An outline of the PhD dissertation:

INVESTIGATION AND MODELLING OF VEGETATION TRANSFORMATIONS INDUCED BY LAND USE CHANGE

by

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I. Introduction and aims

It is widely accepted today that the vegetation pattern we perceive does not depict an equilibrium. It is rather a snapshot of the ongoing transformation of the vegetation (DeAngelis and Waterhouse 1987, Pickett et al. 1992). This is especially true in habitats influenced by humans, where human disturbances or the cessation of those have long-lasting effects on the vegetation dynamics. The investigation of vegetation changes and the detection of their drivers help to understand the processes of vegetation dynamics, as well as to estimate the potential effects of human disturbance. The knowledge of the patterns and drivers also supports the prediction of future changes.

The way we perceive and interpret vegetation response, however, can depend greatly on the spatial and temporal scale of our investigations. On one hand, short term vegetation response may be misleading, the trends observed closely after the human or natural disturbance may be different from the global and long-term response. On the other hand, the effects of human intervention or those of its cessation may be different on different spatial scales as well (see DeAngelis and Waterhouse 1987 among others).

The aim of my PhD research was to analyse the vegetation changes induced by the abandonment of grazing and to understand the drivers of these at multiple spatial and temporal scales, based on a case study well-supported by archive data.

To achieve this, my first aim was to describe the vegetation transformations that occurred since the abandonment. I also formulated transition rules among the vegetation types, based on which I created a rough model of the expected vegetation dynamics for the future.

Secondly, I wanted to explore the relative importance of the abiotic environment and past vegetation patterns as drivers of the observed vegetation dynamics. Within past vegetation patterns I also investigated whether the identity of the preceding vegetation type or the neighbourhood configuration in the past has more influence on the vegetation dynamics.

I dedicated a separate chapter to the consequence of the expansion of *Calamagrostis epigejos*, which induces a vegetation transformation most typical after abandonment of human management in Central Europe nowadays. By studying species turnover pattern in natural steppe fragments and in a patch, which has been overgrown by *C. epigejos,* I aimed at detecting how and why the species rich natural grassland turns into the species poor *C. epigejos* dominated stand. I also set the goal of finding which characteristic of *C. epigejos* (percentage cover, number of shoots, duration of presence, litter cover) is most closely related to these changes.

Finally, I participated in the development of a new method, which is capable of reconstructing the vegetation dynamics on a mechanistic basis. The aim of this chapter was to provide a method,

which finds the transition rules and vegetation maps for intermediate years, that fit best the snapshots of the dynamics observed.

According to the above aims I formulated the following questions:

1. What kind of vegetation transformations occurred at the study site following the abandonment of grazing? What regularities can be deduced based on these and what do these suggest regarding future vegetation development?

2. What is the relative importance of the abiotic background and past vegetation conditions in determining vegetation transformations? How important is the spatial configuration of the past in this aspect?

3. How does the transformation from a natural steppe grassland into a *C. epigejos* dominated one proceed? Which characteristic of *C. epigejos* explains the observed species loss the best?

4. How can we model vegetation dynamics in a realistic and possibly objective way based on a few snapshots of vegetation maps only? Which intermediate states can we assume between the snapshots?

II. Materials and methods

Field sampling was carried out in a dry temperate loess grassland area at the southern foot of the Bükk Mountains (NE-Hungary, N 47° 54', E 20° 35'), at an elevation of about 150-200 m. The subcontinental climate of this gentle hilly country has a transitional character between the climate of the Great Hungarian Plain and that of the mountainous region. The mean annual temperature at the site is 9 °C and the mean annual precipitation is about 600 mm with a slightly semiarid period in late summer. Brown forest soils of chernozemic type are typical on the loess substrate (Virágh 1991).

