Plant diversity patterns of a Hungarian steppe-wetland mosaic in relation to grazing regime and land use history

Muster der Phytodiversität in ungarischen Steppen-Feuchtwiesen-Mosaiken in Abhängigkeit von der Beweidungsintensität und Landnutzungsgeschichte

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Abstract

Steppes used to cover large areas of Hungary, but most of this vegetation has since been destroyed. In Central Hungary, some patches have survived on ridges in wet meadows. These habitat complexes face profound land use changes and their optimal management regime is uncertain. We identified seven annually mown steppe and wet meadow types according to their grazing regime and history and aimed to answer the following questions: (1) Does grazing have beneficial effects on mown steppes and wet meadows? (2) Should the presently homogeneous management of neighbouring steppes and wet meadows be maintained? (3) Is annual mowing sufficient in assisting the recovery of steppes and wet meadows on former croplands?

We selected three localities for each of the seven vegetation types and sampled them with 50 quadrats (50 × 50 cm) in each locality, making a total of 1,050 quadrats. Vascular plant diversity relations were evaluated using the total number of species per habitat type (species richness) and the average number of species per quadrat (microsite diversity). The effect of grazing and history on microsite diversity was tested with linear mixed-effect models. We used Redundancy Analysis to disentangle the role of grazing intensity and management history on species composition. Plant species were then sorted into functional groups, and the proportions of these groups were used to evaluate community structure.

Our results indicate that mowing alone cannot maintain as high a diversity as the combination of the two land use types, thus grazing should be introduced to non-grazed areas. Steppes, however, were found more sensitive to the intensity of grazing than wet meadows. Under heavy grazing, no increased microsite diversity was detected in the steppes and the proportion of disturbance indicators tended to increase. In contrast, the same grazing intensity resulted in only positive effects in wet meadows. Thus, uniform land use on adjacent steppes and wet meadows is not recommended but intensive grazing should be stopped on steppes. Secondary steppes were less diverse than primary ones and their community structure was also poorer, whereas wet meadows had a better regeneration potential. Thus, mowing alone is an incomplete tool to restore the plant diversity of secondary steppes; they should also be grazed and/or should be supported by other active interventions.

Keywords: calcareous *Molinia* meadow, Danube-Tisza Interfluve, dry grassland, heterogeneous landscape, land use change, mowing, Pannonic sand steppe, species richness, wet grasslands

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Traditional, low-intensity management of grasslands has maintained high biodiversity throughout Europe. However, recent land use changes including both intensification and large-scale abandonment pose a threat to these ecosystems (ZECHMEISTER et al. 2003, BÁLDI et al. 2013). Fortunately, extensively managed farmlands are still wide-spread in the eastern countries of the European Union (KŐRÖSI et al. 2012). Land use practices are also changing in this region, showing tendencies similar to western and northern European countries, although the different economic and social history means that the processes are somewhat different (BIRÓ et al. 2013). After the end of the socialist era, the amount of livestock decreased by around 40–50% in the lowlands of Hungary, resulting in the abandonment of vast pastures (BIRÓ et al. 2013, HARASZTY 2013). Instead of grazing, the introduction of crop production has become more profitable for farmers in many cases. As a consequence, large pastures and hayfields, some of which had hosted steppe communities since the late Pleistocene, have been tilled (CZÚCZ et al. 2005, MOLNÁR et al. 2008). In contrast, some former arable fields have been abandoned and secondary grasslands have started developing on them (CSECSERITS & RÉDEI 2001).

One herbaceous community strongly affected by these developments is the closed subtype of the Pannonic sand steppe (*Astragalo austriacae-Festucetum sulcatae* Soó 1957), which is listed as priority habitat type 6260 in Annex I of the Habitats Directive (COUNCIL OF EUROPEAN COMMUNITIES 1992). Closed sand steppe is a two-layered, species-rich community with plant coverage usually close to 100% (BORHIDI et al. 2012). This community used to be the most common primary grassland type in the Danube-Tisza Interfluve of central Hungary until the Middle Ages, covering 280,000 hectares, which equals 20% of the total area of the interfluve (MOLNÁR et al. 2008). Due to their fertile soils, large areas of these steppes have been transformed into croplands and forest plantations. On the other hand, secondary closed sand steppes appeared spontaneously on deforested areas, on dried-out wetlands and particularly on abandoned croplands, resulting in a historically diverse set of closed sand steppes in the region. Nevertheless, the present area of closed sand steppes is only 3.3% of the original, and the area of pristine vegetation within this is estimated to be less than a hundred hectares (BIRÓ et al. 2008, MOLNÁR et al. 2008). Thus, it is imperative to protect these fragments from the detrimental effects of the above-described recent land use changes and to maintain their diversity.

A large proportion of the remaining closed sand steppes (henceforth 'steppes') occur in the so-called Turjánvidék (Fig. 1). The Turjánvidék is a narrow strip of land running parallel with the Danube, and lies in the discharge zone of the groundwater seeping from the nearby Danube-Tisza Sandy Ridge (MÁDL-SZŐNYI & TÓTH 2009). This excess water supply resulted in the development of various wetland types ranging from fen lakes to wet meadows along slight topographic gradients. The most common vegetation type is the calcareous purple moor-grass wet meadow (*Succiso-Molinetum hungaricae* [Komlódi 1958] Soó 1969) (henceforth 'wet meadows'), which is also a priority habitat type (No. 6410) according to Annex I of the Habitats Directive (EUROPEAN UNION, 1992). Wet meadows of this type are usually very dense, with two herbaceous layers and a thick moss layer (BORHIDI et al. 2012). Most wet meadows of the Turjánvidék avoided destructive human impact in earlier centuries due to their water-logged, peaty soil, but the drop in the water table in the entire Danube-Tisza Interfluve in the last couple of decades enabled land owners to start breaking them up in some places. Besides this, shrub and reed encroachment and the spreading of invasive

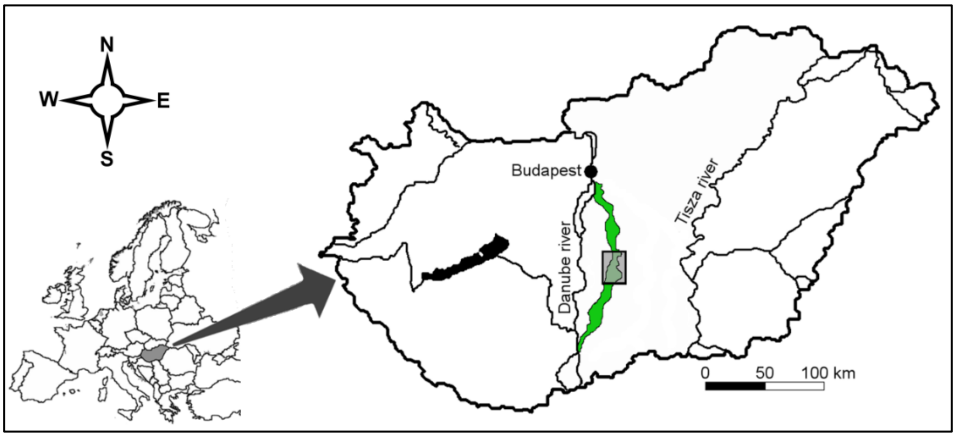

Fig. 1. Location of the Turjánvidék (green strip in central Hungary) and its section where the fieldwork was carried out (grey window).

