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Diversity patterns in transitional grassland areas in floodplain landscapes with different heterogeneity

Diversitätsmuster in Graslandkomplexen von Auen mit unterschiedlicher Landschaftsheterogenität

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Abstract

The complex topography of floodplains provides conditions for high diversity and density of transitional areas between different grassland plant communities. Nevertheless, transitions have been almost completely neglected in previous studies of diversity patterns in semi-natural floodplain grasslands.

We analyzed α-, β- and γ-components of plant species diversity in transitional areas between neighbouring wet and dry grassland communities in two landscapes of the Gauja River floodplain (Latvia) differing in landscape heterogeneity created by land use history and current management type (grazing *versus* mowing). In total 9 transition areas and their adjacent vegetation were sampled in 1 m wide and 8 to 28 m long belt transects gridded into 0.5 m × 1 m plots. Cluster analysis was used to analyze variation in species composition of transitional areas and adjacent vegetation. Indicator species analysis was used to determine species specific to transitional areas (ecotonal species).

Transitional areas of the homogeneous site had a more distinct species composition (clear division in clusters by cluster analysis) and significantly lower β-diversity than those of the heterogeneous site. α-Diversity was significantly higher in transitions than in wet grasslands and lower than in dry grasslands in both sites. Comparing the two sites, α-diversity was significantly higher in wet grasslands of the heterogeneous site, but no differences were found between transitions and dry grasslands in the two sites. Higher β-diversity of transitional areas in the heterogeneous site could be attributed to a higher density of different habitats per unit area in combination with grazing. No species were restricted to transitions, and no differences were apparent in the number of generalist species (indifferent species *sensu* Ellenberg indicator values for edaphic factors) between transitions and adjacent grasslands. Nevertheless, the total number of generalist species was considerably higher in the investigated floodplain grasslands than usually reported for respective vegetation types in Latvia.

It was concluded that transitions of neighboring floodplain grassland plant communities were more important in shaping β-diversity compared to α- and γ-diversity. Our results suggest that destroying transitional areas between dry and wet grasslands by leveling the ground or by abandonment of the management practices will decrease habitat heterogeneity and lead to less pronounced ecotonal processes in the whole riverine landscape. Thus further studies about the role of fine-scale transitional areas for biodiversity of floodplains are important for ecological restoration of floodplain grasslands.

Keywords: boundary, diversity, ecotone, generalists, grazing, mowing

Erweiterte deutsche Zusammenfassung am Ende des Textes

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1. Introduction

In the boreal and nemoral zone of Europe, a high proportion of semi-natural grasslands are located in floodplains. For example, EU Habitats Directive habitat type 6450 (Northern Boreal Alluvial Meadows) covers 43% of all EU-protected semi-natural grassland habitats in Latvia, 22% in Lithuania and 27% in Estonia (ANONYM 2012). Floodplains are disturbance-dominated ecosystems characterised by a high level of habitat and landscape heterogeneity (BAKER 1989, TOCKNER & STANFORD 2002). Microtopography formed by erosional and depositional processes of rivers provide conditions for high diversity and density of transitional areas between different plant communities. Transitional areas (ecotones, ecoclines, boundaries (KENT et al. 1997, STRAYER et al. 2003, KARK & VAN RENSBURG 2006)) are important components of landscape heterogeneity (AHLQVIST & SHORTRIDGE 2010) because much of the floristic diversity at the habitat and landscape scale is attributable to transitional areas (TOCKNER & STANFORD 2002). Transitional areas are influenced both by natural factors and by management activities. Management is a driving factor in the development and patterning of ecotones/ecoclines in human-dominated landscapes (KARK & VAN RENSBURG 2006, DUTOIT et al. 2007).

Theoretical frameworks of ecotones include a hierarchy of spatial scales. Three main spatial levels of transitional areas can be distinguished. Macroecotones are transitions between biomes. Mesoecotones are ecotones on the scale of a landscape (forest-grassland, grassland-fen etc.) or a catena (a sequence of soils and plant communities down a slope, created by the balance of processes such as precipitation, infiltration and runoff). Microecotones are boundaries between individual plants and populations (CADENASSO et al. 2003, PETERS et al. 2006, ERDÖS et al. 2011). Generalisations about transitions may apply only to a subset of boundaries with common attributes (STRAYER et al. 2003).

With regard to structure, mesoecotones differ in the degree of structural complexity. Two main categories can be distinguished. Transitions between two structurally different ecosystems (such as the transition from a system dominated by one life form to a system dominated by another life form, e.g. forest-grassland, grassland-fen, grassland-mire etc.) are boundaries between two systems (KOLASA & ZALEWSKI 1995) and can be considered ecotones of asymmetric interface (VAN DER MAAREL 1990, MARGALEF 1994). The second category includes transitions that are part of a single system (KOLASA & ZALEWSKI 1995). Such transitions develop between two structurally similar ecosystems (both of which are dominated by the same life form, e.g. grassland-grassland, forest-forest etc.) and can be considered environmental ecoclines (VAN DER MAAREL 1990) or symmetric interfaces (MARGALEF 1994). Our research was focused on the symmetric grassland-grassland interface in floodplains, i.e. on mesoscale transitional areas.

Mesoecotones between plant communities within the same vegetation formation at fine spatial scale have gained far less attention in biodiversity studies (e.g. ZALATNAI & KÖRMÖCZI 2004, ZALATNAI et al. 2007) than other types of transitional areas (see KENT et al. 1997, KARK & VAN RENSBURG 2006, HUFKENS et al. 2009 for a review). To our knowledge no biodiversity data are available about catena-scale transitional areas in grassland ecosystem complexes. However, it should be emphasised that transitional areas, regardless of their spatial resolution, have important ecological functions including maintenance of biodiversity (PETTS 1990, PINAY et al. 1990, KOLASA & ZALEWSKI 1995, NAIMAN & DÉCAMPS 1997, MARSHALL & MOONEN 2002, BERGER et al. 2003, STRAYER et al. 2003).

The aim of this research was to assess the diversity of transitional areas between dry and wet semi-natural grasslands in a riverine landscape with reference to landscape heterogeneity.

To reveal the diversity patterns of dry-wet grassland transitional areas, we analyzed species diversity by partitioning it into α-, β- and γ-components. β-Diversity is both turnover (the change in species composition along a spatial or an environmental gradient) and variation (dissimilarity among communities, variance in community structure) (ANDERSON et al. 2011). To address the latter and to reveal the importance of transitional areas in creating grassland community diversity, we also examined community structure by means of cluster analysis. We expected higher spatial heterogeneity of vegetation in transitional areas (higher β-diversity and more clusters in transitional areas than in adjacent vegetation) because of the spatial mosaic of plant assemblages created both from ecotonal species and species of adjacent vegetation (STOWE et al. 2003).

