

Unexpected ecotone dynamics of a sand dune vegetation complex following water table decline

Csaba Tölgyesi^{1,*}, Márta Zalatnai¹, László Erdős¹,
Zoltán Bátorfi¹, Nicole Rosemary Hupp² and László Körmöczi¹

¹ Department of Ecology, University of Szeged, Szeged H-6726, Hungary

² Wildlife Biology Program, College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, Montana, MT 59812, USA

*Correspondence address. Department of Ecology, University of Szeged, 52 Közép fasor, Szeged H-6726, Hungary. Tel: +36-62-546-951; Fax: +36-62-546-949; E-mail: festuca7@yahoo.com

Abstract

Aims

Central Hungarian inland dune ranges harbor heterogeneous grassland vegetation with an extensive network of ecotones, arranged perpendicular to topography-driven hydrologic gradients. The area suffers from severe aridification due to climate change and local anthropogenic factors, which have led to a dramatic decline of the water table. As a result, groundwater is no longer reachable for low-lying plant communities; thus, we expect they are bound to undergo profound changes. This study investigates how the plant communities respond to this changing environment over time by monitoring ecotones, since they are frequently the hotspots of ecosystem change. We monitored five ecotones along permanent belt transects for 15 years to characterize their dynamic response, and to identify the internal structural changes of the plant communities the ecotones delimit.

Methods

Ecotones were delineated with the split moving window technique. The dynamics of two ecotone parameters, location and contrast, were analyzed with linear regression models incorporating two independent variables: study year as a measure of time since the loss of groundwater, and precipitation as a possible driver of inter-annual variations. The internal changes of the patches separated by the ecotones were analyzed using plant functional groups.

Important Findings

Precipitation had no detectable effect on the ecotone descriptors, but study year influenced ecotones in an unusual fashion.

The position of the ecotones appeared to be very stable in time; their dynamics are stationary, not directional as we predicted. The contrasts had clear tendencies; two ecotones disappeared, one new one was formed and two ecotones showed no trend. The internal changes of the patches over time were dramatic, showing a shift toward more xeric and more open plant assemblages in most stretches of the transects. Thus, the dynamic response of the vegetation was not patch expansion vs. shrinking, but fusion vs. division, which profoundly restructured the vegetation pattern. Analysis of plant functional groups revealed that the trends of the ecotone contrasts could be traced back to internal changes of the patches and not to processes within ecotones. Hence, in situations where stationary ecotone dynamics prevail, ecotone position may be a poor indicator of the effects of strong directional environmental changes. However, in this study we show that ecotone contrast can serve as a sensitive tool for monitoring landscape pattern transformations in these cases. Also, this highlights the long-term nature of ecotone responses, which can have implications in landscape planning and restoration measures.

Keywords: groundwater decline, plant functional group, sand dune vegetation, split moving window, stationary ecotone

Received: 1 September 2014, Revised: 27 February 2015,
Accepted: 13 March 2015

INTRODUCTION

The vegetation of landscapes is complex and rarely homogeneous. Basically, vegetation contains two kinds of components: patches and intervening ecotones. Ecotones are transitional

zones where spatial changes occur more rapidly than inside the areas they separate and connect (Cadenasso *et al.* 2003; Erdős *et al.* 2011a; Risser 1995; Yarrow and Marín 2007). Ecotones are dynamic entities with the potential to vary temporally (Cadenasso *et al.* 2003; Strayer *et al.* 2003; Wiens *et al.* 1985),

though the scope of many studies is not large enough to capture variation in ecotones over time. This tendency to change over time, combined with the reality that species may be at their physiological limits in these transitional zones, can make ecotones sensitive indicators of local and global environmental changes (Fortin *et al.* 2000; Goldblum and Rigg 2005; Gosz and Sharpe 1989).

Peters *et al.* (2006) outline three main types of spatial ecotone dynamics: stationary, directional and shifting. These types are different in the nature of their driving forces and the constraints they face. There are, however, additional parameters besides location that carry useful information about ecotones, but they are less commonly emphasized in studies of ecotone dynamics. For example, contrast, i.e. the compositional difference between the plant communities separated by the ecotone (Strayer *et al.* 2003), is an interesting example of a parameter that can change through time. Studying such additional parameters requires long-term and very fine-grained vegetation data, which are challenging to collect. This difficulty can be avoided to a certain extent by using space-for-time substitutions (e.g. Boughton *et al.* 2006). There are limitations to these substitutions, though. Handling parameters of ecotones from different localities as if they belonged to the time series of the same ecotone is subject to uncertainties, because there may be differences in the local factors influencing each ecotone individually (cf. Gosz 1993). Furthermore, space-for-time substitution study designs are not suitable for detecting spatial ecotone movements, because no spatial trend can be inferred from the positional data of different and independent ecotones. Hence, there is a need for long-term studies that monitor ecotones on permanent sampling areas to gain a comprehensive understanding of the multiple

aspects of ecotone dynamics (Hufkens *et al.* 2009; Ludwig and Cornelius 1987).