The northern slopes of the valley where our study site is located, were originally covered by a climatic zonal forest steppe forest of low woody cover, although the forest itself was cleared at least three hundred years ago. Following deforestation, up to the 1970s, sheep grazing of various intensity has shaped the vegetation. Vegetation dominated by *Festuca rupicola* solely, and vegetation co-dominated by *Danthonia alpina*, *Festuca rupicola* and *Avenula praeusta* are among the most species rich communities in the studied area and can be considered as steppe grasslands close to a natural status (Virágh and Fekete 1984). Grazing and anthropogenic disturbances have resulted in the appearance and persistence of communities poorer in species in general and characterized by a different set of subordinated plant species. These were described as separate vegetation types and named after their dominant species by Virágh and Fekete (1984), such as

Chrysopogon type, dominated by *Chrysopogon gryllus* and *Calamagrostis* type, dominated by *C. epigejos*.

Our species turnover results are based on a repeated sampling in 2002, 2003, 2004 and 2005 in 15 1 m x 1 m plots, divided into 20 cm x 20 cm subplots. The plots have been part of a previous experimental scheme (Virágh 1991). In each subplot, percentage cover of each vascular plant species was recorded. In addition to this, the number of *C. epigejos* shoots per subplot was also counted and the cover of living shoots and percentage cover of the litter of the species per 1m x 1 m was estimated independently from subplot investigations. The approximate length of the *C. epigejos* occupation in each affected 1 m x 1 m plot was calculated based on archive data starting from 1979. The rest of the investigations was based on three successive vegetation maps depicting the spatial distribution of all the vegetation types at the study site. The maps were drawn at 1:1400 resolution in 1983, 1988 by Virágh and Fekete (1984 and unpublished) and by myself in 2002.

The dissertation has four main chapters corresponding to the four main questions posed, a distinction also reflected in the methods.

First, the successive vegetation maps were compared to reveal the temporal changes of the landscape pattern, in terms of number, size, proportion and replacement of different types of vegetation patches (i.e. stands of vegetation types). Transition probabilities were calculated between each pair of vegetation types for each period (1983-1988, 1988-2002, 1983-2002). The transition matrix of 1983-1988 was cubed, in order to make it comparable to the matrix of 1988-2002. Finally, the relative cover distribution of vegetation types in 2002 was multiplied three times by the 1983-2002 matrix, so as to give the first few steps of a Markov Chain covering a 60 year period.

Second, I fitted generalised linear models based on conceptual hypotheses to explain the distribution of three vegetation types, the *Calamagrostis*, the *Danthonia* and the *Chrysopogon* type, in 2002. Specifically, I wanted to examine whether current abiotic topo-environment, past neighbourhood configuration, or historical vegetation patterns or a combination of these determine the current distribution of vegetation types the best. I developed basic predictor sets for each hypothesis and using GLMs I tested to what degree these predictor sets were capable of explaining the currently observed patterns of individual vegetation types. Model accuracy was compared by two measures: AUC values and maximised kappa.

For the comparison of species turnover, appearance and disappearance rates of grassland species were calculated for pairs of consecutive years in grassland plots dominated by and free from *C. epigejos*. First, average appearance and disappearance rates were compared in 6 of each type of plots by Monte Carlo randomisation. Second, average appearance rates were assessed for categories of *C. epigejos* performance and their confidence intervals were calculated via Monte Carlo randomisation. Significance levels served as a measure for deciding on the strength of the

relationships between appearance rate and background variables. For two performance variables (percentage cover and shoot number) analyses were performed at two scales (20 cm x 20 cm and 1 m x 1 m).

Finally, I participated in the development of a Bayesian Markov Chain Monte Carlo method, which uses a discrete time stochastic cellular automaton to reconstruct vegetation dynamics among vegetation maps drawn in the field. Expansion capability of each vegetation type was characterized by a lateral spread parameter and by another describing establishment from species pool. The former imitates vegetative spread, the latter establishment from species pool. These two appearance options are governed by parameters arranged into two transition matrices which are further weighted by a function of the frequency of vegetation types in the neighbourhood cells. This yields the final transition weights for individual map cells. The simulation starts form the first input vegetation map and proceeds with one-year intervals. Transition matrix parameters and intermediate estimated maps of vegetation distribution are iteratively adjusted so that these together fit the input vegetation maps, which are fixed throughout the simulation, the best. Actually, not only the best parameter and intermediate vegetations maps, but a full probability distribution of them is produced. As a test of the method the simulation was run both with all three maps supplied as fixed input and also with only the first and last included.