Ecotonal and generalist species are important components of transitional area species diversity. True ecotonal species are species that are restricted to the transitional area and are absent from the two communities flanking the ecotone (WALKER et al. 2003). Transitional areas can possess more generalist species than the neighboring communities because environmental conditions in transitional areas are more stochastic and species with higher dispersal ability and ecological plasticity can establish more easily in transitional areas (ZELENÝ et al. 2010). We hypothesized that transitional areas of dry and wet grasslands will be characterized by the existence of ecotonal species and by higher numbers of generalist species than dry and wet grasslands on either side of the transitional areas.

Finally we examined whether the diversity patterns of dry-wet grassland transitional areas differ depending on landscape heterogeneity. Landscape heterogeneity, alongside with vegetation and land-use history and management practices, is one of the most important landscape-scale factors creating high biodiversity in semi-natural grasslands (COUSINS & ERIKSSON 2001, LINDBORG & ERIKSSON 2004, OKLAND et al. 2006, COUSINS et al. 2007, WELLSTEIN et al. 2007). Landscape heterogeneity is scale-dependent (GOSZ 1993, WIENS 2000) and determined both by natural environmental heterogeneity and by management history (BENTON et al. 2003). The importance of landscape characteristics for species diversity has been shown in several studies: β-diversity is positively associated with spatial heterogeneity (VAN DEN BOS & BAKKER 1990, DE BELLO et al. 2007, KOMAC et al. 2011), species richness is higher in geomorphologically more diverse landscapes (WELLSTEIN et al. 2007), and species richness is promoted by the mass effect or vicinism, which is higher in more heterogeneous landscapes (ZELENÝ et al. 2010). We therefore expected higher plant species diversity in a heterogeneous landscape than in a homogeneous landscape.

2. Material and methods

2.1 Study area

The research was carried out in the middle reaches of the Gauja River Valley, Northern Latvia, in the Protected Landscape Area „Northern Gauja" (Fig. 1). Due to the light sedimentary rocks in the area, the river has formed a characteristic valley landscape with many meanders, oxbow lakes and floodplains. The river flow rate is 800 $m^3 s^{-1}$ during flooding (5–20 days in spring) and 6 $m^3 s^{-1}$ in winter; fluctuations of the water table are 3.2–4.8 m (ĀBOLTIŅŠ 1971). The climate is relatively cool and moist. The average temperature is +5.5 °C (the coldest month is January with -6.5 °C, the warmest July with +16.5 °C). The average annual precipitation is 600 mm.

Fig. 1. Location of the study area.

Abb. 1. Lage des Untersuchungsgebiets.

2.2 Landscape characteristics of the study sites

Two sites differing in landscape heterogeneity and management regime were chosen; they are referred to as the heterogeneous site (grazed) and the homogeneous site (mown) throughout this paper (Fig. 2).

The heterogeneous site was located in the Middle Gauja forested landscape region with a forest cover of 60% (*Pinus sylvestris*-dominated on poor fluvioglacial sandy podzols). Agricultural lands are concentrated mainly in the valley of the Gauja River on sod-gley and alluvial soils.

The homogeneous site was located about 21 km upstream from the heterogeneous site in the Gaujiena-Lejasciems half-open landscape region with extensive tracts of arable fields on sod-gleyic and sod-pseudogley soils and a forest cover of 58% (mostly *Picea abies*-dominated on sod-podzolic soils).

The width of the valley was 3.5 km in the heterogeneous site. Floodplains and terraces were characterized by a much segmented floodplain relief (height differences were 2 m) with many oxbow-lakes of different sizes and depths, oxbow-lake fens, abandoned river beds (channels), levees and small depressions created by floods.

The width of the valley was 1–1.5 km in the homogeneous site. Floodplains were wide and flat with uniform relief. Height differences were 2 m. Oxbow-lakes were mainly wide and not as numerous as in the heterogeneous site.

At a local scale, both sites were dominated by semi-dry grasslands (further referred to as dry grasslands) of the North European alliance *Filipendulo vulgaris-Helictotrichion pratensis* Dengler & Löbel 2003 (*Festuco-Brometea* Br.-Bl. et Tx. ex Klika et Hadač 1944) (DENGLER et al. 2003), mesic *Arrhenatherion* Koch 1926 and *Calthion* Tx. 1937 grasslands on slopes of depressions and wet *Magnocaricion* Koch 1926 communities in depressions and old oxbow-lakes. The homogeneous site contained mostly semi-natural grasslands and old fallow lands and only some trees (Fig. 2, 3). The heterogeneous site was more diverse with a mosaic of secondary scrub, fallow lands and dry and wet grasslands (Fig. 2, 4).

Landscape heterogeneity of both sites was compared using the Shannon-Wiener diversity index, $-\Sigma p_i * \ln p_i$, where p_i is the proportion of the area covered by patch type i (FORMAN 1995). The different habitats included in the calculation were rivers; forests; secondary scrub; dry, moist and wet grasslands