A suitable location for a long-term monitoring study design is the Kiskunság Sandy Ridge of Central Hungary, which is a sandy alluvial fan located between the rivers Danube and Tisza (Fig. 1). These dune ranges are predominantly covered by wooded steppe vegetation. Though the plant communities in the study region are variable, the steppe is mostly comprised of dry, grassy vegetation on the sand dunes which transition into less xeric plant assemblages in the dune slacks and grooves. The result is a patchy landscape where ecotones exist in the interface between the two grassland patch types. The Kiskunság Sandy Ridge, along with most regions in SE Europe, suffers from aridification caused by the combined effects of climate change (Kertész and Mika 1999) and local anthropogenic factors, like the maintenance of draining canals, the extensive exploitation of groundwater for irrigation and the high transpiration rate of newly established exotic tree monocultures (Berényi and Erdélyi 1990). As a result, the water table has dropped dramatically and affected the entire Kiskunság Sandy Ridge. The process became detectable in the mid-1970s, and by the end of the 20th century the groundwater level had decreased by 2–4 m on average (Kertész and Mika 1999; Zsákovics *et al.* 2007). This drop in water availability has had profound consequences for the local biota. These changes in the environment have created an interesting opportunity for long-term ecological research projects to focus on a broad range of issues, including habitat loss, alterations in productivity, plant invasions and socioeconomic factors (Kovács-Láng *et al.* 2008).

Considering the above-described dynamic nature of ecotones, we expect the ecotones in the Kiskunság Sandy

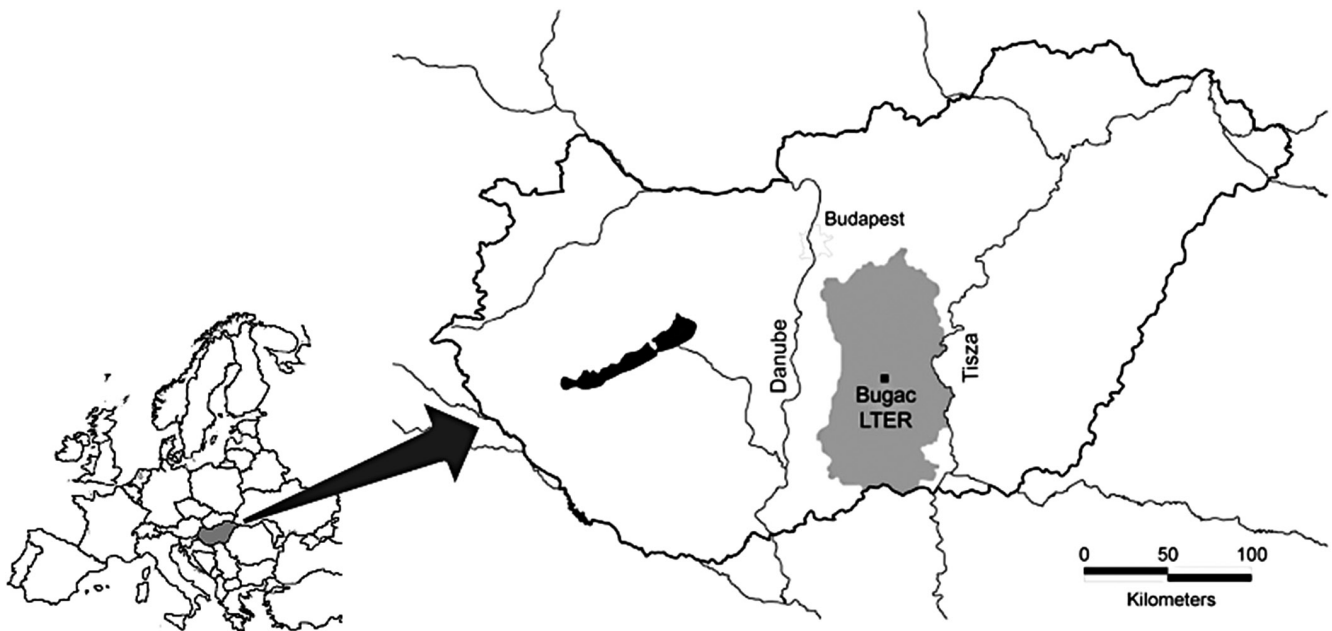


Figure 1: location of the Bugac long-term ecological research site (LTER) site in the Kiskunság Sandy Ridge (gray territory).

Ridge to be highly responsive to the drying conditions. For this reason we monitored a number of ecotones in a sandy steppe area near the village of Bugac for 15 years and aimed to characterize their dynamic properties. We also identified potential trends that can have community and landscape level consequences for the vegetation of the Kiskunság Sandy Ridge. Specifically, we addressed the following questions: (i) Does annual precipitation explain a significant proportion of the inter-annual variation of the two ecotone parameters of interest, spatial ecotone dynamics and contrast? (ii) Can directional movements of the ecotones be detected during the 15-year study period? (iii) Does the contrast these ecotones bridge show distinct trends? (iv) Are there detectable structural changes within the patches delimited by the ecotones?