Abb. 1. Lage des Untersuchungsgebiets (grauer Kasten) im Turjánvidék-Gebiet (grüner Streifen) in Zentral-Ungarn.

neophytes (e.g. *Solidago gigantea*) also threaten them (MÁTÉ 2014). Luckily though, approximately 24,000 ha of wet meadows are still in a relatively good condition in the Turjánvidék (BIRÓ et al. 2007). Apart from their role in providing habitat for dozens of Red List species (BORHIDI et al. 2012, MÁTÉ 2014), the aforementioned steppe remnants could survive on small but never inundated sandy humps and ridges wedged into these wet meadows, which further emphasises their conservation value (MOLNÁR et al. 2008) (Fig. 2).

Steppe-wet meadow mosaics of the Turjánvidék have been used by pastoral cultures since the early Bronze Age (KNIPL & SÜMEGI 2012) and the areas that have not been destroyed by humans are still used in the same way, i.e. mowing and grazing without intensive management techniques like sowing or fertilisation (BÁLDI et al. 2013, BIRÓ et al. 2013). However, they were not completely spared from the land use changes of recent decades. Luckily though, most of them are now under protection either as part of the Kiskunság National Park or the Natura 2000 ecological network, thus the legal background of land use control for maintaining biodiversity is available. For this purpose, the majority of these areas, primary and secondary ones alike, are mown in mid-summer and where livestock is still available they are also grazed at various intensities. However, the optimal conservation measures to maintain or restore target diversities are uncertain. Therefore, scientific data are needed to choose the most favourable land use regime, which takes into account the present landscape pattern and livestock population as well as the history of the sites. In the present study we examined the vegetation composition, diversity and structure of mown steppe-wet meadow mosaics and asked the following questions: (1) Does grazing have beneficial effects on annually mown steppes and wet meadows? (2) Should the presently homogeneous management of neighbouring steppes and wet meadows be maintained in the future? (3) Is annual mowing sufficient in assisting the recovery of steppes and wet meadows on former croplands in this mosaic landscape?

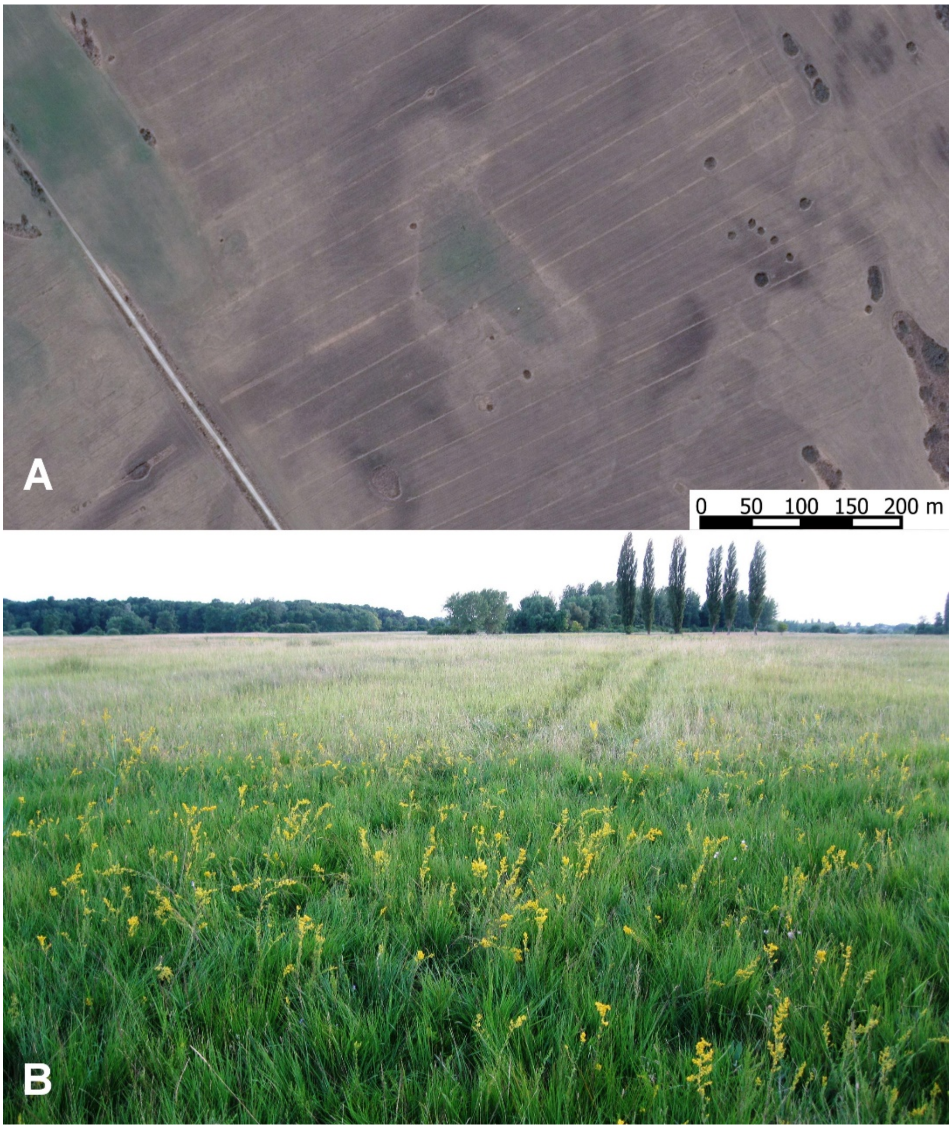

Fig. 2. A) Typical landscape structure of the wet meadow-steppe mosaic in the Turjánvidék in central Hungary (N 46°48’59”–45”, E 19°16’05”–36”, 93 m a. s. l). The central green area, embedded into the matrix of wet meadows, is a sandy hump covered by closed steppe vegetation. **B)** Non-grazed secondary wet meadow dominated by *Molinia caerulea* and *Galium verum* (foreground) and a sandy hump covered by non-grazed secondary steppe with *Festuca pseudovina* and *Elymus repens* (background).

Abb. 2. A) Typisches Steppen-Feuchtwiesen-Mosaik im Turjánvidék-Gebiet in Zentral-Ungarn (N 46°48’59”–45”, E 19°16’05”–36”, 93 m NN). Die grünliche Fläche im Zentrum zeigt einen sandigen Rücken mit Steppenvegetation innerhalb einer Matrix aus Feuchtwiesen. **B)** Im Vordergrund ist eine unbeweidete, sekundäre und von *Molinia caerulea* und *Galium verum* dominierte Feuchtwiese und im Hintergrund ein sandiger Rücken mit unbeweideter sekundärer Steppe mit *Festuca pseudovina* und *Elymus repens* zu sehen.

2. Materials and methods

2.1 Study area

The study was carried out in steppe-wet meadow complexes of the Turjánvidék, central Hungary. The climate of the region is continental with a sub-Mediterranean influence; the annual precipitation is 500–600 mm and the mean annual temperature is 10–11°C (BIRÓ et al. 2013). The climate of the Turjánvidék shows increasing aridity from north to south (FEKETE et al. 2002, KUN 2001), which, combined with anthropogenic effects, has resulted in decreasing species richness in this direction (MOLNÁR et al. 2008). To avoid the confounding effect of this regional pattern, sampling sites were chosen only within a 15 × 5 km zone, located between the towns of Szabadszállás and Páhi (Fig. 1).

