



Hydrologic fluctuations trigger structural changes in wetland–dry grassland ecotones but have no effect on ecotone position

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Abstract: Ecotones between plant communities have received considerable attention among ecologists in the context of fragmentation, climate change and the management of heterogeneous landscapes. However, the predictability of ecotone dynamics is low and the processes taking place within ecotones are still poorly understood. In this study we aimed to characterize the positional and structural dynamics of thirteen ecotones in an ecotone-rich steppe–wetland landscape of Hungary in relation to the inter-annual fluctuations of water regime and the gradients of elevation and of soil composition. According to our results, the ecotones between steppe and wetland communities were sharp and their positions coincided with those places in the landscape where the rate of change in elevation was the highest, confirming that microtopography is a major determinant of ecotone position. Soil boundaries were also detected, mostly downhill to the ecotones. Interestingly, the fluctuations of the water supply had no effect on the position of the ecotones but significantly influenced a structural ecotone parameter, the compositional contrast bridged by the ecotones. High water supply caused high contrast, while low supply went along with low contrast. We explain these changes by asymmetric sensitivities to edge effects. When the water supply was low, the wetland edges became similar to the steppe edges due to the decrease of wetland specialists and to the increase of steppe specialists, but steppe edges did not exhibit an opposite change in wet years, suggesting that steppe communities dominated over wetland communities. The asymmetry in the interaction between the two communities may have pushed the soil boundaries downhill to the ecotones but the currently steppe-like soil of wetland edges could also make wetland edges more sensitive to edge effects; thus, the cause-effect relationship is difficult to disentangle.

Introduction

Ecotones, the transitional zones between adjacent plant communities, have long been in the spotlight of ecological research (e.g., Risser 1995, Walker et al. 2003, Hufkens et al. 2009). The concept of ecotone has been refined multiple times since its introduction by Clements (1907), and currently, ecotones are regarded as three-dimensional structural and functional components of the landscape, which have the potential to vary spatially and temporally (National Research Council 1995, Fagan et al. 2003). In some studies only one of the neighbouring communities is of interest (like a tropical forest patch next to a deforested patch), which is usually divided into a homogeneous patch interior and a more heterogeneous marginal zone, the ‘edge’ (e.g., Harper et al. 2005), and the patterns and processes typical of this zone are studied. However, by definition, it takes both neighbouring patch edges to form the ecotone (Yarrow and Marín 2007).

Several species reach the limit of their tolerance in ecotones; therefore, ecotones can represent the hotspots of landscape-level vegetation change as a response to environmental changes (Fortin et al. 2000). The fact that ecotones can constitute a significant proportion of land cover in fragmented or naturally patchy landscapes further increases the importance of mechanisms taking place in or controlled by ecotones

(Harper et al. 2005, Yarrow and Marín 2007). Thus, there is a growing need for understanding and predicting multiple aspects of ecotone dynamics. Peters et al. (2006) proposed a conceptual framework for studying the positional dynamics of ecotones and described three main types of dynamics: stationary, directional and shifting. These types are different in the nature of their driving forces and the constraints they face. Directional dynamics, i.e., the unidirectional migration of an ecotone by the expansion of one of the neighbouring communities against the other one, has the most voluminous literature as climate change and land use change are among the typical causes of such dynamics (among others, Chen 2002, Gehrig-Fasel et al. 2007, Bodin et al. 2013). Stationary dynamics prevails along, for example, abrupt elevational or geomorphic gradients where spatially stable changes in the microclimate or soil composition occur, anchoring the corresponding ecotones over long periods (Körner 1998). Shifting dynamics are expected when the direction or intensity of major environmental drivers (like the water level in wetland–upland interfaces) change in time (Fortin et al. 2000, Muñoz-Reinoso 2009), or the fluctuations of different drivers (like fire, grazing or climate) favour different communities of species, which, therefore, shift back and forth over time (Gosz and Gosz 1996, Peters et al. 2006). In real life situations, however, there can be a number of different drivers and determinants influencing the position of ecotones simultane-

ously; thus, it can be challenging to predict positional dynamics (Risser 1995).

Besides position, ecotones have several other properties that can also change over time and thus have landscape level consequences (Strayer et al. 2003). From among these parameters, ecotone contrast, the difference in species composition or physiognomy bridged by an ecotone, has an outstanding importance, as many mechanisms that regulate the exchange of materials, organisms and energy across ecotones depend on this structural property (Johnston 1993, Collinge and Palmer 2002, Cadenasso et al. 2003). Ecotone contrast is also influenced by edge effects, i.e., the effects of a community on the edge of the neighbouring community (Murcia 1995); therefore, ecotone contrast provides information on the interaction of the communities as well. Despite the obvious importance of ecotone contrast, very few studies are available that address the dynamics of this parameter. However, there is evidence that ecotone contrast can change during succession (Boughton et al. 2006) and can change in stationary ecotones as a response to directional changes of environmental drivers (Tölgyesi et al. 2016). Thus, to understand fully the dynamics of ecotones and mosaic landscapes as a whole, an integrated examination of ecotone position and structure, especially contrast, is a promising approach.

