications

Since the start of the project 49 publications have been published (with NKFI/OTKA support acknowledged). We published 7 papers in ISI journals, 2 paper in Hungarian journals, 2 plenary talks, and 38 other presentations (posters or lectures).

The total **IF** of these publications is **51,329**

The number of **independent citations** received by the publications of this OTKA grant is **143**.

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