MATERIALS AND METHODS

Study area

The study was carried out on the long-term ecological research site (LTER) of the University of Szeged, located in the middle of the Kiskunság Sandy Ridge, N46.697 E19.602, 110 m a.s.l. (Fig. 1). The climate of the area is continental with some sub-Mediterranean influence, and the area belongs to the wooded steppe biome (Magyari *et al.* 2010). In the last 30 years the mean annual precipitation and temperature of the site were 574 mm and 11.4°C, respectively. The precipitation has extreme inter-annual variations, ranging from 295 mm (in 2001) to 835 mm (in 2010) (Fig. 2). The topography of the area is mostly undulating small sand dunes and wind-grooves, with a difference of up to 3 m between the highest and lowest points. Until the early 1980s the water table lay only a few decimeters below the surface of the grooves (Körmöczi 1991) but then it receded abruptly in the following years. At our study site, there is a groundwater well extending 3 m below the lowest point of the study area that has not reached the water table since at least 1990. This means

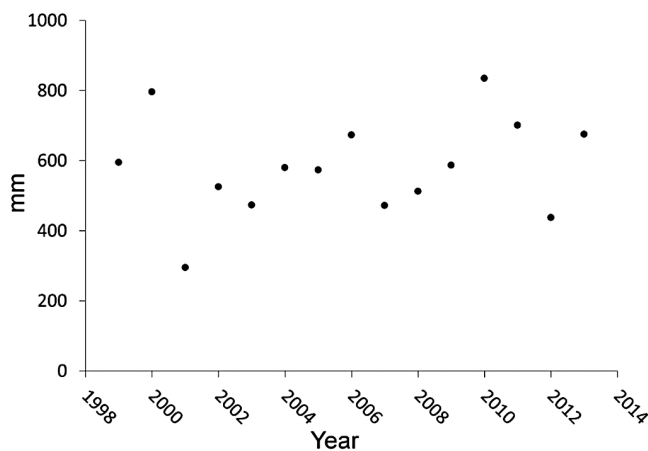


Figure 2: annual precipitation of the Bugac LTER site between 1999 and 2013. Precipitation for year X is expressed as the amount between the June of year X-1 and the May of year X.

that the groundwater has probably not been reachable by the roots of the grassland species in the area for at least 20 years.

The soil of the highest points is pure sand with low humus content and low water-holding capacity, whereas the soil of the lower points contains more organic matter and has a more favorable water balance for plant growth (Körmöczi 1983). Due to climatic and edaphic conditions, the higher parts of the dunes are covered with various forms of the psammophytic *Festucetum vaginatae* Rapaich ex Soó 1967 plant association, which is dominated by xerotolerant perennial grasses and forbs and a dense layer of cryptogams. Elements of the *Secali sylvestris-Brometum tectorum* Hargitai 1940 association, a community rich in pioneer species, are also wide-spread in the driest parts of the area. The grooves and dune slacks used to contain the hydric *Molinio-Salicetum rosmarinifoliae* Magyar ex Soó 1933 association, but these patches have become much drier since the water table declined. A description of the plant communities can be found in Borhidi *et al.* (2012). The environmental conditions and vegetation ecology of the Kiskunság Sandy Ridge are thoroughly discussed by Molnár (2003).

Data collection

We sampled vegetation within two belt transects between 1999 and 2013. The first transect, hereafter called the long transect (55 × 1 m), was oriented from NW to SE. It started on a small, undulating hump then sank into a deep dune slack, traversed the highest dune of the area and ended in a flat zone with intermediate elevation (see also Torma and Körmöczi 2009). The second transect, hereafter called the short transect (30 × 1 m), was oriented from NE to SW. This transect started on a dry ridge with a slightly uneven surface, and ended in a flat depression (see also Zalatnai and Körmöczi 2012). Both transects ran perpendicular to the elevation contour lines, i.e. they were gradient oriented, offering the most efficient layout to characterize the compositional patterns of the vegetation caused by elevation gradients (Gillison and Brewer 1985). We divided each transect into a contiguous grid of 0.25 × 0.25 m microquadrats, resulting in 880 (220 × 4) microquadrats in the long transect and 480 (120 × 4) in the short transect. In each microquadrat, we collected presence/absence data of every vascular plant species, lichen species and moss species. The vegetation data in the four parallel microquadrats of every 0.25-m section of the transects were later merged; so the abundance value of each species could vary between 0 and 4 in every 0.25 × 1 m kernel. We surveyed the vegetation in the long transect every spring (late May/early June) between 1999 and 2013 except in 2010. We sampled the short transect every spring between 2003 and 2007 but later only in 2009 and 2013.

Data processing

We used the split moving window (SMW) analysis (Ludwig and Cornelius 1987; Webster 1978) to locate the ecotones and to determine the cross-ecotone difference (or contrast)