Grazing in the area is conducted mostly by cattle and to a lesser extent by sheep. Grasslands are grazed by cattle in two different ways: areas in the vicinity of their home farm are grazed during most of the vegetation period, thus vegetation is always short and not suitable for mowing. Sites further away are spared in the first half of the growing season, mown for winter hay in mid-summer and when vegetation starts to regrow, they are also grazed. Here, the movement of cattle is restricted by portable electric fences, which are regularly relocated once the animals have removed the available fresh biomass. However, due to the low livestock population, the majority of the mown areas are not grazed. This management regime is identical on steppe patches and wet meadows, and where it takes place, it can be considered intensive according to local standards, though the absolute stocking rate is difficult to assess. A more moderate grazing pressure is achieved by sheep in some parts of the area. Sheep are constantly herded by shepherds and graze mostly on drier sites, most of which are out of the scope of the present study because they are embedded in landscape matrices other than wet meadows (like tree plantations, croplands, etc.) and are usually highly degraded. Infrequently though, sheep visit some of the ridges and humps covered by the precious closed sand steppes, thus their possible impact should also be investigated. Wet meadows are not grazed this way; therefore no moderate grazing level could be defined in them.

Steppe and wet meadow patches can be divided into primary and secondary ones in the area. In the present study, we defined primary ones as grasslands that have been covered with the same plant community continuously (steppe or wet meadow) for the last 100 years. Secondary ones are present in various conditions and with diverse origins and ploughing histories. Therefore, we selected a relatively uniform set of secondary grasslands, namely those that were tilled around 50–60 years ago in a drier period but were abandoned soon after as the ground became wetter again. These areas are mown but not grazed. Thus, a total of seven different mown vegetation types were identified in the area:

1. Intensively grazed primary steppes (IGPS)
2. Moderately grazed primary steppes (MGPS)
3. Non-grazed primary steppes (NGPS)
4. Non-grazed secondary steppes (NGSS)
5. Intensively grazed primary wet meadows (IGPW)
6. Non-grazed primary wet meadows (NGPW)
7. Non-grazed secondary wet meadows (NGSW)

2.2 Sampling design and data analysis

Field work was conducted in late May and early June 2013. We selected three localities for each of the seven vegetation types and sampled them using 50 randomly distributed quadrats (50 × 50 cm) at each locality, making a total of 1,050 sampling quadrats. Presence/absence data of all vascular plant species were recorded in the quadrats. The distance between neighbouring localities ranged from 500 m to 3 km and the different types were randomly distributed relative to each other. The size of the steppe patches ranged from 0.2 ha to 0.5 ha; therefore, for consistency, wet meadows were also sampled within territories of this size range, although their total area was usually much larger. Corresponding steppe and wet meadow localities were not necessarily next to each other.

We used species richness and microsite diversity to describe the diversity relations of the different vegetation types. Species richness was calculated as the total number of plant species in the different vegetation types. Microsite diversity was defined as the number of plant species in the 0.5 × 0.5 m quadrats and was tested across groups using linear mixed-effect models (LMM). Locality was used as a random factor, and the fixed factors were grazing intensity and history. Steppes and wet meadows were analysed separately. Grazing had three levels in steppes (intensive, moderate and no grazing) and two levels wet meadows (intensive and no grazing). History had two levels in both cases (primary and secondary). The normality assumption of the model residuals was tested with Q-Q plot. To test the effect of grazing and history on the composition of the vegetation types, we merged the data from the 50 quadrats in each locality and performed a single Redundancy Analysis (RDA) on the 21 study localities as the objects and grazing regime (intensive, moderate and no grazing), history (primary and secondary) and humidity (steppic and wet) as the factors. The significance of the effect of the variables was tested with Monte-Carlo permutation tests (5000 permutations).

To shed light on the ecological mechanisms operating within each vegetation type, we sorted the species into functional groups, based on the system of BORHIDI (1995), who adapted Grime's C-S-R system (GRIME 1979) to the Pannonian flora. We used the following six groups: natural competitors, generalist stress tolerant species, specialist stress tolerant species, pioneers, disturbance tolerant species, disturbance indicators and non-native species. Our group of disturbance indicators included two categories of Borhidi's system, namely weeds and ruderal competitors, but the other groups have been adopted without modification. We calculated the proportion of each group in the pooled data of each vegetation type and evaluated the resulting spectra.

Statistical analyses were carried out in an R environment (R DEVELOPMENT CORE TEAM 2013). Linear mixed-effect models were generated with the lme function of the nlme package (PINHERIO et al. 2015). The relevel function was used to carry out *post hoc* sequential comparisons among factor levels and the Holm-Bonferroni method was used to correct the p values. The Redundancy Analysis was carried out using the vegan package (OKSANEN et al. 2010). Nomenclature of vascular species follows KIRÁLY (2009).

3. Results

We recorded a total of 191 vascular species in our plots. The most common graminoids were *Festuca pseudovina*, *F. rupicola*, *Cynodon dactylon* and *Dactylis glomerata* in the steppes, and *Molinia caerulea*, *Deschampsia caespitosa* and *Carex flacca* in the wet meadows. The most abundant forbs included *Achillea pannonica*, *Centaurea scabiosa* ssp. *sadleriana*, *Securigera varia*, etc. in the steppes, and *Achillea asplenifolia*, *Galium verum*, *Succisa pratensis* and *Serratula tinctoria*, etc. in the wet meadows. The sampling quadrats included 16 species listed in the Red list of the vascular flora of Hungary (KIRÁLY 2007) and 15 of these are legally protected in Hungary (Supplement E1).

Species richness in the steppes was highest under moderate grazing; intensive grazing resulted in lower numbers but the absence of grazing reduced it more dramatically. Secondary steppes were the least species-rich and provided habitat for around half as many species as the moderately grazed primary ones. Grazing yielded higher species richness in wet meadows as well but the difference between the primary and secondary ones was not as pronounced as in steppes (Table 1).

According to the linear mixed-effect model of the steppes, the microsite diversity of the non-grazed and intensively grazed primary types did not differ from each other, but the moderately grazed type was significantly more diverse. Secondary steppes were less diverse than primary ones. Intensive grazing significantly increased the microsite diversity of wet meadows compared with the non-grazed type. Secondary wet meadows were less diverse than primary ones but the difference was found only marginally significant (Table 2, Fig. 3).

Table 1. Species richness of the seven studied vegetation types and the average microsite diversity (number of species/quadrat) ± standard deviation. MGPS: moderately grazed primary steppe; IGPS: intensively grazed primary steppe; NGPS: non-grazed primary steppe; NGSS: non-grazed secondary steppe; IGPW: intensively grazed primary wet meadow; NGPW: non-grazed primary wet meadow; NGSW: non-grazed secondary wet meadow.

Tabelle 1. Gesamtartenreichtum und kleinräumige Diversität (Anzahl Arten pro 0,25 m²-Quadrat) in sieben Habitattypen. Mittelwerte mit Standardabweichungen sind dargestellt. MGPS: Moderat beweidete primäre Steppe; IGPS: Intensive beweidete primäre Steppe; NGPS: Unbeweidete primäre Steppe; NGSS: Unbeweidete sekundäre Steppe; IGPW: Intensiv beweidete primäre Feuchtwiese; NGPW: Unbeweidete primäre Feuchtwiese; NGSW: Unbeweidete sekundäre Feuchtwiese.