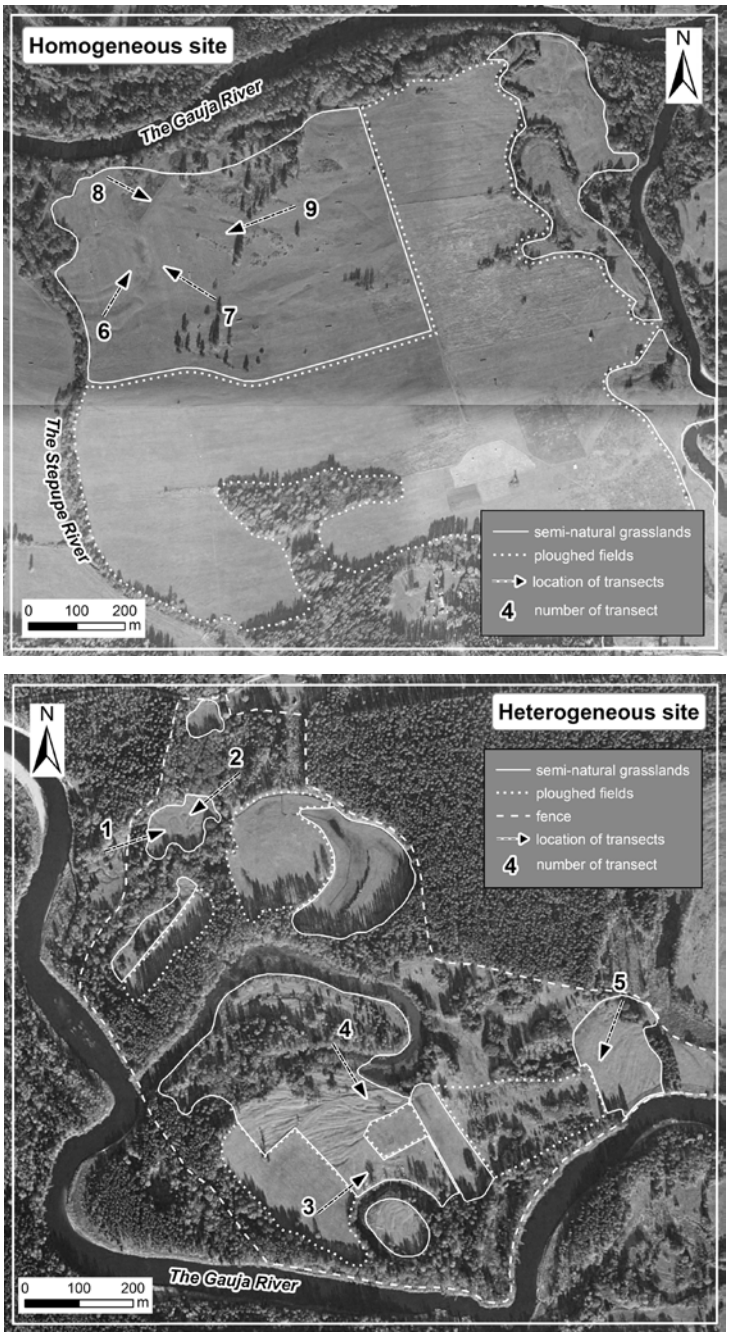

Fig. 2. Location of transects and land-use of study sites between 1950 and 1990. Note the very articulated microrelief creating high habitat density in the heterogeneous site (best visible in the area of transect no. 4).

Abb. 2. Lage der Transekte sowie Landnutzung der Untersuchungsflächen von 1950 bis1990. Beachte das stark ausgeprägte Mikrorelief in dem heterogenen Gebiet (untere Abb.) mit hoher Dichte an verschiedenen Habitaten (besonders gut sichtbar im Bereich von Transekt Nr. 4).

Fig. 3. Characteristic landscape of the heterogeneous site with dry grassland vegetation on levees and wet grasslands in depressions. The left photo is taken in the area where transect no.4. is located. The right photo shows the location of transect no. 2, which was located on the right side of the depression. Wet grassland with *Carex vulpina* was found in the depression. Differences of transitional grassland and dry grassland are smoothed out by grazing.

Abb. 3. Charakteristische Landschaft des heterogenen Gebiets mit trockenem Grasland auf den Dämmen und Feuchtgrasland in den Senken. Das linke Foto wurde im Bereich von Transekt Nr. 4. aufgenommen. Das rechte Foto zeigt die Lokalität von Transekt Nr. 2 (der rechts neben der Senke liegt). In der Senke wächst *Carex vulpina*. Die Grenze zwischen dem Übergangsbereich und trockenem Grasland ist durch Beweidung verwischt.

Fig. 4. Characteristic landscape of the homogeneous site with a flat and wide floodplain. The right photo shows the location of transect no. 8. Wet grassland with a stand of pure *Carex acuta* on the left, transitional grassland with *Alopecurus pratensis* and *Filipendula ulmaria* in the middle and dry grassland with *Helictotrichon pratense* on the right.

Abb. 4. Charakteristische Landschaft des homogenen Gebiets in der weiträumig ebenen Flussaue. Das rechte Foto zeigt die Lage von Transekt Nr. 8. Links ist eine Feuchtwiese mit reinem *Carex acuta*-Bestand zu erkennen, rechts ein trockenes Grasland mit *Helictotrichon pratense*. Dazwischen liegt der Übergangsbereich mit *Alopecurus pratensis* und *Filipendula ulmaria*.

on flat or rugged relief; oxbow-lakes with water or with grassland vegetation as well as oxbow-lakes with steep or flat slopes. For the calculation both research territories were divided into 16 smaller squares, and the diversity index was calculated for each square. The mean of the 16 values was used as a measure of the landscape heterogeneity for each site. The Shannon-Wiener diversity index was 1.29 (standard error 0.12) in the heterogeneous site and 0.92 (SE 0.08) in the homogeneous site. The sites differed significantly in their landscape diversity according to one-way ANOVA ($P < 0.05$).

2.3 Land-use history of study sites

To obtain information on management history, the landowners were interviewed. Until the middle of the 20th century, both sites were divided into small parcels for local farmers (about 4 ha per farm). Each farmer had meadows (mown in the end of June with horse mower or scythe and subsequently grazed) and small fields fertilized by stable dung on their parcel of land. Starting in the 1950s, some areas were leveled (this was done in larger areas in the homogeneous site) and converted into fields treated with artificial fertilizers. Grassland strips around oxbow-lakes and unlevelled grasslands were left as meadows, and the remaining moist and wet grassland strips were grazed. In the heterogeneous site, abandonment started in 1990. Some patches were abandoned in 1992/1993, some only in 2003, and several patches were not abandoned. Mowing of overgrown areas was resumed in 2001–2003; in 2004 a pasture was established (fenced area is shown in Fig. 2). Cattle (Charolais beef breed) grazing pressure was about 1.5 animals per ha, and grazing was performed all year round with supplementary hay feeding in winter. In the homogeneous site, the entire area was abandoned at the same time in 1994. Mowing with hay removal was resumed in 2000. Late mowing after July 15 was introduced in 2004. Grazing has not been reintroduced.

2.4 Transects

Transects were chosen to encompass the range of visual variation in dry-wet grassland transitional areas. They were located in grassland patches that have never been ploughed or fertilised according to the knowledge of the grassland owners. Fieldwork was done in July 2009. For each transect the elevation profile relative to the lowest point was obtained using a theodolite at 0.5–2 m intervals. In total, nine 1 m wide and 8 to 28 m long belt transects (gridded into 0.5 m × 1 m plots) were sampled. Five transects were sampled in the heterogeneous and four transects in the homogeneous site (Figs. 2–4). Each transect was visually divided into three sections: wet, transitional and dry grassland. The transitional section was sampled entirely (in contiguous 1 m × 0.5 m plots). Five contiguous plots were also sampled in both wet and dry sections starting from the visual border between the transitional and the wet/dry section. In addition, plots with a distance of 1.5 m between them were sampled in dry and wet grasslands up to the middle of the grassland patch. In total 15 to 32 plots were sampled per transect. Only15 plots could be sampled in patches where narrow strips of wet grasslands were intersected by narrow ridges (Fig. 4). The cover of each herbaceous species was estimated using Braun-Blanquet cover classes (+ – less than 1%, 1 – 1–5%, 2 – 6–25%, 3 – 26–50%, 4 – 51–75%, 5 – 76–100%). Vegetation data were stored in a database using the software program TURBOVEG (HENNEKENS & SCHAMINÉE 2001).