the ecotones bridge between the neighboring patches (Strayer *et al.* 2003). In SMW analysis, a dissimilarity function is calculated to describe the difference in floristic composition between two halves of a window of set size (window width). These windows are moved along the transect with constant intervals (0.25 m in the present layout) from one end of the transect to the other, resulting in a dissimilarity value for every window mid-point. We used the squared Euclidean distance as the dissimilarity function because it has been shown to efficiently identify vegetation ecotones (Erdős *et al.* 2014; Johnston *et al.* 1992; Wierenga *et al.* 1987). To distinguish between significant ecotones and dissimilarity peaks created by random chance, we carried out a Monte-Carlo randomization procedure. According to Fortin *et al.* (1996) randomizations that apply certain spatial constraints during the shuffling procedure are more efficient in testing the peaks than complete randomizations. Therefore, we chose the random shift method, in which the abundance pattern of each species is shifted along the transect randomly. The sections overhanging the transect due to the shifting were cut off and replaced to the other end of the transect. Thus, the distribution pattern of every species was preserved as much as possible but the spatial correlations of these patterns—a necessary condition for the emergence of ecotones—were lost. After carrying out the randomizations, the observed dissimilarities were Z-transformed by subtracting the overall expected mean (the mean of all dissimilarities, including the observed ones and the random ones, gained from 1000 randomizations) from the observed dissimilarities, and dividing the results by the overall expected standard deviation (Cornelius and Reynolds 1991). Z-scores above 1.65 were considered significant (Boughton *et al.* 2006; Erdős *et al.* 2011b; Hennenberg *et al.* 2005). To avoid arbitrarily choosing window sizes, we calculated the Z-scores for every window size between 1 and 20 (i.e. from 0.25 to 5.00 m) and carried out a preliminary evaluation by checking them separately. Larger window sizes were not considered because they would have been unable to detect ecotones near the end points of the transects. As expected, small window sizes were sensitive to noise (cf. Brunt and Conley 1990), thus the four smallest widths were discarded. While increasing the window widths from 5 till 20, we observed that certain peaks in Z-scores disappeared, whereas some others remained relatively constant or even increased. According to the SMW simulations by Erdős *et al.* (2013) those peaks that disappear have small-scale importance, which we considered in the present case as intra-patch heterogeneity and disregarded them. Those peaks that proved consistently significant with a wide range of window widths were accepted as real inter-patch ecotones. No ecotone that was significant with window width 10 (i.e. 2.5 m) dropped below the significance level when the window width was further increased; however, their location was subject to minor changes. We attributed this effect to the decreasing influence of noise. Thus, the position of the peaks with the largest window width, i.e. with window width 20, were used to mark the position of the

ecotones along the transects. If a significant ecotone position was located, we identified all corresponding peak positions in the entire time series regardless of their significance, to see the history of the underlying compositional dissimilarity. The compositional dissimilarity between the adjacent patches (i.e. the ecotone contrast) was expressed with the Z-scores of the above-described peaks at window width 20.

After identifying the ecotone locations and Z-scores of the corresponding peaks for each year, we performed multiple linear regressions with stepwise selection using SPSS 11.5 (SPSS Inc.) to characterize their dynamics in relation to study year and annual precipitation. Study year was used to approximate the amount of time since the water table dropped below available depth, whereas the annual precipitation was used as a possible explanation for the inter-annual fluctuations of the ecotones. The annual precipitation values covered 12-month periods from June to May. No collinearity existed between the two predictors.

Dynamics of ecotones cannot be fully understood without characterizing the adjacent patches (Fagan *et al.* 2003); therefore, we compared the floristic composition of the two window halves at the ecotones in years that held special importance according to the detected trends of the ecotone properties. Instead of examining all species separately, we sorted them into functional groups using similar guidelines as Kirkman *et al.* (1998) and Cornelius *et al.* (1991). We distinguished six main functional groups: xeric perennials, mesic perennials, xeric annuals, mesic annuals, ephemerals and cryptogams. The distinction between xeric and mesic species was based on Borhidi's relative indicator values for moisture (Borhidi 1995), which is the adaptation of Ellenberg's indicator values for moisture (Ellenberg 1952; Ellenberg *et al.* 1992) for the Hungarian flora. This indicator system expresses the moisture demand of each species along a 12-grade ordinal scale, where low scores are allocated to species with low moisture demand and higher scores to species with higher moisture demand. Species with scores from 1 (plants of extremely dry habitats) to 5 (plants of semi-humid habitats) were typical of the transects. As a rule of thumb, we treated species with scores 1 and 2 as 'xeric', while those with higher scores as 'mesic'. Ephemerals and cryptogams were lumped together, since they both depend on open surfaces to grow, which is their most relevant characteristic in the present situation. We provided the absolute numbers of occurrences, since not only the relative but also the absolute changes were interesting for understanding the processes.

RESULTS

Detected ecotones and their dynamics

The SMW tests identified four positions along the long transect where significant ecotones occurred in at least one of the study years (Fig. 3). The first ecotone was located on a gentle, south-facing slope between meters 6.0 and 6.5. The Z-scores of this dissimilarity were above 1.65 only in four early years

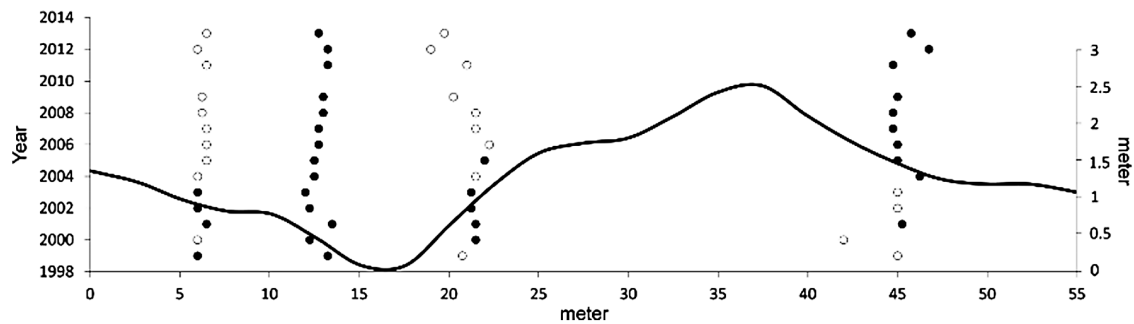


Figure 3: ecotone profile of the long transect. Full circles indicate the positions of significant ecotone centers, empty circles indicate non-significant but corresponding dissimilarity peaks. The black line illustrates the relief of the transect (not to scale).