The Turjánvidék of central Hungary is typically such a complex landscape. It is a narrow but long geographic region (approx. 5 km × 120 km) of the Great Hungarian Plain. It runs parallel to the Danube River, and lies in the discharge zone of the groundwater seeping from the nearby Danube–Tisza Sandy Ridge (Mádl-Szőnyi and Tóth 2009) (Fig. 1). This excess water supply resulted in the development of various wetland types, including fen lakes, reed beds and swampy meadows along slight microtopographic gradients and steppe enclaves on never inundated humps (Tölgyesi et al. 2015). However, the water supply shows extreme fluctuations, which is likely to have a profound effect on the vegetation pattern of this mosaic landscape. In the present study, we aim to characterize this special dynamics by monitoring ecotones between wetland and steppe communities. Specifically, we ask the fol-

lowing main questions: (1) Do the ecotones between never inundated and regularly inundated patches form abrupt vegetation ecotones, or are they blurred by the unstable water regime? (2) Does the position of these ecotones follow the inter-annual fluctuations of the water regime, i.e., are they shifting ecotones? (3) How is the vegetation pattern of other, comparatively stable environmental gradients, like microtopography and soil composition, related to the position of the ecotones? (4) How does water regime affect the structure, in particular the contrast and composition, of these ecotones?

Materials and methods

Study area

The study was carried out in steppe–wetland mosaics of the Turjánvidék, central Hungary (Fig. 1; Appendix S1). The climate of the region is continental with a sub-Mediterranean influence; mean annual precipitation is 500–600 mm and mean annual temperature is 10–11°C (Biró et al. 2013). The area is located about 100 m above sea level and its surface is slightly undulating with a difference of only 2–3 m between the highest and lowest elevations. Steppe communities are grasslands that have evolved on humps of calcareous sandy substrate that are elevated above the level of inundation. These steppe communities are exceptionally species-rich communities with plant coverage usually close to 100%. Dominant species include *Chrysopogon gryllus* (Torn.) Trin., *Festuca pseudovina* Hack. ex Wiesb., *F. rupicola* Heuff., *Poa angustifolia* L., etc., and dicots are also present in large numbers. Adjacent wetland zones are dominated by *Carex disticha* Huds, *C. panicea* L., *Deschampsia caespitosa* (L.) P. B., *Molinia coerulea* (L.) Moench, etc. and, similarly to steppes, the resulting communities are tall and dense. Species richness of the wetlands is usually somewhat lower than in steppes, especially if the cover of tall sedges is high (Tölgyesi et al. 2015). The hydroperiod of the wetlands varies in winter and early summer, depending on precipitation, while surface water is usually absent between mid-summer and autumn.

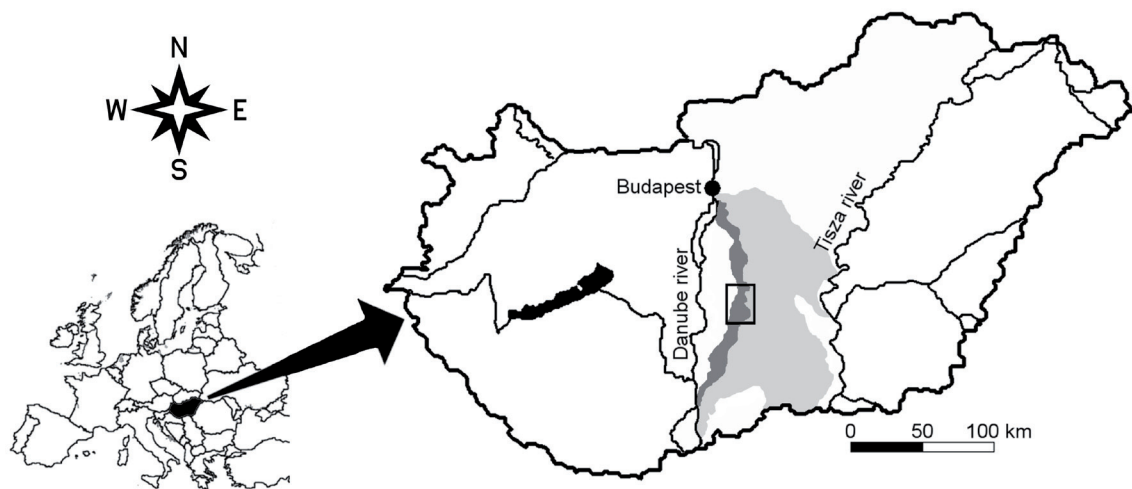


Figure 1. Location of the Turjánvidék (dark grey) and the Danube–Tisza Sandy Ridge (light grey) in central Hungary. Sampling areas were located within the black window.

Owing to the waterlogged conditions, peat deposition is common. The precipitation of the region shows extreme variation; in some years, it can exceed 800 mm (like in 2010), but sometimes, it can be lower than 300 mm (like in 2001). For the inter-annual fluctuations of the precipitation of the region in the last two decades, see Tölgyesi et al. (2016). Accordingly, the amount of groundwater seeping from the nearby Danube–Tisza Sandy Ridge (located 120–130 m above sea level) also shows high fluctuations, increasing the difference between humid and droughty years.

Data collection

We selected 20 steppe–wetland transitions for the study within a 15 km × 5 km landscape window in the central zone of the Turjánvidék using aerial photographs. These transitions were validated in the field during the spring of 2013, and five had to be discarded, as their steppes showed signs of recent tilling and/or were infested with invasive species like *Solidago gigantea* Ait. At the 15 remaining sites we established gradient oriented permanent belt transects with size of 40 m × 1 m. Each transect started in a steppe patch and ended in a wetland patch, their midpoint (meter 20) was positioned at the visually assessed point of highest rate of vegetation change and the transect was oriented perpendicular to the ecotone. We divided the transects into contiguous grids of 0.5 m × 0.5 m quadrats, resulting in 160 (2×80) quadrats in each transect. The presence/absence data of all vascular plant species were recorded in the quadrats between late May and early June in 2013, 2014 and 2015. Data in parallel quadrats were pooled; thus, each species could have an abundance value of zero, one or two in every 0.5 m × 1 m section of the transects. Due to relocation difficulties two transects were lost during the study period; thus we present data from 13 transects.