III. Results

Transformation regularities among vegetation types following abandonment of grazing

1. Strongly directional transitions were discovered among vegetation types, source and sink vegetation types were distinguishable.

2. The cubed 1983-1988 transition matrix was found to be different from the 1988-2002 matrix, indicating a lag period before the effects of the abandonment of grazing became observable.

3. According to the Markov model estimation, the *Calamagrostis* type and the shrub type, which were characterised by self-replacement in the first ca. 20 years, are predicted to expand considerably in 60 years time. At the same time, a decrease of the extent of previous sink types (which have expanded heavily recently) is predicted.

The relative importance of abiotic background and past vegetation in determining the expansion of selected vegetation types

1. The distribution in 2002 of the three vegetation types investigated was determined by different

background variables.

2. Knowledge of past conditions was sufficient to predict the distribution of two (the *Calamagrostis* and the *Danthonia* type) of the three investigated vegetation types alone, thus no topo-environmental predictors were needed for a successful prediction of these.

3. The distribution of the *Calamagrostis* type in 2002 depended on the location of its patches in 1988 (i.e. on the past neighbourhood configuration) only.

3. The distribution of the *Chrysopogon* type was best explained by current topo-environmental predictors. And these were also equivalently good predictors of the distribution of the *Danthonia* type compared to the variable groups characterising past conditions.

A vegetation transformation of special interest: the effects of the establishment and dominance of C. epigejos *on the species turnover of a natural grassland*

1. *C. epigejos*-dominated plots differed from unaffected ones by significantly lower appearance rates. This indicates that *C. epigejos* lowers species number by hindering reappearance of component species of the original grassland.

2. Appearance rate changed in a non-linear manner with changing levels of *C. epigejos* performance. Low level *C. epigejos* performance enhanced appearance rate compared to intact stands, while high level performance decreased it, regardless of the choice of performance measure.

3. Change in appearance rates was best explained by differences in percentage cover of *C. epigejos*.

4. Coarser scale *C. epigejos* performance had a closer correspondence with appearance rate change than fine-scale performance. Therefore, the broader scale conditions seem to have a greater effect on turnover than local ones.

Reconstruction of the vegetation dynamics by Monte Carlo Markov Chain simulation

1. We estimated the trajectory of change for each vegetation type, which was sufficiently diverse and flexible. The estimated dynamics also bore a considerable non-linear element in most cases.

2. For several types (e.g. *Festuca* and *Danthonia* type) these nonlinearities unveiled a hidden minimum or maximum point in the amount of area occupied at dates, when no data are available.

3. The estimated intermediate vegetation maps resulting from the simulation based on two vegetation maps resembled those from the simulation based on all three maps available.

4. Vegetative spread capability was generally more expressed than establishment capacity from species pool for our vegetation types.

IV. Conclusions

Three of the four studies in this PhD dissertation aimed at contributing to the reconstruction and understanding of the vegetation changes over the full study area. Each of these proved that vegetation types reacted individually to abandonment: some vegetation types benefited from the land use change, while others suffered from it.