(in 1999, 2001, 2002 and 2003) of the study, though the position of all corresponding non-significant peaks in subsequent years remained highly constant, with a standard deviation of only 0.24 m. According to the regression model of the positions, neither predictor, precipitation and year, had a significant effect. The Z-scores, however, showed a significant negative relationship with year ($R^2 = 0.675$, $B = -0.146$ unit/year, $t = -4.779$, $P = 0.001$), indicating that the difference between the two sides of the ecotone gradually disappeared (Fig. 4a). Annual precipitation was excluded from the model, as its effect was not significant.

The second ecotone, located on a south-facing slope between meters 12.0 and 13.5 (SD = 0.45 m) had persistently significant Z-scores (Fig. 4b). Neither predictor had a significant effect on its parameters according to the multiple linear regression analysis.

The third ecotone was located on a north-facing slope between meters 19.0 and 22.25 (SD = 0.88 m) and was significant only in the first half of the study (in years 2000–03 and 2005), while in the second half the Z-scores of the corresponding peaks fell below significance level (Fig. 4c) and the variance of their position increased, while the ecotone seemed to shift downhill. The regression models confirmed year as a significant predictor of both position ($R^2 = 0.312$, $B = -0.109$ m/year, $t = -2.333$, $P = 0.038$) and Z-score ($R^2 = 0.498$, $B = -0.177$ unit/year, $t = -3.447$, $P = 0.006$), but precipitation had no significant effect in these cases either.

The fourth ecotone, whose peaks scattered between meters 42.0 and 46.75 (SD = 1.05 m), at the foot of a south-facing slope, showed an opposite trend: the peaks were not significant in some early years (in 1999, 2000, 2002 and 2003) but later on the increasing Z-scores indicated a clear, significant ecotone (Fig. 4d). The regression models for the position of this ecotone were not significant for either predictor; the Z-scores were significantly influenced only by the year ($R^2 = 0.443$, $B = 0.112$ unit/year, $t = 3.087$, $P = 0.009$). The relationship was positive, indicating that the contrast increased between the adjacent stretches of the transect during the study period.

In the short transect there was only one detectable ecotone, located between meters 15.0 and 18.75 (SD = 1.41), in the lower section of the only apparent slope of the transect

(Fig. 5). The dissimilarity peaks were found above the significance level in all surveyed years (Fig. 4e) but their position had a high variance. According to the multiple linear regression models, neither predictor had significant effect on either of the studied descriptors of this ecotone.

Comparisons by functional groups

The absolute numbers of plant occurrences that served as a basis for the comparisons can be found in Table 1. To compare functional groups, we looked into the structural changes of the vegetation units on the two sides of an ecotone. For the first ecotone, we utilized data from 2001 and 2013, because the Z-score was highest in 2001 and lowest in 2013. In 2001, mesic perennials were five times more abundant in the second window half than in the first half. By 2013 they had declined dramatically in both halves, yet the decline was more severe in the second half of the window. The amount of xeric perennials was more or less constant over time, with slightly higher amounts in the second window half. Mesic annuals, just like mesic perennials, were more common in the second window half; their amount decreased in the first window half, but interestingly they showed a moderate increase in the second one. Xeric annuals behaved as expected, with some increase in both halves over time. Ephemerals and cryptogams exhibited an almost 2-fold increase in the first window half and a >4-fold increase in the second one, resulting in similar final amounts in 2013.

The Z-scores of ecotone 2 showed no trend; therefore, the first and the last years of the study were chosen for comparison. The second half of the window was located in the lowest point of the transect; so it was expected to be moister than the first window half. Mesic perennials were the most numerous functional group on both sides but they decreased by >50% in the first window half and remained relatively unchanged in the second one. Xeric perennials, a group with an intermediate share in both halves of the window in 1999, had doubled by 2013 in the second half of the window. Both annual groups were more abundant in the first half of the window, and their abundance hardly differed between 1999 and 2013. In contrast, ephemerals and cryptogams increased over time in both window halves considerably, though they also had higher numbers in the first window half.