We also mapped the relief of the transects using a MOM Ni-C4 theodolite with a precision of 0.5 cm and collected soil samples from, at least, every 2 m interval along the transects using a tubular soil sampler. We determined the organic matter content of the samples, as this parameter was an easy-to-measure parameter of soil composition and was expected to reflect the long-term interactions of vegetation and hydrology (Bot and Benites 2005). Only the upper 15 cm of the soil (making a total of approx. 200 cm³) was sampled because deeper layers had an apparently lower root density and frequently contained freshwater limestone fragments, a rather widespread component of deeper soil layers of the region (Pécsi et al. 2014). Organic matter content was determined with the method of loss on ignition (Heiri et al. 2001).

We also set up a groundwater measuring station in the area (N46°49'06" E19°16'37") in January 2013, which was suitable for measuring water level both below and above the surface. Groundwater level was read every other month. Furthermore, we obtained the monthly precipitation data of the area between June 2012 and May 2015 from the 'Időkép' online meteorological portal (www.idokep.hu) to characterise the water regime of the study years.

Data processing

Ecotone positions were objectively identified with the split moving window (SMW) technique. As most methods used for identifying ecotone positions, SMW is also unable to properly account for the dimensionality of ecotones but delineates them with a single point along a transect, the point where the rate of vegetation change is the highest (Fortin et al. 1996, Fortin et al. 2000). Accordingly, we also use the phrase 'ecotone position' for such points, although the corresponding real ecotone is a broader zone between the interiors of the wetland and steppe patches as described in the Introduction.

In the SMW analysis, dissimilarities are calculated to describe the difference in species composition between two halves of a window of a preset size (window width). These windows are moved along the transect step-by-step (with 0.5 m intervals in the present sampling design) from one end of the transect to the other, resulting in a dissimilarity value for every window mid-point. We applied the squared Euclidean distance, as it has been shown to delineate efficiently ecotone positions (Wierenga et al. 1987, Erdős et al. 2014). To distinguish between significant ecotones and dissimilarity peaks created by chance, we performed a Monte-Carlo randomisation procedure. Randomisation that applies certain spatial constraints during the shuffling procedure is more efficient when testing the peaks than are complete randomisations (Fortin et al. 1996). Therefore, we chose the random shift method, in which the abundance pattern of each species is shifted along the transects randomly (Tölgyesi et al. 2016). After the randomisations, the observed dissimilarity values were Z-transformed by subtracting the overall expected mean (the mean of all dissimilarities, including the observed and random ones, gained from 1000 randomisations) from the observed dissimilarities, and dividing the results by the overall expected standard deviation (Boughton et al. 2006). Z-scores above 1.65 were considered significant (Hennenberg et al. 2005, Boughton et al. 2006).

Choosing the right window width in the SMW analysis is a critical step (Erdős et al. 2014). We calculated Z-scores for every window size from 1–10 m. Z-score profiles were very noisy with window sizes from 1–3 m, while distinct ecotones started to appear at 4 m. The position of the peaks changed slightly when the window size was further increased, which we associated with the decreasing effect of noise (cf. Boughton et al. 2006); however, at window widths of 9 and 10 m, double peaks started to coalesce, making their evaluation difficult. Thus, we chose window size 8 m for all SMW analyses. Double peaks were averaged, so all ecotones positions were delineated with a single position along the transects. For expressing ecotone contrast, we used the Z-scores; in double peaks, Z-scores were averaged similarly to the positions.

To test the spatial dynamics of the ecotones, we compared the changes of the ecotone positions between 2014 and 2013 and between 2015 and 2014 using one-sample tests with zero as the hypothetical value. Changes in the Z-scores of the ecotone positions (ecotone contrasts) were also tested this way. To confirm that the fluctuations of the water regime and the temporal pattern of the ecotone descriptors are in a causa-

tive relationship, we further analysed the composition of four transect sections, which we called steppe edges, wetland edges, steppe interiors and wetland interiors. Since there is no universal method for measuring the width of edges and thus it is mostly an arbitrary decision what is considered an edge and what a patch interior (Chen et al. 1992, Hennenberg et al. 2005), we simply handled the 4-meter window halves at the ecotone positions as edges and the terminal 4-meter sections of the transects as patch interiors without stating that 4 meter would be the exact width of the edges (or 8 m would be the width of the corresponding ecotone) (Fig. 2).

In each of the four transect sections, we calculated frequency weighted average Ellenberg-type indicator values for moisture (Ellenberg et al. 1992) as adapted to the Hungarian flora by Borhidi (1995). This indicator system expresses the moisture demand of each plant species along a 12-grade scale, where low scores are allocated to species with low moisture demand and higher scores to species with higher moisture demand. The changes of the four transect sections were compared to a theoretical value of zero and also to one another with linear mixed-effects models with transect section type as the fixed factor (four levels: wetland interior, wetland edge, steppe edge and steppe interior) and location (transect) as the random factor. One model was developed for the changes between 2014 and 2013 and another one for the changes between 2015 and 2014. Since the changes were especially large in wetland edges, we tested the absolute changes of wetland specialists and steppe specialists between consecutive years using one-sample tests to determine if the compositional changes of the wetland edges were caused by the encroachment/retraction of steppe specialists, the retraction/encroachment of wetland specialists or both. Wetland and steppe specialist species were defined as the species with the lower and the upper third of the occurring Ellenberg-type indicator values present in a transect; the changes of species with intermediate values (middle third of the spectrum) were ignored.