The positions and the widths of the transitional areas were determined by two methods: visually in the field (ZALATNAI et al. 2007) and from DCA (Detrended Correspondence Analysis, HILL & GAUCH 1980) ordination scores using the moving-window regression method (MWR) (WALKER et al. 2003) after fieldwork. After performing preliminary analyses at a range of widths, a 4 m moving window was chosen. DCA was performed with the program PC-ORD 5 (MCCUNE & MEFFORD 1999).

2.5 Data analysis

To analyze species diversity, the Shannon-Wiener diversity index and Pielou's evenness index ($H'/\ln S$) were calculated (KENT & COKER 1994). Five plots from both ends (dry and wet) of each transect and five plots (in two transects with narrow transitional areas only four plots were present) from the middle of the transitional area were used in the analysis. The α-, β- and γ-components of species diversity were partitioned in a multiplicative way ($\beta = \gamma / \alpha$) as suggested by WHITTAKER (1960, cited in LEGENDRE et al. 2005).

To compare species composition of transitional areas and adjacent vegetation, Cluster Analysis (Sørensen distance measure, beta-flexible clustering (flexible beta set to −0.25)) was used. Cluster Analysis was performed separately for the heterogeneous and the homogeneous site. All transects of each site were pooled. The number of clusters was set to 15 for the heterogeneous site (5 transects multiplied by 3 sections (wet, transitional, dry) per transect) and 12 for the homogeneous site (4 tran-

sects). Classification stability was determined by without-replacement bootstrap resampling with Goodman-Kruskal's lambda (TICHÝ et al. 2011). Sørensen's dissimilarity (%) of vegetation in wet, transitional and dry sections of the transects was calculated with the software program JUICE (TICHÝ 2002).

Indicator Species Analysis (DUFRENE & LEGENDRE 1997) was used to determine ecotonal species specific to transitional areas. Species classified as indifferent with respect to moisture, nitrogen or reaction by ELLENBERG (1992) were considered generalist species. Their proportion of all species recorded in a given transect section was calculated. Calculations were done separately for both sites.

Mean Ellenberg indicator values for moisture, reaction and nitrogen (ELLENBERG et al. 1992) were calculated for each plot using the software program JUICE (TICHÝ 2002) to test for edaphic differences between the sites.

Shapiro-Wilk's test of normality was used to test the normality of data. Significances of differences in transitional area metrics, species richness and diversity indices between two sites and among grassland types were evaluated by one-way ANOVA using Tukey's post hoc tests. Significances of differences in mean species richness, evenness and Shannon diversity index between two sites were evaluated by Welch's test because the homogeneity of variance assumption was not met. Differences in mean Ellenberg indicator values and proportions of generalist species were evaluated by non-parametric Wilcoxon test because the data were not normally distributed. Statistical analyses were performed using the software package SPSS for Windows, version 19.0.

Nomenclature for vascular plants followed GAVRILOVA & ŠULCS (1999).

3. Results

3.1 Morphology and site conditions of transitional areas

Transitional area width varied from 1.8 to 8 m. The visual method resulted in wider transitional areas than those obtained by the MWR method. Slope inclination ranged from 7° to 18°, and elevation differences were 0.87 to 1.76 m. Significant differences in mean transect length, length of DCA gradient and transitional area width were found between the sites (Table 1). Ellenberg indicator values indicated very similar edaphic conditions in both sites with the exception of nitrogen values for wet grasslands, which indicated more fertile conditions in wet grasslands of the homogeneous site (Table 2).

3.2 Species diversity

In total 126 species were recorded. 78 species were common for both sites. Comparing the two sites, α-diversity was significantly higher in wet grasslands of the heterogeneous site when compared to the homogeneous site, but no differences were found between the two sites' transitions and dry grasslands (Table 3). Wet grassland γ-diversity was two times higher in the heterogeneous than in the homogeneous site, but transitional areas and dry grasslands did not differ significantly. Transitional area β-diversity was significantly higher in the heterogeneous site indicating that individual transition plots in the heterogeneous site encompassed less species in comparison to the total number of species present in transitions.

At the within-site level, species richness and Shannon diversity index were significantly higher in transitions than in wet grasslands and lower than in dry grasslands in both sites (Table 3). No significant differences were found between the evenness of dry and transitional areas in the heterogeneous site, but the evenness of all sections differed significantly in the homogeneous site. γ-Diversity was lower in wet grasslands than in transitional and dry grasslands in both sites. γ-Diversity of wet grasslands in the heterogeneous site was significantly higher than in the homogeneous site. There was a tendency of β-diversity to be

Table 1. Topography and transitional area width in the nine studied transects of transitional areas in floodplain grasslands. Significant differences between sites are given in bold ($P < 0.05$, one-way ANOVA). Standard errors of means are given in parentheses.

Tabelle 1. Topographie der neun Transekte und Breite der Übergangsbereiche. Signifikante Unterschiede zwischen den beiden Gebieten sind fett dargestellt ($P < 0{,}05$, einfaktorielle ANOVA). Standardfehler der Mittelwerte in Klammern.

	Transect No.	Length of transect (m)	Slope orientation	Relative height of the slope (m)	Slope inclination on transitional area (°)	Length of gradient of DCA axis 1	Transitional area width (visual method)	Transitional area width (MWR method)
Heterogeneous site – Ht	1	16	NW	0.87	7	312	4.0	3.0
Ht	2	13	SW	1.68	18	362	2.0	2.0
Ht	3	13	E	1.25	12	355	2.5	2.0
Ht	4	10	NE	1.35	11	338	1.8	2.5
Ht	5	26	SW	1.24	7	259	3.5	3.0
Average Ht	–	**15.6** (2.8)	–	1.28 (0.13)	11.0 (2.0)	**325** (18.7)	**2.8** (0.4)	2.5 (0.2)
Homogeneous site – Hm	6	21	SE	1.25	13	428	6.0	3.5
Hm	7	28	NW	1.76	13	371	8.0	8.0
Hm	8	16	W	0.90	8	441	5.0	2.5
Hm	9	26	N	1.92	12	533	4.5	5.0
Average Hm	–	**23.0** (2.6)	–	1.46 (0.23)	11.5 (1.2)	**443** (33.6)	**5.9** (0.8)	4.8 (1.2)

Table 2. Mean Ellenberg indicator values and standard deviations for edaphic conditions in wet, transitional and dry sections of transects in the homogeneous and the heterogeneous sites of floodplain grasslands. Significant ($P < 0.05$, Wilcoxon test) differences between sites are given in bold. Hm – homogeneous site, Ht – heterogeneous site

Tabelle 2. Mittlere Ellenberg-Zeigerwerte (mit Standardabweichungen) der Standortbedingungen im feuchten (Wet) und trockenen (Dry) Bereich sowie im Übergangsbereich (Transitional) entlang der Transekte in einem homogenen (Hm) und einem heterogenen (Ht) Auengebiet. Signifikante ($P < 0{,}05$, Wilcoxon-Test) Unterschiede sind fett dargestellt.