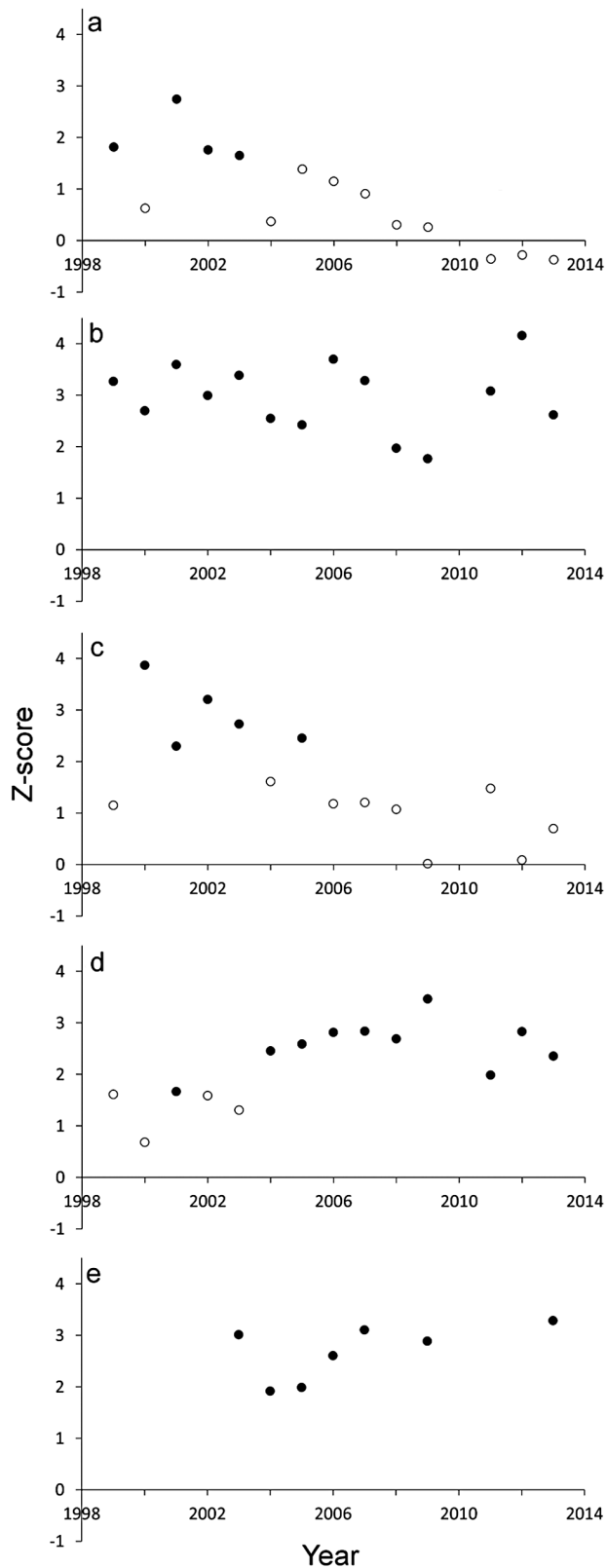


Figure 4: Z-scores of the five monitored ecotones according to years. Full circles indicate significant dissimilarity peaks, empty ones indicate non-significant peaks. Diagrams from a to e correspond to ecotones 1–5, respectively.

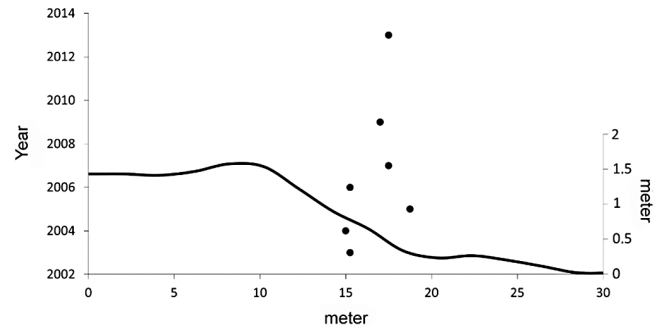


Figure 5: ecotone profile of the short transect. Full circles indicate the positions of the ecotone centers in the studied years. The black line illustrates the relief of the transect (not to scale).

The third ecotone gradually disappeared during the study; therefore, an early year with the highest Z-score (year 2000) and a late year with the lowest Z-score (year 2009) were used for comparison. As expected, the most dominant group of the first window half was the mesic perennials but they showed an obvious decline between the two chosen years. Mesic perennials were also common in the second window half, but their abundance remained constant over time. There were roughly twice the amount of xeric perennials in the second window half than in the first window half in 2000, but by 2009 their abundance in the first half doubled, which resulted in very similar amounts in both sections. Mesic annuals decreased markedly in both window halves but their relative amounts stayed more or less unchanged. Xeric annuals were absent in 2000 in both halves and were rare in 2009 as well. Ephemerals and cryptogams were very scarce in the first window half and had moderate amounts in the second one in 2000. By 2009 their amount increased in both halves considerably.

The Z-scores of ecotone 4 showed a significant increase during the study period; therefore, the years with the lowest and highest Z-scores (2000 and 2009, respectively) were chosen for comparison. Mesic perennials were twice as common in the second window half than in the first window half in 2000. Due to their parallel decrease over time, this relative difference increased to almost 6-fold by 2009, while the absolute difference had not changed much. The amount of xeric perennials was higher in the first window half than the second half, and their amounts did not notably change between the 2 years. Mesic annuals were more numerous in the second window half than the first, and their absolute amount decreased a bit in both sections. In 2000, xeric annuals were not common in the first section and were especially rare in the second one, but their amounts doubled in the first section by 2010, making them one of the dominant groups, while they remained low in the second section. Ephemerals and cryptogams had similar amounts in both window halves in 2000 but their amounts increased by 2009 in the first window half while they stayed the same in the second.