In order to determine the points along the transects where soil organic matter content and microtopography had the

highest rates of change (henceforth, soil and elevation boundaries), we fitted smooth splines to the values, calculated the first derivative of the resulting curves for every 0.5 m and identified the highest absolute values. We then measured the distance between these environmental boundaries and the ecotone positions and tested if they coincide along the transects using one-sample tests.

All data analyses were carried out in an R environment. For one sample tests, we used either one-sample t-test if data did not deviate from the normality assumption (checked visually with Q-Q plots), or Wilcoxon, one sample, signed rank test if we detected an apparent deviation. Linear mixed-effects models were built using the 'lme' function of the nlme package (Pinheiro et al. 2015). The 'relevel' function was used to perform post hoc sequential comparisons among the levels of the fixed factor, and the Holm-Bonferroni method was used to correct the p-values. Spline fittings were carried out with the 'smooth.spline' function. SMW analyses were performed using the freely available 'Bord-ER' software, specifically designed to identify discontinuities along multivariate transect data (accessed at www.staff.u-szeged.hu/~kormoczi/bordER/index.html).

Results

Water regime

Precipitation values of the 12-month periods preceding each vegetation survey indicated that 2013 was more or less an average year (493 mm), while 2014 was much drier (392 mm) and 2015 was wetter (673 mm) than the average (500–600 mm, Biró et al. 2013). The amount of snow in February and March 2013 was unusually high and resulted in extreme floods in the Turjánvidék in the spring of 2013 (personal observation). Thus, 2013 was also considered a humid year. Our groundwater level measurements were in line with this pattern, as the level was very high at the beginning of the growing season of 2013; it dropped sharply during the summer months and by November 2013, it had decreased 65 cm

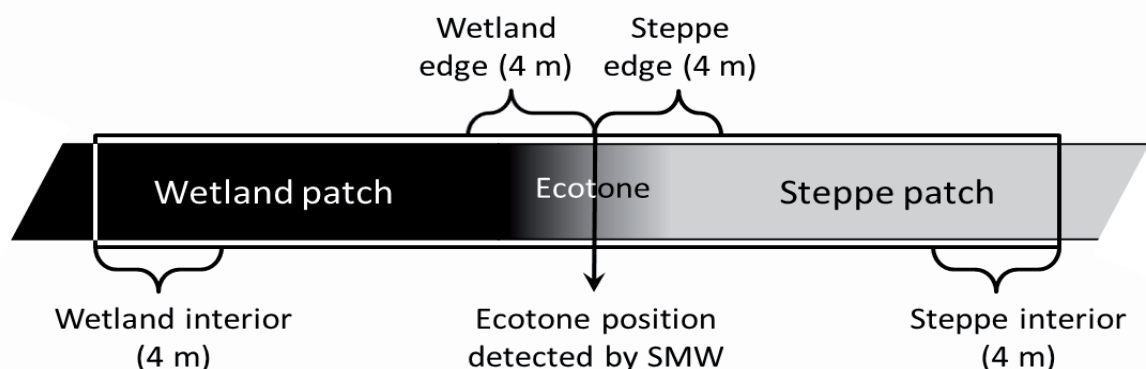


Figure 2. Illustration of the studied parts of the transects. The two adjacent vegetation patches transit into one another through the ecotone. The position where the rate of change in species composition is the highest is defined as the ecotone position; the spatial extent of the ecotone is not defined. Adjacent 4 m wide zones next to the ecotone position are handled as wetland and steppe edges. Steppe and wetland interiors are 4 meter sections at the terminal zones of the transects. The black rectangle indicates the 40 m long transect, aligned perpendicular to the elevation gradient.

below the spring level. Thus, the groundwater level was approximately 35 cm lower in March 2014 than in March 2013. We detected a temporary drop in the level during June and July 2014, but it started to rise again in August, and remained constantly high between September 2014 and April 2015, resulting in conditions similar to the spring of 2013 (Fig. 3). In line with the general humidity patterns of the region, we encountered large stretches of surface water in the lower sections of all transects during the surveys of 2013 and 2015, but surface water was absent in all but one transect (transect 3) in 2014.

Ecotones

We detected significant vegetation ecotones in all the 13 studied transects. These appeared as narrow, unimodal peaks

on the SMW profiles of transects 1, 4, 5, 6, 7, 8, 9 and 11, and unimodal but ragged peaks in transects 2, 3 and 12. In transects 10 and 13, the ecotones were bounded by two significant peaks with sub-zero Z-scores between the peaks (Figs. S2 and S3).