Habitat type	MGPS	IGPS	NGPS	NGSS	IGPW	NGPW	NGSW
Species richness	92	80	70	46	91	64	61
Species/quadrat	21.0 ± 3.3	15.5 ± 2.5	13.6 ± 2.7	9.0 ± 1.8	17.2 ± 2.6	14.3 ± 2.7	12.3 ± 2.0

Table 2. Results of the linear mixed-effect models of the steppe and wet meadow habitat types using grazing intensity and history as the fixed factors and locality as the random factor. NGP: non-grazed primary; IGP: intensively grazed primary; MGP: moderately grazed primary; NGS: non-grazed secondary. * indicates significant *p*-values.

Tabelle 2. Ergebnisse der *Linear mixed-effect models* der verschiedenen Steppen- und Feuchtwiesentypen mit Beweidungsintensität und Beweidungsgeschichte als feste Faktoren und Lokalität als Zufallsfaktor. NGP: Unbeweidet-primär; IGP: Intensiv beweidet-primär; MGP: Moderat beweidet-primär; NGS: Unbeweidet-sekundär. Sternchen (*) zeigen signifikante *p*-Werte an.

Comparisons in Steppes	*t*	Adjusted *p*
NGP vs. IGP	1.833	0.104
NGP vs. MGP	7.405	0.001*
MGP vs. IGP	-5.572	0.005*
NGP vs. NGS	-4.673	0.008*
Comparisons in Wet Meadows		
NGP vs. IGP	3.199	0.008*
NGP vs. NGS	-2.250	0.058

According to the RDA, humidity and grazing significantly affected the plant composition of the landscape, but no significant effect could be confirmed for history (Table 3). The ordination plot shows that the four steppe types form rather distinct groups, whereas this pattern is not so clear in wet meadows (Fig. 4).

In steppes, disturbance tolerant species and generalists were the most common functional groups across all vegetation types. The proportion of competitors was more than two times higher in the non-grazed types than in the moderately grazed ones, but intensively grazed sites also tended to have fewer competitors than the non-grazed ones. Natural pioneers, however, had an opposite trend with low proportions in the non-grazed types, 3-times higher share in the MGPS sites and an intermediate amount in the IGPS. Disturbance indicators showed an increasing tendency in the primary types with increasing grazing intensity, but their amount was the highest in the secondary steppe. Non-native species were absent and specialists were negligible (Fig. 5).

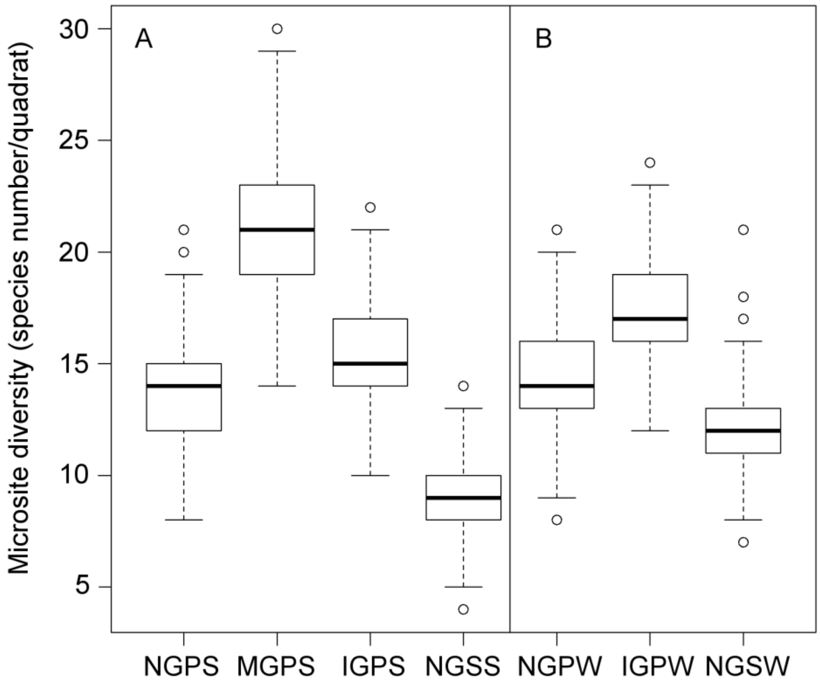

Fig. 3. Species numbers of the Steppe (A) and Wet Meadow (B) types. Empty circles indicate outliers. See Table 2 for significance values. NGPS: non-grazed primary steppe; MGPS: moderately grazed primary steppe; IGPS: intensively grazed primary steppe; NGSS: non-grazed secondary steppe; NGPW: non-grazed primary wet meadow; IGPW: intensively grazed primary wet meadow; NGSW: non-grazed secondary wet meadow.

Abb. 3. Artenzahlen der unterschiedlichen (A) Steppen- und (B) Feuchtwiesentypen. Leere Kreise zeigen Ausreißerdaten an. Die entsprechenden Signifikanzwerte siehe in Tabelle 2. NGPS: Unbeweidete primäre Steppe; MGPS: Moderat beweidete primäre Steppe; IGPS: Intensiv beweidete primäre Steppe; NGSS: Unbeweidete sekundäre Steppe; NGPW: Unbeweidete primäre Feuchtwiese; IGPW: Intensiv beweidete primäre Feuchtwiese; NGSW: Unbeweidete sekundäre Feuchtwiese.

Table 3. Redundancy analysis of the plant community composition of the studied habitat types according to humidity (steppic or wet meadow), grazing regime (no grazing, moderate grazing or intensive) and history (primary and secondary). * indicates significant *p* values.

Tabelle 3. Redundanzanalyse der Artenzusammensetzung der untersuchten Habitattypen mit Feuchtigkeit (Steppe oder Feuchtwiese), Beweidungsintensität (keine, moderate, intensive Beweidung) und Natürlichkeitsgrad (primär, sekundär). Sternchen (*) zeigen signifikante *p*-Werte an.

Variables	Variation %	pseudo-*F*	*p*
Grazing	11.82	1.711	0.009*
History	4.66	1.351	0.132
Humidity	28.26	8.183	0.001*