The only ecotone of the short transect (ecotone 5 in Table 1) showed no detectable trend; therefore, the first and the last

Table 1: absolute numbers of plant occurrences sorted according to functional groups within the window halves at the ecotone peaks in years that have special importance in the dynamics of the ecotones

Ecotone 1				
Year	2001		2013	
Window halves (m)	1.0–6.0	6.0–11.0	1.5–6.5	6.5–11.5
Mesic perennials	27	136	16	30
Xeric perennials	148	198	153	165
Mesic annuals	47	85	28	137
Xeric annuals	136	43	182	82
Ephem. and Crypt.	221	89	382	376
Ecotone 2				
Year	1999		2013	
Window halves (m)	8.25–13.25	13.25–18.25	7.75–12.75	12.75–17.75
Mesic perennials	362	483	150	451
Xeric perennials	93	86	96	176
Mesic annuals	141	91	136	92
Xeric annuals	39	3	44	5
Ephem. and Crypt.	165	42	318	158
Ecotone 3				
Year	2000		2009	
Window halves (m)	16.5–21.5	21.5–26.5	15.25–20.25	20.25–25.25
Mesic perennials	522	148	324	160
Xeric perennials	84	209	153	173
Mesic annuals	125	109	47	57
Xeric annuals	0	0	1	8
Ephem. and Crypt.	10	89	86	166
Ecotone 4				
Year	2000		2009	
Window halves (m)	37.0–42.0	42.0–47.0	40.0–45.0	45.0–50.0
Mesic perennials	106	253	31	185
Xeric perennials	133	61	104	76
Mesic annuals	86	123	54	96
Xeric annuals	54	9	99	18
Ephem. and Crypt.	98	85	151	74
Ecotone 5				
Year	2003		2013	
Window halves (m)	10.25–15.25	15.25–20.25	12.5–17.5	17.5–22.5
Mesic perennials	233	415	110	357
Xeric perennials	135	232	215	247
Mesic annuals	57	21	37	17
Xeric annuals	2	0	59	2
Ephem. and Crypt.	159	73	274	151

study years were compared. This ecotone was similar to ecotone 2 of the long transect as it was also located between a south-facing slope and a low-lying, wet section, thus the changes over time were also similar. Mesic perennials decreased considerably in the first window half over the years, and there was a moderate decrease in the second half as well. Interestingly, xeric perennials were found more abundant in the second section than the first in 2003, but over time their amount increased in the first half while remaining constant in the second, consequently their amounts were nearly identical in 2013. Mesic annuals were scarce in both sections and their amount showed little variation between the two examined years. Xeric annuals, which were practically absent in both sections in 2003, increased in the first window half but not in the second one. Ephemerals and cryptogams were quite common in the first window half and had a moderate share in the second one in 2003. By 2013 they had doubled in both sections, which made them the most dominant group in the first section and a common one in the second.

DISCUSSION

In our study we monitored five ecotones located between herbaceous plant assemblages with different water regimes. The dynamics of two ecotone parameters, namely position and contrast, were studied in relation to annual precipitation and study year. We could not confirm that annual precipitation is a significant driver of the inter-annual variation of either ecotone parameters. However, this does not necessarily mean that precipitation has no effect on the ecotones but only that the assumed relationship is not this direct. The precipitation of earlier years may modulate the effect of the precipitation of the current year and it is also likely that the within-year distribution of precipitation is of great importance (Gosz 1993).

As for the relationship between study year and ecotone position, only one ecotone showed significant directional spatial change, and even in this case it was apparent only when the contrast became low, i.e. when the compositional dissimilarity was not significant any more. The other ecotone positions showed no temporal trend but were stable in space, with extremely low variation in ecotones 1 and 2 and somewhat higher in ecotones 4 and 5. This behavior after a dramatic change of a key environmental factor confirms that these ecotones fall into the category of stationary ecotones, as described by Peters *et al.* (2006). According to them, stationary ecotones are typical along abrupt geomorphologic gradients where major differences in environmental factors lead to spatial changes in the vegetation pattern. Basically, this used to be true for the plant assemblages of the Bugac LTER as well, since lower points were very close to the water table, while higher ones benefited much less from its effect. This environmental difference, which is widely accepted as a major reason for the heterogeneity and ecotone formation of sand dune areas (Körmöczki 1991; Munoz-Reinoso and Novo 2005), had vanished several years before the study period. But why did the position of the ecotones not react to this? The long existence of the hydrologic gradient between lower and

higher zones could result in different plant production rates and nutrient flows, which could bring about different organic matter contents and physicochemical soil properties (Munoz-Reinoso 2009). This has been confirmed for the short transect with actual soil analyses as well (Zalatnai and Körmöczki 2012). Such soil patterns can persist for a long period of time even after the supporting mechanisms cease to function (Carter 1994), which reduce the potential reactivity of ecotone positions to the changes in the primary environmental factors. Moreover, it has been shown that some microclimatic differences still exist between the lower and higher points of the area. Bátori *et al.* (2014) detected significant differences between the daily temperature and relative humidity cycles of the lower and higher points of the long transect. This was especially distinct during night measurements, when the frequently still air led to the formation of a cold air puddle with 100% relative humidity in the depression between ecotones 2 and 3; this phenomenon was independent of the water table.

Furthermore, it should be mentioned that in most studies reporting directional ecotone movements, the adjacent vegetation patches had very different physiognomies, such as alpine grasslands vs. mountain forests (e.g. Gehrig-Fasel *et al.* 2007; Stanisci *et al.* 2000) or dry grasslands vs. dry scrubs (e.g. Gosz 1993, Grover and Musick 1990, Mueller *et al.* 2007). In such cases ecotone movements can at least partly be traced back to the population dynamics of one or a very limited number of woody species. The advance of these species can make the occupied area uninhabitable for grassland species and can facilitate the colonization of woodland or shrubland species (cf. Bruno *et al.* 2003), which leads to the expansion of the entire forest or shrub community, and hence to the movement of the ecotone at their edge. In the present study, however, the physiognomical differences were mild and there were no dominant, ecosystem engineering species, which also hampered spatial ecotone movements.