The average differences in ecotone positions were -0.08 m and 0.13 m between 2013 and 2014 and between 2014 and 2015, respectively; neither of these differed significantly from 0 m (one sample t-tests: $t = -0.43, P = 0.67$ for 2014 vs. 2013 and $t = 0.71, P = 0.49$ for 2015 vs. 2014) (Fig. 4A). The average differences in ecotone contrasts were -0.915 between 2013 and 2014 and 0.903 between 2014 and 2015, and both were significantly different from 0 (one sample t-tests: $t = -2.39, P = 0.036$ for 2014 vs. 2013 and $t = 2.75, P = 0.019$ for 2015 vs. 2014) (Fig. 4B), which meant that the contrast de-

Figure 3. Water regime of the study area between June 2012 and May 2015. Bars indicate monthly precipitations; different shadings identify the 12-month periods preceding each field survey (dark grey before the survey of 2013, empty bars before 2014 and light grey before 2015). The black line indicates groundwater levels. Groundwater levels were standardized with respect to the lowest value (November 2014), which was set at zero.

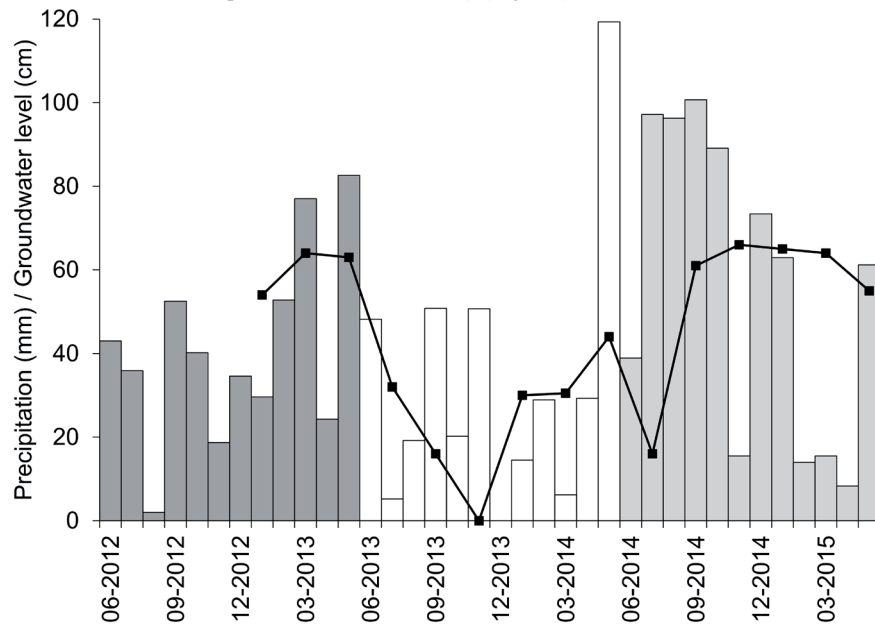


Figure 4. Changes of ecotone positions (A) and ecotone contrasts (B) between consecutive study years. Black dots indicate outliers.

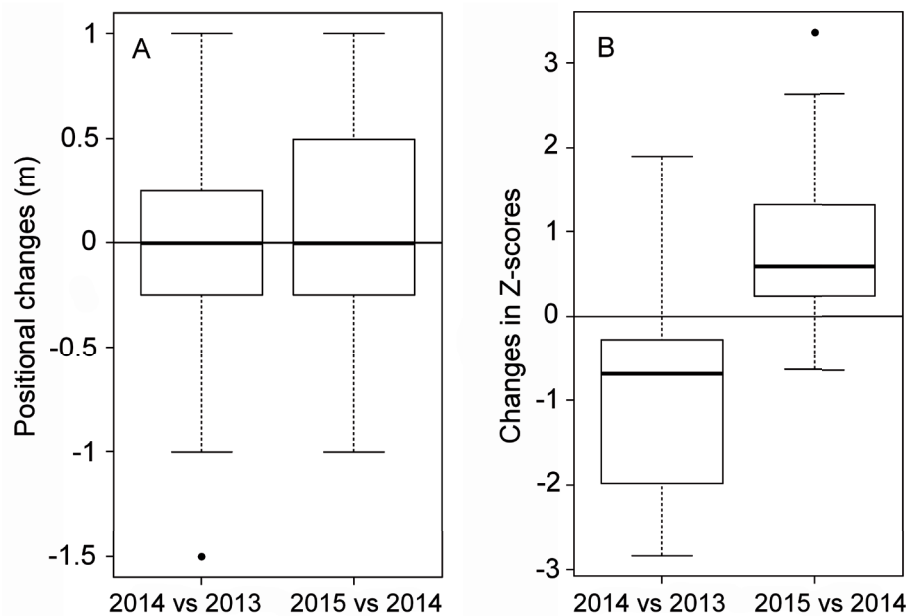
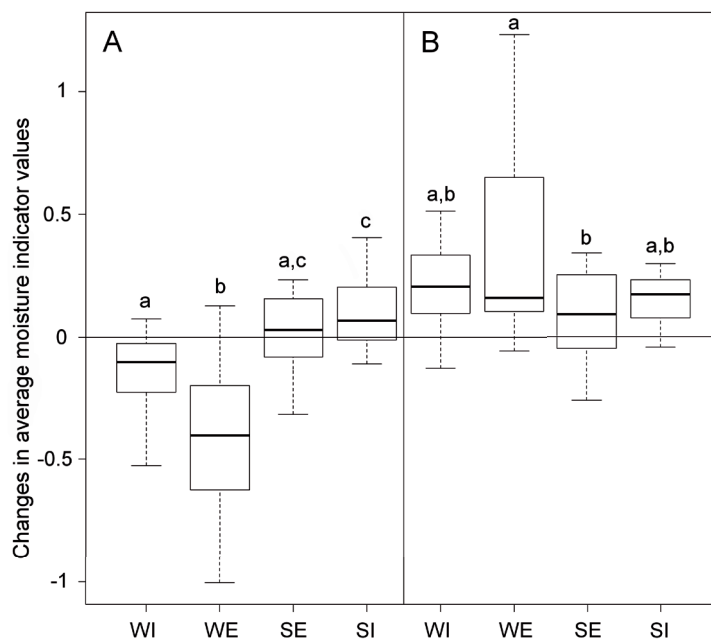