Parameter	Wet		Transitional		Dry	
	Ht	Hm	Ht	Hm	Ht	Hm
No. of relevés	32	20	35	20	35	20
Ellenberg moisture	7.55 ± 0.40	7.71 ± 0.79	6.53 ± 0.77	6.13 ± 0.74	5.20 ± 0.32	5.04 ± 0.19
Ellenberg nitrogen	**4.68** ± 0.50	**5.54** ± 0.96	4.32 ± 0.46	4.67 ± 0.69	3.87 ± 0.32	3.80 ± 0.36
Ellenberg reaction	6.72 ± 0.53	6.55 ± 0.35	6.18 ± 0.43	6.27 ± 0.51	6.10 ± 0.37	5.88 ± 0.32

higher in the transitional area than in adjacent dry and wet grasslands in the heterogeneous site. In contrast, in the homogeneous site, β-diversity of the transitional area was lower (significantly in comparison to wet grasslands) than in adjacent communities (Table 3).

Cluster analysis revealed different patterns in the two sites (Table 4). In the heterogeneous site, no clear division between wet and transitional transect sections was obtained – half of the transitional grassland plots were classified as dry grassland, and almost half of all wet grassland plots were classified as transitional grassland. In the homogeneous site, classification by cluster analysis was more similar to the division of the plots into three sections according to their position in dry, transitional, or wet grassland sections. Dry grasslands were

Table 3. Species diversity partitioned in α-, β- and γ-component in wet, transitional and dry grasslands in the homogeneous and heterogeneous floodplain sites. Letters indicate significant ($P < 0.05$) differences among grassland types within each site according to one-way ANOVA with Tukey post hoc tests; SD = standard deviation, P = significance level of differences between sites (ANOVA), n.s. = not significant.

Tabelle 3. α-, β- und γ-Bestandteile der Artendiversität des feuchten (Wet) und trockenen (Dry) Graslands sowie des Übergangsgraslands (Transitional) in einem homogenen und einem heterogenen Auengebiet. Buchstaben zeigen signifikante Unterschiede ($P < 0{,}05$; einfaktorielle ANOVA mit Tukey-*Post-hoc*-Test) zwischen den drei Graslandtypen innerhalb eines Gebiets; SD = Standardabweichung, P = Signifikanzniveau der Unterschiede zwischen Flächen; n.s. = nicht signifikant.

	Heterogeneous site	SD	Homogeneous site	SD	P
Total diversity in a site calculated from mean values of transects					
α-diversity: Species richness	20.32	2.50	19.88	3.51	n.s.
β-diversity	3.22	0.44	3.41	0.67	n.s.
γ-diversity	65.45	3.06	66.25	4.78	n.s.
Diversity in wet, transitional and dry transect sections calculated from mean values of respective sections					
α-Diversity: Species richness					
Wet	12.92 [a]	2.45	5.70 [a]	2.66	< 0.05
Transitional	23.13 [b]	8.20	21.45 [b]	8.53	n.s.
Dry	30.05 [c]	3.50	32.50 [c]	3.71	n.s.
α-Diversity: Shannon index					
Wet	1.72 [a]	0.32	0.84 [a]	0.52	< 0.05
Transitional	2.32 [b]	0.29	2.16 [b]	0.48	n.s.
Dry	2.54 [c]	0.55	2.66 [c]	0.20	n.s.
α-Diversity: Evenness					
Wet	0.67 [a]	0.10	0.47 [a]	0.18	< 0.05
Transitional	0.74 [b]	0.08	0.71 [b]	0.09	n.s.
Dry	0.74 [b]	0.07	0.76 [c]	0.04	n.s.
β-Diversity					
Wet	1.80 [ac]	0.31	1.87 [a]	0.20	n.s.
Transitional	1.90 [a]	0.11	1.63 [b]	0.14	< 0.05
Dry	1.64 [bc]	0.12	1.66 [ab]	0.20	n.s.
γ-Diversity					
Wet	23.30 [b]	3.31	10.50 [b]	5.00	< 0.05
Transitional	44.00 [a]	1.40	35.00 [a]	13.93	n.s.
Dry	48.00 [a]	5.34	53.50 [a]	2.65	n.s.

Table 4. Distribution of plots (%) of wet, transitional and dry grasslands in the first three clusters of the cluster analysis performed separately for the heterogeneous and the homogeneous site.

Tabelle 4. Verteilung der Probeflächen (in %) auf das feuchte (Wet), trockene (Dry) und Übergangsgrasland (Transitional) für die ersten drei Aufnahmegruppen der Cluster-Analyse bzw. das heterogene und homogene Gebiet.

	Heterogeneous site			Homogeneous site		
Cluster	1	2	3	1	2	3
Wet grassland	52	48	0	83	17	0
Transitional grassland	0	47	53	0	67	33
Dry grassland	0	0	100	0	0	100

classified correctly in both areas (Table 4). Analysis of classification stability resulted in Goodman-Kruskal's lambda values from 71 to 86 in the heterogeneous and from 82 to 98 in the homogeneous site indicating that the classification of the heterogeneous site plots was less stable and vegetation gradients were more gradual there.

3.3 Ecotonal species

Indicator species analysis resulted in determination of indicator species – species with significantly higher abundance in one grassland type compared to the other two types (Appendix 1). The highest number of such species was obtained in dry grasslands, followed by wet grasslands. The lowest number of indicator species was observed in the transitional area in both sites although the total number of species was higher in this section compared to wet areas. There were almost no true ecotonal species (species with high abundance restricted to transitional areas). Although species richness was intermediate in transitional areas, the number of indicator species for transitional areas was the lowest. Transitional areas of the heterogeneous site had six and of the homogeneous site four species that occurred only in transitional areas, but since their constancy was only 13–34%, they cannot really be called ecotonal species. Species occurring only in transitional areas were species typical for moist grasslands, e.g. *Thalictrum flavum*, *Elytrigia repens*, *Lysimachia vulgaris*, *Anthriscus sylvestris*, *Alopecurus pratensis*, *Deschampsia cespitosa*, *Filipendula ulmaria*, *Inula salicina* (Appendix 1). Such a pattern indicates that environmental conditions in transitional areas were intermediate between those of the adjacent communities and species with higher occurrence in transitional areas were adapted to these conditions. Therefore, the species composition of transitional areas was similar to dry and wet grasslands, but species abundances were different.