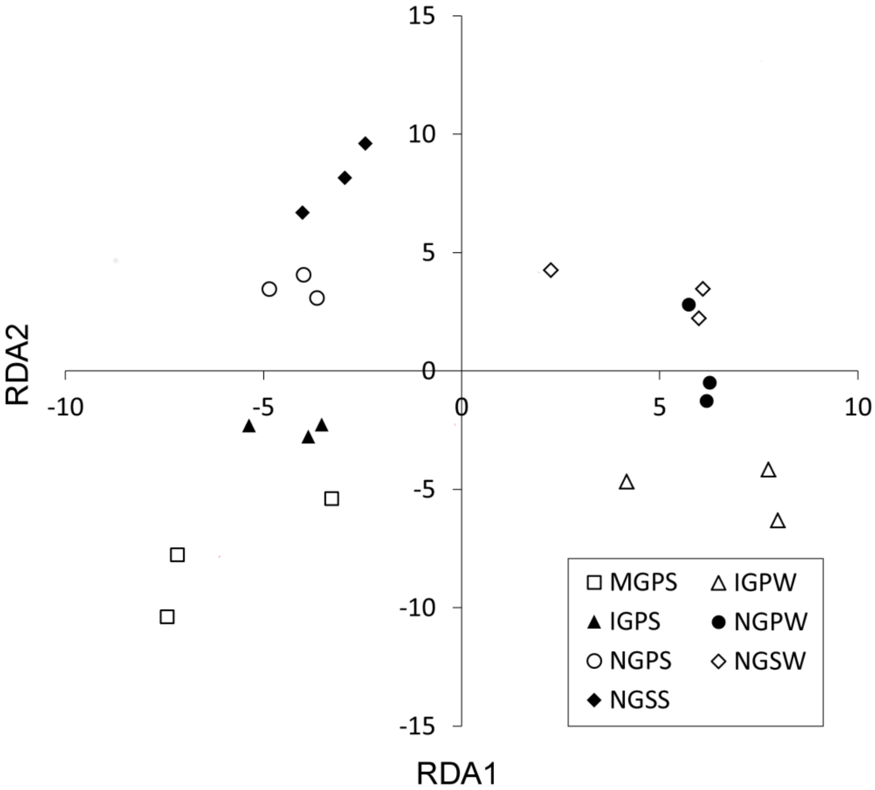

Fig. 4. RDA ordination plot of the 21 studied localities labelled according to habitat type. MGPS: moderately grazed primary steppe; IGPS: intensively grazed primary steppe; NGPS: non-grazed primary steppe; NGSS: non-grazed secondary steppe; IGPW: intensively grazed primary wet meadow; NGPW: non-grazed primary wet meadow; NGSW: non-grazed secondary wet meadow.

Abb. 4. RDA-Ordination der Artenzusammensetzung der 21 untersuchten Lokalitäten. MGPS: Moderat beweidete primäre Steppe; IGPS: Intensiv beweidete primäre Steppe; NGPS: Unbeweidete primäre Steppe; NGSS: Unbeweidete sekundäre Steppe; IGPW: Intensiv beweidete primäre Feuchtwiese; NGPW: Unbeweidete primäre Feuchtwiese; NGSW: Unbeweidete sekundäre Feuchtwiese.

Wet meadows also had the disturbance tolerant species and the generalists as the most abundant groups but competitors were present in similar numbers as well. Disturbance tolerant species tended to be more abundant in the IGPW type than in the two non-grazed types, meaning that there was a lower proportion of generalists and competitors. Specialists had a moderate but similar share in the IGPW and NGPW types but were absent in the NGSW type. Disturbance indicators were equally rare in all the three studied types; pioneers and non-natives were practically absent (Fig. 6).

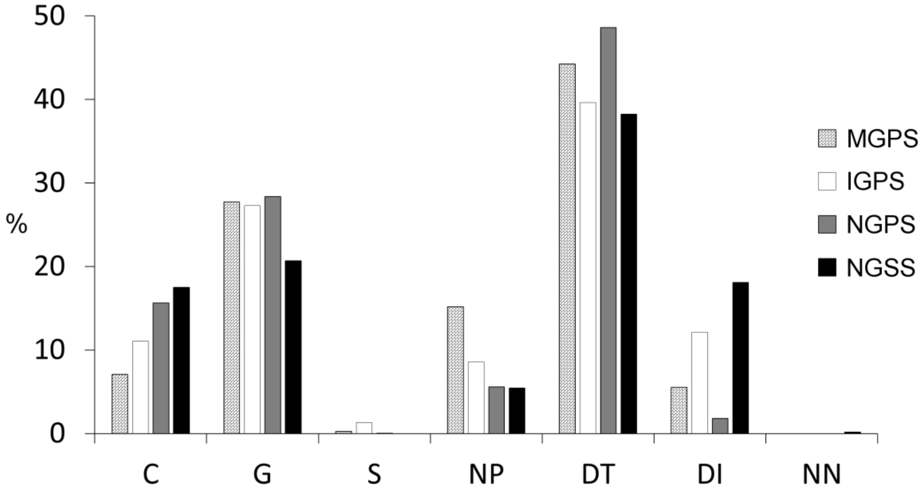

Fig. 5. Functional group spectrum of the steppe types. The bars indicate the proportions of each functional group in the pooled data of the four steppe types. C: natural competitors; G: generalist stress tolerant species; S: specialist stress tolerant species; NP: natural pioneers; DT: disturbance tolerant species; DI: disturbance indicators; NN: non-native species; IGPS: intensively grazed primary steppe; MGPS: moderately grazed primary steppe; NGPS: non-grazed primary steppe; NGSS: non-grazed secondary steppe.

Abb. 5. Spektren von sieben funktionellen Gruppen in vier Steppentypen. Die Balken zeigen die relativen Anteile der funktionellen Gruppen an. C: Natürliche Konkurrenzarten; G: Generalistische stresstolerante Arten; S: Spezialisierte stresstolerante Arten; NP: Natürliche Pionierarten; DT: Störungstolerante Arten; DI: Störungszeiger; NN: Nichteinheimische Arten; IGPS: Intensive beweidete primäre Steppe; MGPS: Moderat beweidete primäre Steppe; NGPS: Unbeweidete primäre Steppe; NGSS: Unbeweidete sekundäre Steppe.

4. Discussion

4.1 Does grazing of mown steppes and wet meadows have beneficial effects?

In the present paper we aimed to investigate the effects and possible conservation implications of grazing regime and land use history on the vegetation of annually mown steppes and wet meadows in Hungary. The effects of both mowing and grazing have been studied extensively in vegetation science, showing that both land use forms can be regarded as disturbances, but if their intensity is carefully chosen, they have beneficial effects on diversity and community structure alike (e.g. ROSENTHAL et al. 2012). The combined effects of mowing and grazing, however, have rarely been looked into.

According to our results, grazing had significant consequences for the composition and diversity of the mown steppe and wet meadow components of the landscape. Species richness was higher in all grazed forms than in the non-grazed ones, microsite diversity was higher in the MGPS and IGPW sites than in the corresponding non-grazed sites and the community structure was also more complex in the grazed steppes than in the non-grazed ones. Such differences between grazed and mown grasslands are frequently encountered (e.g. RUSINA et al. 2013), and can be explained by the phenomenon that grazing suppresses strong competitors (HARTNETT et al. 1996) and creates gaps in the vegetation (LOUCOU-

408

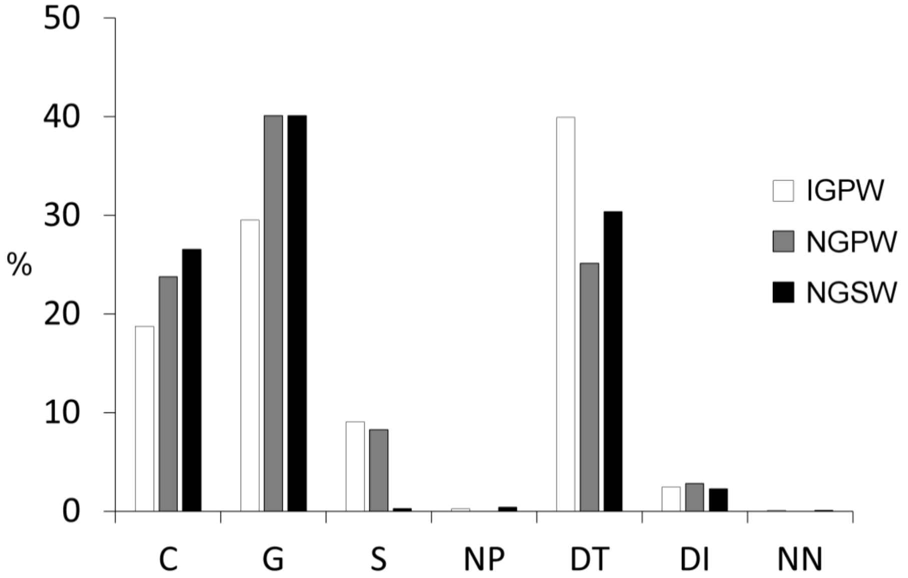

Fig. 6. Functional group spectrum of the wet meadow types. The bars indicate the proportions of each functional group in the pooled data of the three wet meadow types. C: natural competitors; G: generalist stress tolerant species; S: specialist stress tolerant species; NP: natural pioneers; DT: disturbance tolerant species; DI: disturbance indicators; NN: non-native species; IGPW: intensively grazed primary wet meadow; NGPS: non-grazed primary wet meadow; NGSW: non-grazed secondary wet meadow.