Table 1. Comparisons of the changes of mean Ellenberg-type indicator values of different transect sections to a hypothetical value of zero. *P*-values were calculated using linear mixed-effects models. Asterisks indicate significant differences ($P < 0.05$).

| | 2014 vs. 2013 | | 2015 vs. 2014 | |
|------------------|---------------|----------|---------------|----------|
| | <i>t</i> | <i>P</i> | <i>t</i> | <i>P</i> |
| Wetland interior | -2.21 | *0.034 | 2.70 | *0.011 |
| Wetland edge | -6.37 | *< 0.001 | 4.93 | *< 0.001 |
| Steppe edge | 0.380 | 0.71 | 1.10 | 0.28 |
| Steppe interior | 1.46 | 0.15 | 1.92 | 0.064 |

Table 2. Pairwise comparisons of the changes of mean Ellenberg-type indicator values of different transect sections between consecutive years. *P*-values were calculated using linear mixed-effects models and were corrected with the Holm-Bonferroni method. Asterisks indicate significant differences ($P < 0.05$).

| | 2014 vs. 2013 | | 2015 vs. 2014 | |
|--------------------------------------|---------------|----------|---------------|----------|
| | <i>t</i> | <i>P</i> | <i>t</i> | <i>P</i> |
| Wetland interior vs. Wetland edge | -3.02 | *0.020 | 1.88 | 0.29 |
| Wetland interior vs. Steppe edge | 1.88 | 0.14 | -1.35 | 0.56 |
| Wetland interior vs. Steppe interior | 2.67 | *0.036 | -0.66 | 0.99 |
| Wetland edge vs. Steppe edge | 4.91 | *< 0.001 | -3.23 | *0.018 |
| Wetland edge vs. Steppe interior | 5.69 | *< 0.001 | -2.54 | 0.080 |
| Steppe edge vs. Steppe interior | 0.79 | 0.44 | 0.69 | 0.99 |

**Figure 5.** Changes of mean Ellenberg-type moisture indicator values of different transect sections between 2014 and 2013 (A) and between 2015 and 2014 (B). WI: wetland interior; WE: wetland edge; SE: steppe edge; SI: steppe interior. Boxes with different lowercase letters are significantly different from each other within each subplot.

creased between 2013 and 2014, but increased between 2014 and 2013.

According to the linear mixed-effects model of the changes of the Ellenberg-type indicator values for moisture, wetland edges and wetland interiors had significantly lower values in 2014 than in 2013, while steppe edges and steppe interiors did not show any significant change between these two years (Table 1). The pairwise comparisons between the transect sections revealed that the change of the wetland edges was significantly larger than in all other transect sections, that is, the indicator value of wetland edges decreased more dramatically than in the other transect sections. The change between the steppe interiors and the wetland interiors was

also significantly different, with lower values in the wetland interiors (Fig. 5A; Table 2).

The mixed effects-linear model developed for the changes between 2015 and 2014 indicated that it was again the wetland edges and the wetland interior that had a change significantly different from zero, and this time, the direction of the change was positive (Table 1). The pairwise comparisons revealed only one significant difference; the changes of wetland edges and steppe edges were different, with the wetland edges having higher values (Fig. 5B, Table 2). It should also be noted that the indicator values of the steppe interiors also tended to change in a positive direction, although we detected only a borderline significance. Steppe interiors also had a sig-

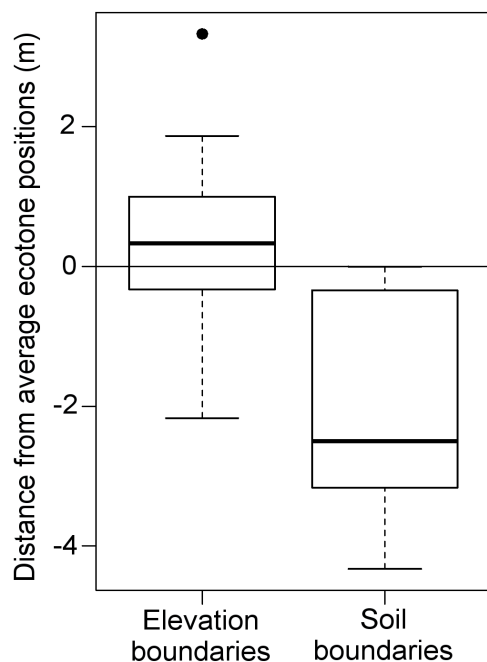


Figure 6. Distance of elevation boundaries and soil boundaries from ecotone positions averaged across the three study years. Positive values indicate uphill locations, negative values downhill locations. Black dot indicates an outlier.

nificantly lower change according to the uncorrected p-value in the comparison to the wetland edges, but this significance was lost owing to the correction.