The proportion of generalist species (indifferent species *sensu* Ellenberg indicator values for edaphic factors – moisture, nitrogen and reaction) was intermediate in transitional areas compared to wet and dry sections in both sites. The lowest proportion of generalist species was found in wet sections. However, in the heterogeneous site, the difference in the proportions of generalist species was significant ($P < 0.05$) only between wet and dry sections, but not between wet and transitional sections. Transitions in the homogeneous site contained more moisture generalists, but less nitrogen generalists, than transitions in the heterogeneous site (Fig. 5).

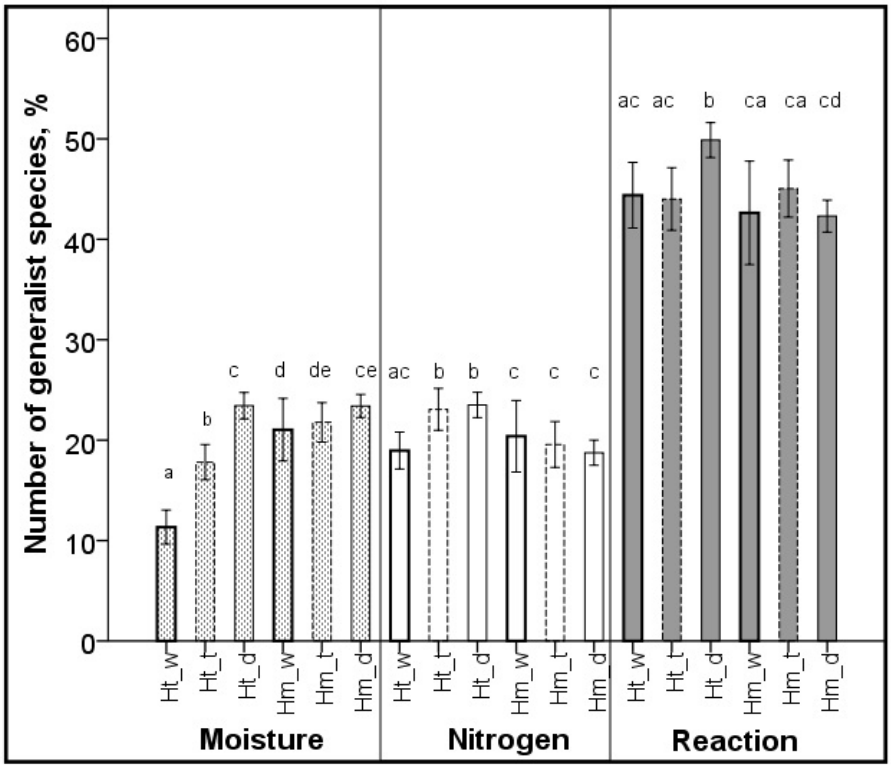

Fig. 5. Percentages (%) of generalist species (species classified as indifferent with respect to moisture, nitrogen or reaction by ELLENBERG (1992)) in wet, transitional and dry grasslands in the homogeneous and the heterogeneous floodplain grassland sites. Ht – heterogeneous site, Hm – homogeneous site. Bold line – wet section, punctuated line – transition, solid line – dry section. Bars represent 2 standard errors; different letters indicate significant differences (Wilcoxon test, $P < 0.05$) among sections of the same site and between the same sections of both sites.

Abb. 5. Prozentsätze an generalistischen Arten (indifferente Arten hinsichtlich der Ellenberg-Zeigerwerte für Feuchte, Nährstoff und Reaktion) im feuchten, trockenen und Übergangsgrasland in einem homogenen (Hm) und einem heterogenen (Ht) Auengebiet. Fette Linie – feuchter Transektabschnitt, Punktlinie – Ökoton, durchgezogene Linie – trockener Transektabschnitt. Balken zeigen zweifache Standardfehler und unterschiedliche Buchstaben signifikante Unterschiede (Wilcoxon-Test, $P < 0{,}05$) zwischen gleichen Transektabschnitten innerhalb eines Gebiets bzw. zwischen beiden Gebieten.

4. Discussion

4.1 Species diversity patterns of grassland-grassland transitional areas

Most of the transitions previously described are transitions between two structurally different ecosystems. Few studies can be found dealing with transitions between structurally similar vegetation types (e.g. KIMSA 1991, ZALATNAI & KÖRMÖCZI 2004, ZALATNAI et al. 2007, MUNOZ-REINOSO 2009, TSUYUZAKI & HARAGUCHI 2009, BECKER et al. 2012), but none of them describes diversity patterns of transitional areas. We hereby discuss our results in the framework of general relationships described for ecotones at different spatial scales.

Species richness and Shannon diversity index were intermediate in transitional areas in this study, but closer to the higher-diversity community (dry grassland) than to the lower-diversity community (wet grassland). In other studies of hydro-ecotones (transitions governed by steep groundwater level gradients), varying results have been obtained (LLOYD et al. 2000, WALKER et al. 2003). It is likely that species richness in grassland-grassland transitional areas is not governed purely by ecotonal processes (e.g. community patchiness, spatial mass effect, environmental stochasticity). Instead, environmental factors that govern species richness in semi-natural grasslands could be more important, the most important being moisture, nutrient availability and management (SCHAFFERS 2002, PYKÄLÄ 2005, MERUNKOVÁ & CHYTRÝ 2012).

Our results are consistent with the observed diversity gradients along moisture and nutrient gradients in Northern and Central European semi-natural grasslands where species richness is the highest in areas with intermediate moisture availability (SHAFFERS 2002). In our study the highest species richness was observed in dry grasslands where the mean Ellenberg indicator value was 5.0–5.2 indicating their intermediate position in the moisture gradient. In floodplains a gradient of increasing moisture is generally also associated with increasing nutrient availability (WASSEN et al. 2003, XIAO et al. 2012).