Vegetation types also differed regarding the drivers of their expansion, which again points to different spread mechanisms for different vegetation types. These differences are well mirrored in the results of the simulation, too. For the expansion of the *Calamagrostis* type, even the Markov Chain showed time homogeneity, i.e. linear spread in time. This also appeared in the corresponding prediction. Such an expansion pattern is only possible if the identity of the vegetation type, which is overtaken by *Calamagrostis* type does not influence this process. If any of the vegetation types had been preferred for transformation into *Calamagrostis* type, the decrease of the area of this preferred type would have slowed down the expansion of *Calamagrostis* type. In accordance with this expectation, the best predictor of the 2002 distribution of *Calamagrostis* type was the past configuration of its patches. The simulation added a final touch only by showing a slight nonlinearity, a faint saturation in the expansion of this type. Nevertheless, this pattern was still very close to linear. These findigs point to a clonal spread strategy, which is further underlined by the result that the *Calamagrostis* type was one of the vegetation types, for which high lateral spread weights were estimated in the simulation study.

In contrast to the pattern found for the *Calamagrostis* type, the Markov Chain predicted a decrease for the formerly increasing *Danthonia* and *Chrysopogon* types. Although the effect of the past vegetation was discernable for the *Danthonia* type according to the spatial prediction study, abiotic background predicted it equally well. The distribution of the *Chrysopogon* type in 2002, on the other hand, was clearly determined by the abiotic environment. Consequently, the *Chrysopogon* type and to some extent the *Danthonia* type as well are close to an equilibrium with the abiotic background, which also makes their further expansion unlikely. Nevertheless, the expansion of other types which are not sensitive to the abiotic background (such as *Calamagrostis* type) can decrease the area occupied by the *Danthonia* and *Chrysopogon* types. This means that implications of the results of the spatial prediction approach are in accordance with those of the Markov Chain Model. Additionally, the simulation study showed that the decreasing trend could have started before 2002, since according to the results, the *Danthonia* type have reached the largest extent before 2002. Of course, such maximum points could not have been detected by the simple Markov Chain Model. Although the simulation shows no maximum point in the past for the *Chrysopogon* type, the ceasing of its expansion is clearly shown.

All four studies within the dissertation clearly pointed out nonlinear features of the vegetation dynamics that followed the abandonment of grazing. The most apparent non-linearity was probably the presence of a lag period in the vegetation response. In the first study, differences of the 1983-1988 and the 1988-2002 transition matrices showed that the first five years of dynamics was much less intense than that of the next 14 years. The lag period in the response is less apparent, but discernable in the second study as well, especially for the *Danthonia* type. The distribution of this vegetation type in 2002 still reflected some of the 1988 vegetation pattern opposed to pure abiotic determination, which could be expected if the response of the type could emerge fully after the abandonment. The lag-period was also apparent in the fine-scale analysis, where the appearance rate of did not decline right after the establishment of the future dominant species as it did later, but it increased in the beginning. The simulation study also showed a lag period in the dynamics. This would not be surprising if it would only be discernable with the simulation based on all three vegetation maps. Nevertheless, it also showed up when the initial and final vegetation maps were used only, which also underlines the reliability of the simulation approach. This last study also pointed out other forms of non-linearity, such as minimum and maximum points in the area curves of some of the vegetation types.

The expansion of the *Calamagrostis* type was an apparent feature in all studies, not only in the third, where this was the main effect studied. Both temporal prediction approaches (Markov Chain and Markov Chain Monte Carlo) estimated linear spread for this type. This is even more interesting as none of the other vegetation types showed such pattern. Furthermore, the *Calamagrostis* type was the only vegetation type the response of which showed no lag period, but could profit from the land use change instantly. At the same time, its effect on the turnover in the natural grassland was only discernable after a lag period. Besides the instant expansion of the type after the abandonment, all other results point to a superior expansion capability of the type, too. The change in the proportion of area occupied by the various vegetation types did not influence its expansion and the location of the *Calamagrostis* patches in 2002 was determined by the location and configuration of its former patches only.

To sum up, the dissertation illustrated the diverse behaviour of vegetation types within one site after abandonment. The regularities of the transformations within vegetation types have been shown, which pointed to non-linear response in many cases. Finally, the dynamics was also successfully reconstructed and its main drivers were identified. The responses of the vegetation found on different spatial and temporal scales as well as with different approaches complemented each other plausibly.

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