Considering the amount of plant records belonging to species with extreme values, the linear mixed-effects models indicated that steppe specialists increased between 2014 and 2013 in the wetland edges ($t = 4.23$, $P = 0.001$) but decreased between 2015 and 2014 ($t = -3.62$, $P = 0.004$). Wetland specialists showed an opposite trend, although the p-values were a bit higher ($t = -3.00$, $P = 0.012$ for the change between 2014 and 2013 and $t = 2.31$, $P = 0.041$ between 2015 and 2014).

Elevation boundaries

In most transects, the first derivatives of the smooth splines fitted to the measured elevation values had a single peak near the ecotones (transects 1, 2, 3, 4, 5, 6, 8, 11 and 12), while double peaks were detected in transects 7, 9, 10 and 13, which bounded terrace-like sections around the ecotones (Figs. S4 and S5). However, the SMW profiles of transects 7 and 9 were not structured into double peaks, but had only solitary significant peaks. Taking all transects into consideration, the average position of the elevation boundaries (inclusive of the averaged positions of the double peaks), was, on average, 0.49 m uphill to the vegetation ecotones averaged across the three years (Figs. 6, S2 and S3). This difference did not prove to be significantly different from 0 m (one sample t-test: $t = 1.34$, $P = 0.21$).

Soil boundaries

Soil organic matter contents were typically higher in the wetland side of the transects, while the soil of steppes contained less organic matter (Appendix S6 and S7). The gradient was opposite in transect 5, but we considered this deviation an artefact, as the wetland side of the transect contained an extreme amount of shell fragments of freshwater snails, which increased the non-organic fraction of the soils. Transect 12 also deviated from the general pattern, as, along this boundary, we failed to detect any gradient. The most likely explanation was that this area was regularly ploughed in the past, which homogenised its soil. The low species richness of this transect compared with the other transects also served as evidence for its disturbed history. Thus, only the soil of the remaining 11 transects was considered for the purposes of the study. The first derivatives of the smooth splines of transects 1, 2, 3, 4, 8, 9, 10 and 13 showed single peaks. In transects 6 and 7, the rate of change in organic matter content was rather smooth and had only a low peak. In transect 11, two peaks were detected, one near the ecotone and the other one at meter 12.5. The latter one had no corresponding peak in the SMW profile of the vegetation, so it may be a relict soil boundary from a historical period with a different water regime in that specific area or caused by some other unknown factor.

The average distance between soil boundaries and corresponding average ecotone positions was 1.89 m, with the soil boundaries downhill from ecotone positions (Fig. 6). The differences followed a bimodal distribution probably due to unknown differences in historical water regimes or land use differences. In transects 1, 2, 6, 7 and 11, the soil boundary was close to the ecotone (0–0.87 m), while it was more downhill in transects 3, 4, 8, 9, 10 and 13 (2.5–4.33 m). These differences were compared to 0 m with a Wilcoxon one-sample, signed-rank test, and the result was significant ($w = 45$, $P = 0.008$). In sum, soil boundaries were never uphill from the ecotones and were always downhill from the elevation boundaries (Figs. S2 and S3).

Discussion

In our study, we monitored steppe–wetland transitions of the Turjánvidék for three consecutive years to understand some general mechanisms determining the vegetation dynamics of this mosaic landscape under fluctuating water supply.

According to our results, the scrutinised transitions were not blurred by the unstable water supply, but formed sharp ecotones in the interface of steppe and wetland communities. The emergence of sharp ecotones in natural landscapes is explained by two non-exclusive mechanisms (Lloyd et al. 2000). Several authors emphasize the causative role of abrupt changes in major environmental gradients like microtopography, soil or microclimate (Wierenga et al. 1987, Pärn et al. 2010, Courtwright and Findlay 2011). However, it has been repeatedly shown that sharp ecotones can form along smooth environmental gradients as well (Lennon et al. 1997, Danz et al. 2013). This non-linear response of the vegetation to

environmental variables can be attributed to self-organising processes within the adjacent communities (Milne 1996). Our findings supported the first theory, since we detected peak rates of change along the gradients of both scrutinised environmental variables near the ecotone positions in most transects. The position of the elevation boundaries did not differ significantly from the ecotone positions, so these boundaries seem to be the primary determinants of ecotone position in this landscape.

Our findings also indicated that the position of the detected ecotones was not affected by the water level fluctuations. This spatial resistance of ecotones is similar to our earlier findings, in which we showed that ecotones between dune slack and dune top grassy vegetation in the Danube–Tisza Sandy Ridge did not crawl downslope as a result of long-term groundwater decline, but held their position for over 15 years (Tölgyesi et al. 2016). However, very few other similar findings can be encountered in the literature (but see Bestelmeyer et al. 2006). Perhaps, the reason for this lack of information is not the exceptionality of this dynamics under changing environmental conditions, but the bias in ecotone-related studies for landscapes where communities with strikingly different physiognomies meet at the ecotone. The overwhelming majority of these studies focus on ecotones between woody and grassy communities, where ecotone movements are frequently traced back to the expansion or retraction of the population of one or a limited number of tree or shrub species (among others Báez and Collins 2008, Gastner et al. 2009), which can “drag” the entire corresponding forest/shrub community with themselves (Bruno et al. 2003). Conversely, the communities in our studies were of similar architecture and did not contain strong ecosystem engineering species capable of overwriting each other’s edaphic or microclimatic properties.

Nevertheless, it should be noted that ecotone positions were not completely frozen in our case either; there were slight fluctuations of up to 1–1.5 m in both directions, including uphill movements of some boundaries even in the dry year and downhill movements of some other ones in the wet years. Such subtle random fluctuations of ecotones have also been predicted in simulated ecotones and are mainly explained by stochastic processes (Lennon et al. 1997, Gastner et al. 2009), which the present study supports with empirical data.