Abb. 6. Spektren von sieben funktionellen Gruppen in vier Feuchtwiesentypen. Die Balken zeigen die relativen Anteile der funktionellen Gruppen an. C: Natürliche Konkurrenzarten; G: Generalistische stresstolerante Arten; S: Spezialisierte stresstolerante Arten; NP: Natürliche Pionierarten; DT: Störungstolerante Arten; DI: Störungszeiger; NN: Nichteinheimische Arten; IGPW: Intensive beweidete primäre Feuchtwiese; NGPW: Unbeweidete primäre Feuchtwiese; NGSW: Unbeweidete sekundäre Feuchtwiese.

GARAY et al. 2004), enabling weak competitors like pioneer species to spread (BULLOCK et al. 2001). Tendencies for both the reduction of competitors and the increase of pioneers were detected in the present study and the high microsite diversity in the MGPS and IGPW sites could also be a consequence of the small-scale succession processes in such small gaps.

As a conclusion it can be said that mowing alone cannot maintain as high a biodiversity as the combined application of the two methods. This is in line with a number of studies emphasising that mowing is an incomplete surrogate for grazing and in areas where grazing has been abandoned, mowing cannot fully restore or maintain target communities (STAMPFLI & ZEITER 1999, ARI-PEKKA et al. 2001), though its application is undisputedly a better choice than ceasing all management (COLLINS et al. 1998, GÜSEWELL & LE NÉDIC 2004). In the Turjánvidék, the reintroduction of grazing to the abandoned areas would therefore be highly advantageous. In the long run, this should be done by increasing the total livestock population but as a more rapid response the adjustment of the grazing pattern of the present population seems also feasible. A possible solution for this can be deduced from the differences of MGPS and IGPS sites. The MGPS type is more diverse, indicating that although intensive grazing is better than a complete lack of grazing, a moderate level of grazing is the best management. Thus, the disturbance intensity at MGPS sites might be the closest to an

409

optimal disturbance level as outlined in the intermediate disturbance hypothesis (cf. CONNELL 1978, MILCHUNAS et al. 1988). Redistributing a certain amount of livestock from IGPS sites to NGPS sites to get closer to a moderate level of disturbance at both areas would also be an advantageous conservation measure. However, it should also be noted that sheep and cattle have somewhat different grazing impacts (DENNIS et al. 2008) and to further fine tune the stocking rates, more studies should be carried out to separate the effect of grazing species and intensity on the steppes.

Furthermore, in the future a broader spectrum of grazing should also be studied in the wet meadows to see whether the intermediate disturbance hypothesis applies in this habitat type as well and whether the presently applied stocking rate needs adjustment similarly to the steppes.

4.2 Should the presently homogeneous management of neighbouring steppes and wet meadows be maintained in the future?

Though a moderate level of grazing was not studied in the steppes, the intensively grazed areas can be directly compared since their grazing intensity was identical. Our results indicate that the steppes and wet meadows do not have the same sensitivity to grazing. The species richness trends were similar in the two groups but we did not detect a difference between the microsite diversity of the IGPS and NGPS sites, whereas the IGPW sites had significantly higher microsite diversity than the NGPW sites. The functional group analysis indicated that the underlying community structures also had different tendencies. Primary wet meadows reacted to grazing by an increasing trend in disturbance tolerant species only, while the other groups did not change in absolute numbers. In contrast, steppes showed more extensive differences and it was the disturbance indicators (i.e. a less desirable group) that generally increased under intensive grazing and not the disturbance tolerant species. Thus, it can be concluded that steppes are more prone to degradation under heavy disturbance than wet meadows.

Differences in sensitivity to grazing along moisture gradients have been reported by some other studies as well but their results were opposite to ours. TÖRÖK et al. (2014) found that dry alkaline steppes are less sensitive than adjacent alkaline wet meadows in eastern Hungary and KISS et al. (2011) had similar results on the Danube-Tisza Sandy Ridge of central Hungary. In both studies the dry components of the landscapes were rather large in size and were also more stressed, which does not favour competitors (salinity in the first case and aridity in the second). The steppe types of the present study, however, are small and isolated in the matrix of extensive wet meadows and have little environmental stress to constrain them. Therefore, dispersal and colonisation processes play a smaller role and when disturbance is low, competition can prevail and can restructure the community.

These findings also mean that intensive grazing can be moved from IGPS sites to NGPW sites as well, even in the same intensive fashion, leaving MGPS-like conditions behind on the steppe. This could be done easily by fixing the portable fences so that they include drier ridges and humps only in every other year or even less frequently. These results confirm the notion that homogeneous management of heterogeneous areas should be avoided (ERDŐS et al. 2011) and should be optimised to the behaviour of the constituting patch types.

Putting more emphasis on the grazing of wet meadows by redistributing the present population and particularly by introducing new herds can have further beneficial effects. It has been shown in North American wetlands that grazing indirectly retains water in the soil by removing biomass that could otherwise evaporate large quantities of water (MARTY 2005).

The Turjánvidék, similarly to the Danube-Tisza Sandy Ridge, faces severe groundwater loss, partly due to climate change (KERTÉSZ & MIKA 1999) and more importantly to local anthropogenic factors like groundwater extraction for irrigation, active draining and the creation of vast exotic tree plantations with extreme evapotranspiration rates (BERÉNYI & ERDÉLYI 1990). The Turjánvidék, being the discharge zone of the Danube-Tisza Sandy Ridge, receives the majority of its water supply in the form of seeping groundwater. This water source, however, is threatened by the above processes and all solutions that conserve available water should be encouraged if they do not interfere with other conservation purposes. Though probably not in a grand scale, the suggested expansion of grazing on wet meadows may increase groundwater seepage by reducing evapotranspiration rates.

4.3 Is annual mowing sufficient to assist the recovery of steppes and wet meadows on former croplands?

The secondary steppes in this study had lower species richness and significantly lower microsite diversity than the primary steppes. In contrast, we did not detect such a difference between the diversity measures of the secondary and primary wet meadows, and probably this is why the RDA could not confirm that history was a significant predictor of the species composition of the landscape. Thus, it can be concluded that steppes are not only more sensitive to disturbance but their regeneration potential is also worse than that of the wet meadows, since even half a century of spontaneous processes was insufficient to restore their diversity to the level of the NGPS sites. Nevertheless, the absence of specialists in the secondary wet meadows indicates that the recovery was not complete in their case either.