We hypothesized that transitional areas between dry and wet grasslands will be characterized by ecotonal species and more generalist species than in dry and wet grasslands. However, no such pattern was visible in the studied transitional areas. The proportions of species indifferent to moisture, nitrogen and soil reaction were not higher in transitional areas. These results suggest that the vegetation adjacent to transitional areas experiences the same amount of disturbance and environmental stochasticity as the transitional areas themselves. It can be concluded that the studied transitional areas belong to the hierarchy of transitions in a riverine ecosystem where both wet and dry grasslands together with their transitions act as a part of a hierarchical ecotonal system between stream and upland environment (DÉCAMPS et al. 2004, VERRY et al. 2004). Patterns of transitional areas at this spatial scale may be less pronounced because of the governing patterns of higher level ecotonal processes (STOWE et al. 2003, YARROW & SALTHE 2008).

This interpretation is supported by the fact that the total number of generalists was considerably higher in the studied grasslands than usually reported for respective vegetation types in Latvia outside floodplains. Dry grasslands of *Festuco-Brometea* have on average 14% moisture generalists, 35% reaction generalists and 14% nitrogen generalists (RŪSIŅA 2007), but dry grassland sections in this research contained 19–23% moisture generalists, 42–50% reaction generalists and 19–23% nitrogen generalists (Fig. 4). Thus our study supports the hypothesis that floodplain grasslands contain more generalists and fewer specialists than upland grasslands because of annual flood disturbance creating environmental stochasticity (MOUW & ALABACK 2003, TOOGOOD et al. 2008, JUNG et al. 2009).

4.2 Effect of landscape heterogeneity

We expected higher β-diversity in transitional areas. It was true for the heterogeneous site, but not for the homogeneous site for which both partitioning of species diversity and cluster analysis results indicated low β-diversity. In the homogeneous site, β-diversity of the transitional section was the lowest in comparison to the adjacent wet and dry sections, and the vegetation composition in the transition was more distinct from the adjacent vegetation (the ecotone between dry and wet grassland was more pronounced, sharper) than that of the heterogeneous site.

As transitional areas in both sites did not differ significantly in slope inclination, elevation or edaphic conditions (characterised by Ellenberg indicator values), the explanation of observed patterns is likely to be connected with differences in landscape heterogeneity and management.

Although all studied transitional areas were located in patches that have never been ploughed or fertilized, the surroundings of both sites differed in landscape heterogeneity created both by topographical factors (amount and diversity of microrelief forms) and by human activities (management practices and land-use history). Higher β-diversity of transitional areas in the heterogeneous site could be created by a higher density of different habitats per unit area in combination with grazing. Grazing can both increase and decrease spatial heterogeneity, and the effect is scale-, time- and environment-dependent (GIBSON 1988, ADLER et al. 2001, FISCHER & WIPF 2002, YARROW & SALTHE 2008, ROSENTHAL et al. 2012). Grazing can create higher β-diversity because a more complex vertical and horizontal structure of vegetation in pastures promotes micro-scale patchiness and β-diversity is positively associated with spatial habitat heterogeneity (VAN DEN BOS & BAKKER 1990, DE BELLO et al. 2007, KOMAC et al. 2011, ROSENTHAL et al. 2012). Similar results have been obtained in a grazing *versus* mowing experiment in floodplain grasslands in Germany (SCHAICH & BARTHELMES 2012) where six years of mowing created higher small-scale species density and grazing created higher patchiness. Grazing also promotes species dispersal across habitats (BAKKER et al. 2008) and could thereby promote the mass effect or vicinism (HOBOHM & HÄRDTLE 1997), which is reported to be an important transitional area property (STOWE et al. 2003, WALKER et al. 2003, ZELENÝ et al. 2010). The mass effect could be more pronounced in the heterogeneous site also because of the high density of different habitats created by microtopography.

If grazing has increased β-diversity at community scale in transitions, why did not it affect wet and dry grassland community heterogeneity? Wet grasslands of both sites did not differ in β-diversity, but there were significant differences in α- and γ-diversity. The heterogeneous site was significantly richer in species both on a plot level and in total number of species per wet section of a transect. Higher α- and γ-diversity could be created by the already mentioned mass effect as most wet grasslands were located in narrow depressions (3–4 m); in addition, cattle trampling could create microtopography promoting the establishment of new species (METERA et al. 2010, ROSENTHAL et al. 2012).

No changes in β-diversity of wet grasslands and no differences in α-, β- and γ-diversity of dry grasslands between sites could be attributed to the rather short history of grazing in the heterogeneous site – it had taken place for only five years and in low stocking density. Several studies have shown that at least three to five years are needed to induce substantial changes in vegetation after the introduction of grazing (BARBARO et al. 2001, PYKÄLÄ 2005, SCHAICH et al. 2010). Concerning wet grasslands it is reported that cattle avoid wet places if mesic and dry ones are available (HESSLE et al. 2008) or graze them mostly in spring when young sedge and grass leaves are soft (GÜSEWELL et al. 2007, HESSLE et al. 2008). In wet grasslands early spring grazing is very important as defoliation creates places for germination of herb species. In fact, grazing in wet grasslands occurred at the heterogeneous site mainly in early spring when tall sedge species (*Carex vesicaria*, *C. acuta*, *C. vulpina* etc.) and graminoids (mainly *Phalaris arundinacea*) were soft (personal observation). In contrast, mowing in late summer after July 15 in the homogeneous site could lead to dominance of tall sedges and graminoids and increase competition for light for forb species, thus decreasing α-diversity (OOMES et al. 1996, GREVILLIOT et al. 1998, HÄRDTLE et al. 2006).

4.3 The importance of transitional areas for shaping grassland diversity in floodplains

We studied fine-scale environmental transitions in floodplain grasslands created by differences in groundwater availability, which is related to topography. Such transitions are inherent in a hierarchy of ecotones within the larger floodplain ecotone and contribute to biodiversity maintenance in floodplain ecosystems (WARD et al. 1999, 2002, DÉCAMPS et al. 2004, VERRY et al. 2004).

Transitional areas can contribute to plant diversity via mass and rescue effect (HOBOHM & HÄRDTLE 1997, STOWE et al. 2003, WALKER et al. 2003, LEIBOLD et al. 2004). Although our research did not focus on the analysis of mass effect, our results suggest that a transitional area can serve both as recipient and donor of propagules, thus enhancing species diversity both in the transitional area and in the adjacent vegetation. In our case mass effect was least pronounced in wet grasslands (the most distinct flora) and most pronounced in dry grasslands where species of wet grasslands (e.g. *Phalaris arundinacea*, *Trollius europaeus* and *Poa palustris*) occurred together with typical dry grassland species (*Filipendula vulgaris* and *Helictotrichon pratense*). The presence of mass effect in the research area is also consistent with the fact that the flora was rich in generalists. Mass effect is reported to be associated with higher numbers of generalists in the flora as they can establish populations in sink habitats more easily than specialists (ZELENÝ et al. 2010).