The fluctuations of the water regime, however, did not leave the ecotones unaffected. Unlike positions, ecotone contrasts sensitively responded to the changing water availability. In the wet years, the contrast was high, meaning that the compositional difference between the wetland edges and the steppe edges was large, while, in the dry year, the contrast was significantly lower. Despite the short period of the study, the analysis of the Ellenberg-type indicators confirmed that this dynamics were driven by the water supply. Furthermore, this analysis revealed that the mechanism of contrast changes could be traced back to the different behaviour of wetland edges and steppe edges. Mean indicator values did not change much in the steppe edges but the indicator values were high in the wetland edges in wet years and lower in the dry year, indicating that the vegetation of steppe edges was resistant to the hydrologic fluctuations, while wetland edges sensitively

followed the water availability. Wetland interiors showed lower magnitudes of change than wetland edges, and steppe interiors tended to be less static than steppe edges; thus, we conclude that the outlined contrast dynamics was restricted to the dynamics of the vegetation around the ecotone positions and did not involve the entire patches, corroborating the concept that ecotones are indeed hotspots of the response of the vegetation to the fluctuating water regime.

According to the models developed for the steppe and wetland specialists, wetland edges exhibited a complete compositional transformation between the years, as the encroachment of steppe specialists came along with the retraction of wetland specialists and vice versa. Interestingly though, the changes are restricted to only one side of the ecotones, the wetland edges. This spatial heterogeneity of ecotone dynamics indicates that the interaction of wetland and steppe communities highly depends on the sensitivity of their edges to edge effects (in this case the effect of the humidity conditions of the neighbouring community).

The high sensitivity of wetland edges to drier, steppe-like water regime and the low sensitivity of steppe edges to wetter, wetland-like conditions imply the dominance of steppes over wetlands in their interaction. The fact that the vegetation of wetland edges can become similar to steppe edges in dry years can serve as a possible explanation why some parts of the soil of the wetland edges are also steppe-like. However, the steppe-like soil conditions, which may have as well been caused by processes like erosion, could also make wetland edges more prone to edge effects. Thus, the cause-effect relationship between the behaviour of the wetland edges and the observed soil patterns is difficult to disentangle; they probably mutually influence each other. In other words, soil boundaries may have been pushed downslope relative to the ecotones by the edge effect of the steppes and/or other factors like erosion, but the resulting soil conditions may have also reinforced the sensitivity of the wetland edges to edge effects.

Processes related to ecotones are rarely explained with dominance relationships between the adjacent communities, although one of the communities is frequently considered dominant over the other one without giving voice to this. In many cases, especially in the already mentioned forest–grassland ecotones, the dominance of forests is taken as granted. The movements of tree lines (e.g., Gehrig-Fasel et al. 2007) or the encroachment of woody species across the borders of forest gaps (Copenheaver et al. 2004) are frequently studied without mentioning any chance for the propagation of grassland species into forested areas, leading to the consequential displacement of the woody community. This concept implies the dominance of woody communities over grassy ones in their interaction. However, we showed in the present study, that this relationship is not limited to communities with strikingly different physiognomies and to communities characterized with ecosystem engineering species, but can also be present between communities with similar physiognomies, even though the hierarchy is more likely to affect ecotone contrast than ecotone position.

In summary, we conclude that the steppe and wetland patches of the studied mosaic landscape are delimited by sharp ecotones. The position of these ecotones is determined by an environmental gradient, the microtopography, while a seemingly important factor, the fluctuating water supply, does not influence the position; thus the patch pattern of the landscape is rather rigid. Ecotone contrast is the reactive parameter of the ecotones to the changing water supply, and the mechanism of this dynamic response can be traced back to asymmetric sensitivities of the edges to edge effects, leading to a seemingly dominant behaviour of steppes over wetlands at the ecotones.

Besides the basic ecological importance, the presented mechanisms have some implications for nature conservation and future restoration plans of the Turjánvidék and similar wetland–dry grassland mosaics. The high sensitivity of wetland edges to dry conditions call attention to their vulnerability if draughty periods get more severe, which is very likely since the entire Danube-Tisza Interfluve is facing a long-term aridification (Kertész and Mika 1999, Ladányi et al. 2015). Little wetland patches are particularly in danger, because the edge/interior ratio increases with decreasing patch size. Nevertheless, our results suggest that short wet periods do not threaten the biodiversity of steppe patches, whatever small their size is.

Fortunately, large-scale measures to restore the water supply of the Danube-Tisza Sandy Ridge are on the way in the form of high-budget EU projects. The higher flexibility of wetland edges mean that they are likely to react to these interventions promptly, which is corroborated by the fact that the regeneration potential of wetlands after disturbance is also better than that of steppes (Tölgyesi et al. 2015). However, the expansion of wetland patches cannot be expected in the short run. Thus, for monitoring short-term effects of such actions, the best indicator remains ecotone contrast, whose value will increase if the water supply of wetlands increases. For this monitoring, we recommend establishing permanent plot pairs with one plot in a wetland edge and its pair one next to it in the steppe edge, and using the compositional difference as the indicator of restoration efficiency. This method can also be useful to assess how far the influence of a wetland restoration measure reaches from its immediate target zone.

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Electronic appendix

Figures S1–S7 may be downloaded from www.akademai.com.