On arid sand steppes of the Danube-Tisza Interfluve of central Hungary, CSECSERITS & RÉDEI (2001) found that most native species can colonise old-fields within 10 years after abandonment and no active restoration is needed. However, they mentioned that on more fertile soils (like the present study area) recovery may be slower. Some other studies indicate that complete spontaneous recovery may be nearly impossible when strong ruderal competitors – a subgroup of disturbance indicators (BORHIDI 1995) – become dominant and arrest succession (FAGAN et al. 2008). Such species, like *Elymus repens* and *Cynodon dactylon* are dominant on the NGSS sites, and without actively reducing their populations, other species will probably be unable to colonise. Grazing has been shown to efficiently reduce the amount of these undesirable species and then to reactivate the seed bank if not depleted yet (SCHWABE et al. 2013, TÖRÖK et al. 2014). Therefore, grazing should be introduced to these sites as well.

Another problem that can hinder secondary succession is the lack of propagule influx (SIMMERING et al, 2006.). This may be an especially important factor in steppe patches, which are rather isolated habitats. The introduction of grazing could mitigate the effect of isolation by endo- and epizoochory (SCHWABE et al. 2013) but other active restoration techniques like hay transfer from diverse primary sites could also assist the colonisation of species with low dispersal ability (TÖRÖK et al. 2011).

In summary, we can conclude that spontaneous succession on the secondary steppes of the Turjánvidék is incomplete and should be actively supported by grazing and/or other restoration techniques. Nevertheless, prevention is better than restoration, therefore future breaking-up of grasslands should be minimised in the area. This should be realised not only by prohibitions and fines, but husbandry on grasslands should be made more appealing to land owners by appropriate EU Agri-Environmental Schemes (cf. BÁLDI et al. 2013).

Erweiterte deutsche Zusammefassung

Einleitung – Europaweit ist durch traditionelle extensive Landnutzung sehr biodiverses Grasland entstanden, das jedoch durch die derzeitigen Landnutzungsänderungen mittlerweile vielerorts stark gefährdet ist. In der ungarischen Tiefebene nahm z. B. der Viehbestand in den frühen 1990er Jahren dramatisch ab, was zur Folge hatte, dass riesige Weideflächen brachfielen. Einige dieser Flächen wurden später in Ackerland überführt. Im Gegensatz dazu wurden andere Ackerflächen aufgegeben, so dass sich dort sekundäres Grasland entwickeln konnte (BIRÓ et al. 2013). Von dieser Entwicklung profitierte besonders der nach der FFH-Richtlinie prioritäre Lebensraumuntertyp 6260 Pannonische Sandsteppen. Dieser Lebensraumtyp war in der Region ehemals weit verbreitet; heute sind allerdings lediglich noch 3,3 % seiner früheren Fläche erhalten und der Anteil der intakten Flächen umfasst kaum 100 Hektar (MOLNÁR et al. 2008).

Im Turjánvidék-Gebiet in Zentral-Ungarn existieren noch zahlreiche Steppen (Abb. 1). Insgesamt dominieren in diesem Gebiet Feuchtlebensräume wie Niedermoorseen oder Feuchtwiesen. Den größten Anteil nehmen mit 24.000 Hektar Pfeifengraswiesen kalkreicher Standorte ein (BIRÓ et al. 2007); sie werden im Folgenden kurz als Feuchtwiesen bezeichnet. Diese Feuchtwiesen bilden einen Lebensraum für etliche Rote Liste-Arten und formen Schutzstreifen um die Steppenreste, die sich auf kleinen Hügeln und Rücken innerhalb der großflächigen Feuchtwiesen befinden (Abb. 2). Die Steppen-Feuchtwiesen-Mosaike des Turjánvidék-Gebiets werden seit Jahrtausenden extensiv beweidet oder gemäht, doch sind auch sie in den letzten Jahren von Landnutzungsänderungen nicht verschont geblieben. Glücklicherweise wurden die meisten der Flächen unter Schutz gestellt, womit eine gesetzliche Grundlage zur Regulierung der Landnutzung geschaffen wurde. Welche Form der Landnutzung zum Erhalt oder zur Wiederherstellung der gewünschten Diversität der Flächen am besten geeignet ist, ist allerdings unklar. In der vorliegenden Studie untersuchen wir die Artenzusammensetzung, Artendiversität und funktionelle Merkmale der Vegetation von beweideten Steppen-Feuchtwiesen-Mosaiken in Zentral-Ungarn und stellen die folgenden Fragen: (1) Hat Beweidung einen positiven Effekt auf jährlich gemähte Steppen und Feuchtwiesen? (2) Sollte die einheitliche Bewirtschaftung von benachbarten Steppen und Feuchtwiesen zukünftig beibehalten werden? (3) Ist zur Wiederherstellung von Steppen und Feuchtwiesen auf früheren Ackerflächen in dieser Mosaik-Landschaft eine jährliche Beweidung notwendig?

Material und Methoden – Diese Studie wurde in Steppen-Feuchtwiesen-Komplexen im Turjánvidék-Gebiet in Zentral-Ungarn durchgeführt (Abb. 1). In den Steppen wurden drei Typen der Beweidungsintensität unterschieden: intensive Beweidung (mit Rindern), moderate Beweidung (mit Schafen) und keine Beweidung. In den Feuchtwiesen wurden – da Schafe feuchte Bereiche meiden – nur zwei Typen der Beweidungsintensität unterschieden: intensive und keine Beweidung. Zusätzlich wurden sowohl in den Steppen als auch in den Feuchtwiesen entsprechend ihrer Entstehungsgeschichte primäre und sekundäre Bestände unterschieden. Die sekundären Bestände wurden ausschließlich gemäht (nicht beweidet), während in den primären Beständen alle drei Beweidungstypen (intensiv, moderat, keine Beweidung) realisiert waren. Insgesamt wurden so sieben Kombinationen (im folgenden kurz Habitattypen) unterschiedlicher Beweidung bzw. Vegetation unterschieden: IGPS = primäre Steppe mit intensiver Beweidung; MGPS = primäre Steppe mit moderater Beweidung; NGPS = primäre Steppe ohne Beweidung; NGSS = sekundäre Steppe ohne Beweidung; IGPW = primäre Feuchtwiese mit intensiver Beweidung; NGPW = primäre Feuchtwiese ohne Beweidung; NGSW = sekundäre Feuchtwiese ohne Beweidung.

Für jeden Habitattyp wurden drei Gebiete ausgewählt und darin auf jeweils 50 zufällig ausgewählten 50 × 50 cm-Quadraten alle Gefäßpflanzenarten bestimmt. Um Beziehungen zwischen Diversität und Habitattyp zu untersuchen, wurde für jeden Habitattyp die kumulative Gesamtartenanzahl (im Folgenden „Artenreichtum“ genannt) und die mittlere Artenzahl pro 50 × 50 cm-Quadrat (im Folgenden kurz „kleinräumige Diversität“) ermittelt. Unterschiede in der kleinräumigen Diversität zwischen den Vegetationstypen wurden mithilfe von *Linear mixed models* mit dem Gebiet als Zufallsfaktor und der Beweidungsintensität als festem Faktor untersucht. Um den Effekt der Beweidung und der Nutzungsgeschichte auf die Zusammensetzung der Vegetation zu untersuchen, wurden die Daten für jede der 21

Gebiete zusammengefasst und eine Redundanzanalyse mit Beweidungsregime (intensiv, moderat, keine), Nutzungsgeschichte (primär, sekundär) und Feuchtetyp (Steppe, Feuchtwiese) als Faktoren durchgeführt.

