

SUMMARY OF THE Ph.D. THESIS

**Dynamics of grassland ecotones under unidirectional  
and fluctuating water regime changes**

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## **Introduction**

Ecotones, the transitional zones between adjacent vegetation patches, have received considerable attention in relation to fragmentation, climate change and the management of heterogeneous landscapes. Since several plant species reach their local limit of tolerance in the ecotones, ecotones can be the most reactive zones of the landscapes during environmental changes. Despite these, the predictability of ecotone dynamics is low and the processes taking place within ecotones are still poorly understood. The aim of the present study was to characterize the ecotones of two landscapes with different trends in their water supply, and to find an explanation for the detected behaviour of the ecotones. Specifically, I asked the following main questions: (1) Are there sharp ecotones in the landscapes, which divide up the vegetation into distinct patches, despite the unstable water regimes? (2) Do ecotone positions follow the changes of the water regimes? (3) What other gradients influence the positions of the ecotones? (4) What structural reactions can be detected in the ecotones as a function of the water regime?

## **Materials and methods**

The first landscape I studied was a sand dune range area of the Danube–Tisza sandy ridge. The vegetation pattern is driven by the differences in elevation, leading to a mosaic of xeric and mesic communities interconnected by an extensive network of ecotones. The entire region is affected by long-term aridification due to water table decline. This tendency has been typical for the study area as well and can be considered a directional drying process. The high differences in the annual precipitation add a fluctuating component to the water regime change.

The other studied landscape is the steppe–wetland mosaic of the Turjánvidék. The character of the plant communities is also determined by the elevation gradients. The water supply is high compared with the other study area because falling precipitation is supplemented by seeping groundwater from the direction of the sandy ridge; however, the inter-annual fluctuations are extremely large.

In the sand dune landscape, vegetation was surveyed in two, gradient oriented permanent transects annually between 1999 and 2013. In the Turjánvidék, I surveyed the vegetation of 13 permanent transects starting in steppe patches and ending in wetland patches in 2013, 2014 and 2015, which corresponded to a sequence of wet, dry and wet years. In 2013, I measured microclimatic and soil moisture data in one of the sand dune transects and also obtained the precipitation data of the area for the full study period. In the Turjánvidék, I measured the ground water levels during the study and obtained the precipitation data to characterize the water regime. Besides these, I mapped the microtopography and soil organic content of the Turjánvidék transects in order to identify boundaries in the gradients of these parameters.

Vegetation data were analyzed with the split moving window technique to delineate the position and contrast (the compositional difference between the two sides of the ecotone positions) of the ecotones. Using multiple linear regressions, I tested if annual precipitation and year (as a measure of time since the loss of water table) influence any of the two ecotone descriptors. As for the ecotones of the Turjánvidék, I used one-sample tests to check if the interannual changes of ecotone positions and contrasts differ from zero and to compare the elevation and soil boundaries to the ecotone positions averaged across the three study years.

In the sand dunes, the internal changes of the patches bounded by the ecotone positions were evaluated using plant functional types. In the Turjánvidék, it was possible to separately analyze the structural dynamics of patch edges (wetland edges and steppe edges) and patch interiors (wetland interiors and steppe interiors) using average relative indicator values for moisture. I used mixed-effects linear models for the purpose, with the inter-annual changes of the average indicators as the dependent variable, the four transect sections as the fixed factors and transect as the random factor. To understand the mechanisms driving the changes of the wetland edges, I checked whether the abundance changes of steppe specialists, wetland specialists or both have a role.

## Results

In the sand dunes, a total of five (four in one of the transects and one in the other) transitions were detected that could be considered significant, sharp ecotones in at least one of the study years. The position of these ecotones was stable; no significant relationship could be found with the precipitations of the 12-months and 3-months periods preceding the surveys and only one ecotone had a directional trend over the years. However, this trend became apparent only after the contrast of this ecotone had fallen below significance level. Only one significant relationship could be detected between precipitation and contrast values, but the years had clearer significant effects. Two ecotone contrasts decreased and had disappeared by the end of the study; one ecotone appeared during the study and its contrast showed a constant increase; the two remaining ecotones showed no trend. According to the evaluations of the functional groups, two main trends prevailed: drying, indicated by the increase of xeric perennials and the decrease of mesic perennials, and the opening up of the vegetation, indicated by the increasing abundance of ephemerals and cryptogams. These two trends, however, did not occur simultaneously with the same magnitude everywhere owing to the initial conditions and the potential end-states of the patches; these differences clearly explained why each ecotone contrast changed in the way they did.