In contrast to ecotone position, the other ecotone parameter, contrast, showed clear trends in three of the five ecotones. These trends resulted in the disappearance of two ecotones (ecotones 1 and 3) and the emergence of a new one (ecotone 4). This means that the plant assemblages on the two sides of ecotone 1 and ecotone 3 gradually became very similar to each other, whereas a formerly low dissimilarity in ecotone 4 gradually became an obvious ecotone.

Finding an explanation for these trends is challenging if looking at the ecotones exclusively; therefore, we performed a 'manual' analysis of the internal structure of the vegetation patches using plant functional types. These comparisons revealed that despite the stability of the ecotone positions, the adjacent plant assemblages underwent profound transformations. Two general tendencies could be identified: the vegetation has become drier and more open. These components of aridification have also been recognized and discussed in other LTERs in the Kiskunság Sandy Ridge (e.g. Bartha *et al.* 2008; Kovács-Láng *et al.* 2000). In the present case, drying was indicated by the decrease of mesic perennials and/or the increase of xeric perennials in most of the scrutinized window halves.

The opening of the vegetation was indirectly indicated by the increase of ephemerals and cryptogams, since these groups have low competitive ability and require open surfaces. Non-ephemeral annuals, including mesic ones, also benefit from open surfaces. Therefore, we consider their trends less indicative of the drying conditions. The amount of xeric annuals was either stable or increased in all cases, which is in line with the expectations. However, the two main trends did not take place simultaneously in all window halves, due to the initial structure of the sections and to other circumstances, such as aspect, that favored some possible changes but hindered others. Consequently, the ecotone trends became easier to interpret. The first ecotone was located between an already dry section and an intermediately dry one, thus the changes could be greater in the second one, which could thus 'catch up' on the vegetation in the first section. The mechanisms were similar in ecotone 3, where a moist and an intermediately dry patch met. In this case the intermediate section (i.e. the second window half) reached its final state with little change because it had a northern aspect, resulting in a lower insolation rate and an inherently more humid microclimate. Whereas the first section had a larger potential to change, though with a similar end-state due to its special microclimatic features. At ecotone 4, both window halves had a more or less intermediately dry initial composition. The first section exhibited both trends of the drying process, probably due to its southern aspect. Whereas the second one became more xeric but the vegetation has not started to open up yet, which led to an increase in dissimilarity. The two remaining ecotones did not show any contrast change because the window halves in both cases could change in a parallel fashion, meaning that they turned somewhat more xeric and started to become more open as well.

To sum up, we can conclude that the main dynamic feature of the heterogeneous vegetation of our transects is not patch expansion vs. shrinking (i.e. ecotone movement) but fusion vs. division (i.e. ecotone disappearance and appearance). [Peters et al. \(2006\)](#) stated that landscapes dominated by stationary ecotones are likely to remain relatively stable through time, regardless of changes in environmental drivers. The present study contradicts this notion; therefore, we need to add that under certain circumstances these landscapes can also show pattern changes in the above-described manner. These pattern changes can be traced back to patch interior changes rather than to processes inside the ecotones, which is against the generally accepted theory that ecotones are the hotspots of landscape change ([Fortin et al. 2000](#); [Walker et al. 2003](#)). So, when studying landscape dynamics with ecotones in the focus, we suggest first identifying the types of the ecotones that are present. Further, if they are likely to behave in a stationary fashion, a study design that scrutinizes ecotone contrast and patch interior properties might be a better choice than those that rely on ecotone position as the indicator of the changes.

The results of the present study also demonstrate that contrast changes require long periods of time to manifest, since the landscape pattern of the Bugac LTER has not reached its

final state after >20 years following the loss of groundwater as a water source. Studies on the dynamics of ecotone contrast are rare in the literature but, i.e. [Boughton et al. \(2006\)](#) also found that post-fire succession in a mosaic landscape resulted in contrast changes only 30 years after the fire events. The low rate of such reactions and/or the long time lag they need can be very important when planning restoration measures, since their success may not become obvious for decades; therefore, it would be extremely difficult to plan the magnitude and temporal arrangement of the interventions. Interventions to raise the water table in the Kiskunság area are being planned by means of drainage water retention and other active methods, though not specifically for conservation purposes but to aid agricultural systems suffering also from aridity. However, it is actually not clear whether the outlined landscape changes of the Bugac LTER can be reversed simply by restoring the groundwater level. The drying of the lower zones has already resulted in the loss of several plant species, like *Schoenus nigricans*, *Gentiana pneumonanthe*, *Molinia caerulea*, etc. and their recolonization is uncertain, since their closest present populations are around 15 km away in the western discharge zone of the Kiskunság Sandy Ridge. Therefore, besides the urgent need for restoration of the water regime, conservationists should also closely monitor the effects of the water table on a long-term basis and, if needed, further interventions, like species reintroductions should be carried out to counteract and reverse the outlined landscape pattern transformations.

FUNDING

European Union and the State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP 4.2.4. A/1-11-1-2012-0001 'National Excellence Program'.

Conflict of interest statement. None declared.

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