Die vorkommenden Arten wurden auf Grundlage des Systems von BORHIDI (1995) sechs funktionellen Gruppen zugewiesen: natürliche Konkurrenzarten, generalistische stresstolerante Arten, spezialisierte stresstolerante Arten, natürliche Pionierarten, störungstolerante Arten, Störungszeiger und nichteinheimische Arten. Aus den gruppierten Daten jedes Vegetationstyps wurden die relativen Anteile der Gruppen errechnet und die resultierenden Spektren evaluiert.

Ergebnisse – Insgesamt zählten wir auf den Probenflächen 191 Gefäßpflanzenarten, darunter 16 Arten der Roten Liste (Anhang E1). In den Steppen war der Artenreichtum unter moderater Beweidung am höchsten; vor allem in nicht beweideten Flächen war der Artenreichtum hingegen geringer. Zudem waren sekundäre Steppen mit etwa halb so vielen Arten wie in den moderat beweideten Steppen am wenigsten artenreich. In den Feuchtwiesen führte Beweidung ebenfalls zu einem höheren Artenreichtum; allerdings waren die Unterschiede zwischen primären und sekundären Feuchtwiesen weniger stark ausgeprägt (Tab. 1).

Unbeweidete und intensive beweidete primäre Steppen unterschieden sich nicht in ihrer kleinräumigen Diversität; moderat beweidete Steppen hatten jedoch eine signifikant höhere Diversität. Zudem waren sekundäre Steppen weniger divers als primäre Steppen. In Feuchtwiesen führte intensive Beweidung zu einer signifikanten Zunahme der kleinräumigen Diversität im Vergleich zu unbeweideten Bereichen. Sekundäre Feuchtwiesen waren weniger divers als primäre Bestände; dieser Unterschied war allerdings lediglich marginal signifikant (Tab. 2, Abb. 3). Feuchtetyp und Beweidungstyp hatten in der RDA-Ordination einen signifikanten Effekt auf die Artenzusammensetzung, während die Geschichte der Flächen sich nicht signifikant auswirkte (Tab. 3, Abb. 4).

In Steppen wurden Konkurrenzarten durch Beweidung tendenziell unterdrückt, während Pionierarten gefördert wurden. Störungszeiger nahmen in den primären Typen mit zunehmender Beweidungsintensität tendenziell zu, der höchste Anteil wurde aber in den sekundären Steppen erreicht (Abb. 5). In Feuchtwiesen kamen störungstolerante Arten unter intensiver Beweidung tendenziell häufiger vor, während die anderen funktionellen Gruppen keinen Trend hinsichtlich der Beweidungsintensität zeigten (Abb. 6). Die Spektren der funktionellen Gruppen waren in primären und sekundären Feuchtwiesen ähnlich, obwohl in den sekundären Feuchtwiesen die Spezialisten fehlten.

Diskussion – Unsere Ergebnisse zeigen, dass die Beweidungsintensität einen signifikanten Effekt auf die Artenzusammensetzung gemähter Steppen und Feuchtwiesen hat. Artenreichtum und kleinräumige Diversität waren in beweideten Flächen höher als in unbeweideten Flächen und die Gesellschaftsstruktur war in beweideten Steppen komplexer. Daraus kann geschlossen werden, dass eine hohe Diversität nicht durch Mahd alleine sondern nur durch eine Kombination aus Mahd und Beweidung erhalten werden kann. In der Turjánvidék-Region wäre daher eine Wiederaufnahme einer bevorzugt moderaten Beweidung der brachgefallenen Gebiete sehr vorteilhaft. Kurzfristig sollte dies durch Neuverteilung des derzeitig verfügbaren Viehbestands erreicht werden und langfristig durch eine Vergrößerung des Viehbestands.

Unsere Ergebnisse zeigen ebenfalls, dass Steppen und Feuchtwiesen nicht gleich empfindlich auf Beweidung reagieren. Zwar waren die Trends des Artenreichtums in Steppen und Feuchtwiesen ähnlich, aber wir konnten keinen Unterschied in der kleinräumigen Diversität zwischen primäre Steppe mit intensiver Beweidung (IGPS) und primäre Steppe ohne Beweidung (NGPS) feststellen. Im Gegensatz dazu zeigte die primäre Feuchtwiese mit intensiver Beweidung (IGPW) eine signifikant höhere kleinräumigen Diversität als die primäre Feuchtwiese ohne Beweidung (NGPW).Die Analyse der funktionellen Gruppen deutete ebenso darauf hin, dass die Gesellschaften auf Störung unterschiedlich reagieren und bestätigt, dass Steppen bei starker Störung anfälliger für Degradation sind. Dies ist ein weiteres Argument dafür, Weidetiere aus den intensiv beweideten primären Steppen (IGPS) in die unbeweideten primären Feuchtwiesen (NGPW) zu verlagern um in beiden Gesellschaften moderate Beweidung zu bewirken. Der Vergleich von Flächen mit unterschiedlicher Geschichte zeigte, dass sekundäre Steppen eine geringere Artendiversität und eine signifikant geringere kleinräumige Diversität als primäre Steppen aufwiesen. Im Gegensatz dazu konnten wir für die Feuchtwiesen keine unterschiedliche Diversität zwischen sekundären und primären Beständen finden. Daraus kann geschlossen werden, dass Steppen nicht nur empfindlicher gegen Störung sind, sondern auch ihr Regenerationspotenzial schlechter als das der Feuchtwiesen ist. Dies kann durch mindestens zwei Gründe erklärt werden. 1) In sekundären Steppen dominieren ruderale Konkurrenzarten wie *Elymus repens* und *Cynodon dactylon*, die die Sukzession deutlich behindern können. Diese Arten können durch Beweidung unterdrückt werden (TÖRÖK et al. 2014) und daher wäre Beweidung hier vorteilhaft. 2) I. d. R. sind die Steppenflecken klein und isoliert; daher sind die Ausbreitungs- und Besiedlungspotenziale von Natur aus unzureichend. Beweidung kann für dieses Problem ebenso eine Lösung sein, aber aktive Maßnahmen wie Heutransfer von primären auf sekundäre Flächen könnte die Wiederherstellung der Diversität zusätzlich unterstützen.

Zusammenfassend schließen wir, dass spontane Sukzession von sekundären Steppen in der Turjánvidék-Region unvollständig ist und daher aktiv unterstützt werden sollte. Trotzdem ist Erhaltung besser als Wiederherstellung. Der Umbruch von Grasland sollte also zukünftig verhindert werden. Dies sollte nicht nur durch Verbote und Strafen, sondern auch durch Steigerung der Attraktivität der Viehwirtschaft für die Landbesitzer durch geeignete EU-Agrar-Umwelt-Programme realisiert werden.

Acknowledgements

The authors thank Csaba Biró, ranger of the Kiskunság National Park, for his help in selecting the study sites. We are also grateful to István Maák and Attila Torma for their suggestions in statistical issues and to the two anonymous reviewers, who contributed to the paper with useful recommendations.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Species list of the studied habitat types.

Anhang E1. Artenliste der untersuchten Habitattypen.

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