In the Turjánvidék transects, one sharp ecotone could be detected in all transects, located between the wetland and the steppe communities. These positions showed some minor interannual shifts but these were unrelated to the fluctuations of the water regime. The ecotone positions averaged across the years did not differ from the position of the detected elevation boundaries but were a bit uphill from soil boundaries. Contrast values sensitively followed the water regime; the contrast was high in the wet years but was low in the dry one. The analysis of the four transect sections revealed that the contrast changes were caused by the intensive reactions of the wetland edges. The average indicator values were high in the wet years and low in the dry year, while the steppe edges remained unchanged. Changes in the patch interiors, if there were at all, were lower than in the wetland edges. Both the

encroachment/retractions of steppe specialists and the retraction/encroachment of wetland specialists could be detected in the wetland edges.

## **Discussion and conclusions**

Based on the results, it can be concluded that the vegetation of the studied landscapes is made up from distinct patches bounded by sharp ecotones, so the changes of the water regime do not blur the transitions between the patches. According to the literature, sharp ecotones can develop due to sharp environmental boundaries and to non-linear responses of the vegetation to gradual environmental changes. The present study corroborates the first theory as I could detect steep gradients of microclimatic parameters and soil moisture at a sharp ecotone of the sand dunes, while a disappearing ecotone corresponded to no such environmental pattern. Ecotone positions in the Turjánvidék coincided with elevation boundaries, which are obviously the steepest points of the hydrologic gradients, regardless of the actual absolute moisture conditions. Soil boundaries were also mostly present, although not really in an overlapping position.

The positional movements of the ecotones were independent of the water regime, meaning that the patch pattern of the landscape appeared rather rigid. There can be several non-exclusive explanations for this. The formerly higher water supply in the sand dunes and the long-term average water supply in the Turjánvidék could cause stable, long-lasting differences (like in organic matter content or physicochemical properties) on different elevations, which could hinder positional responses of the ecotones. Besides, there can be gradients that are unrelated to the water regime, including the already mentioned microclimatic gradients in the sand dunes and the pattern of the elevation gradient in the Turjánvidék. In sum, these factors can anchor the ecotone positions, and, in addition, there are no strong ecosystem engineering species in either communities, which could facilitate the spreading of each community.

Unlike positions, ecotone contrasts sensitively followed the changes of the water regime in both studies. Thus, the typical patch dynamics of the sand dunes was

not patch expansion and shrinking but patch fusion and fission, which went along with the internal changes of the patches. A landscape level loss of species is a natural consequence of such a dynamics, but their re-colonization is doubtful due to the remoteness of source populations. Thus, the restoration of the water table in the Danube–Tisza sandy ridge, or other altered environmental conditions in other mosaic landscapes, should be supplemented by species reintroductions to successfully restore the vegetation.

In the Turjánvidék, the processes leading to the changes in ecotone contrasts did not involve the interiors, corroborating the „hotspot” theory of ecotones during environmental changes. However, the two halves of the ecotones, the wetland edges and the steppe edges, behaved in an asymmetric way, implying the dominant nature of steppe communities over wetland communities in their interaction. This can explain why the soil boundary was located downhill to the ecotone positions, even though the cause and effect relationship is not likely to be this simple. Other factors, like erosion might have also pushed down soil boundaries, and in such a case the asymmetric behaviour of the two edges would be consequential. However, the fact that the vegetation of steppe edges did not become the least bit wetter in the wet years supports the hierarchy between the two community types.

The sensitivity of the wetland edges calls attention to the vulnerability of small patches to prolonged dry periods owing to their large edge/interior ratio. This issue does not apply to steppe patches, whatever small they are. Thus, an overshoot in the restoration of the water supply of the region is not likely to threaten these valuable communities if the water level is not high for too long.

Finally, the results also suggest that monitoring patch limits, either on the spot or by GIS, is not a good choice for keeping track on the responses of the vegetation pattern to environmental changes in mosaic habitats like the ones scrutinized in the present study. Instead, permanent monitoring quadrat pairs should be established within the ecotones (one quadrat of the pair in one patch edge and the other one in the adjacent edge) and their difference should be used as a measure of the response of the vegetation to environmental changes or restoration effectiveness.

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