Another important function of transitional areas in shaping floodplain biodiversity is to sustain the dynamic equilibrium in a floodplain over decades. Landscape dynamics depends on the diversity and spatial configuration of transitions in the landscape (PETERS et al. 2006). The studied wet-dry grassland transitions are ”stationary transitional areas“ according to PETERS et al. (2006). They are relatively stable over time and controlled by inherent abiotic constraints, namely differences in the groundwater table, which result from a sharp elevation gradient. To some degree our studied transitions also possess characteristics of shifting transitions. The latter are governed by strong abiotic drivers not reinforced through time (neither by biotic nor by abiotic feedback mechanisms) or by abiotic constraints (PETERS et al. 2006). These drivers are flooding and groundwater level changes among years (dry and wet years) creating favorable conditions for one or another end state and triggering an increasing abundance of dry or wet species for a period of time. In this aspect the studied transitions are completely different from similar situations outside floodplains (e.g. hill top, slope and the foot) where no strong abiotic drivers are acting.

Our research indicated that transitional areas have the potential to sustain species of wet and dry grasslands in extremely dry or wet periods as about 50% of wet and 45–65% of dry grassland species also occurred in transitional areas. Thus transitions are very dynamic and linked to local species pools of both wet and dry grasslands.

Our results show that grassland-grassland transitional areas are more important in shaping β-diversity and, consequently, community diversity of floodplain grasslands than in shaping γ-diversity. Transitional areas, in comparison to wet and dry grasslands, maintained specific plant assemblages, but almost no unique plant species. A similar pattern has been observed in other studies of transitional areas (LLOYD et al. 2000, WALKER et al. 2003, ZALATNAI & KÖRMÖCZI 2004). The importance of transitional areas for γ-richness of grasslands was higher in the homogeneous site as wet grasslands were species-poor and species of moist places were mostly present in transitional areas in the homogeneous site.

Regarding the hierarchy of ecotones in a riverine landscape, we can hypothesize that decreasing lower-level heterogeneity (e.g. destroying transitional areas between dry and wet grasslands by leveling the ground or by abandonment of the management practices) leads to

less pronounced ecotonal processes in the whole riverine landscape. This should be taken into account in the evaluation of restoration success. The majority of floodplain grassland restoration deals with the resumption of floods or rewetting but is not concerned with the restoration of floodplain microrelief (MANCHESTER et al. 1999, NIENHUIS & LEUVEN 2001, TOCKNER & STANFORD 2002, HÄRDTLE et al. 2006). Further research is needed to reveal the role of local scale transitional areas in structuring species richness patterns within the larger floodplain ecotone, e.g. in the framework of the metacommunity concept (LEIBOLD et al. 2004). Further research should combine several spatial scales and temporal dimensions in order to make generalisations about feedbacks between vegetation and management in the context of ecotone hierarchy and their functions. More case studies are needed to give an insight into the generality of patterns of species diversity and functions of transitional areas in grassland complexes.

Erweiterte deutsche Zusammenfassung

Einleitung – Die vielschichtige Topographie von Flussauen ist Vorrausetzung für eine hohe Diversität und Dichte an Ökotonen und damit auch für zahlreiche Übergänge zwischen verschiedenen Graslandgesellschaften. Ökotone sind ein wichtiges Landschaftselement da sie erheblich zur floristischen Diversität sowohl auf Habitats- wie auch auf Landschaftsebene beitragen. Wir untersuchten den Ökoton zwischen Buckeln/Wällen und Senken im Grasland von Flussauen. Auf den Buckeln/Wällen wuchs trockenes Grasland der Verbände *Filipendulo vulgaris-Helictotrichion pratensis* (*Brachypodietalia*, *Festuco-Brometea*) und *Arrhenatherion* und in den Senken feuchtes Grasland des *Calthion* und *Magnocaricion*. Nach unserem Wissen liegen für solche Ökotone bislang keine Biodiversitätsdaten vor. Das Ziel der Untersuchung war die Einschätzung der Diversität des halbnatürlichen Graslands im Übergangsbereich von trockenen zu feuchten Auenstandorten in Beziehung zur Landschaftsheterogenität. Wir vermuteten, dass sich die Übergangsbereiche durch spezifische Arten sowie eine höhere Beta-Diversität und auch eine höhere Anzahl an Generalisten als die angrenzenden, entweder trockenen oder feuchten Bereiche, auszeichneten. Gleichzeitig erwarteten wir in einer heterogen strukturierten Landschaft mit hoher Dichte an Ökotonen eine höhere Pflanzenartendiversität als in einer homogen strukturierten Landschaft mit geringer Dichte an Ökotonen.

Material und Methoden – Wir untersuchten die α-, β- und γ-Pflanzenartendiversität des Graslands im Übergangsbereich von benachbarten feuchten und trockenen Standorten in zwei Auengebieten der Gauja (Letland) mit einer durch die frühere und heutige Landnutzung (Weide bzw. Mahd; Abb. 1–4) bedingten unterschiedlichen Landschaftsheterogenität. Auf lokaler Ebene dominierte in beiden Gebieten halbtrockenes Grasland. Das homogen strukturierte Auengebiet enthielt überwiegend halbnatürliches Grasland und altes Brachland mit wenigen Bäumen (Abb. 2, 3). Das heterogene Auengebiet war dagegen vielfältiger strukturiert und zeigte ein Mosaik aus Gebüschen, Brachen sowie trockenem und feuchtem Grasland (Abb. 2, 4). Die Landschaftsheterogenität nach dem Shannon-Index lag in dem heterogenen Gebiet bei 1,29 und in dem homogenen bei 0,92 ($P < 0{,}05$; einfaktorielle Varianzanalyse). Die Vegetation des visuell erkennbaren Übergangsbereichs zwischen feuchtem und trockenem Grasland wurde entlang von Linientransekten aufgenommen. Diese lagen in Graslandbeständen, die nach Auskunft der Besitzer nie gepflügt oder gedüngt worden waren. Insgesamt wurden 9 solche Übergangsbereiche untersucht. Dazu wurden 1 m breite und 8–28 m lange Linientransekte, welche in 0,5 m × 1 m-Flächen unterteilt wurden, angelegt. Die α-, β- und γ-Komponenten der Artendiversität wurden multiplikatorisch aufgeteilt ($\beta = \gamma / \alpha$). Um die Übergangsbereiche und angrenzenden Bereiche zu vergleichen, wurde eine Cluster-Analyse (Sørensen-Distanzen, *flexible beta clustering* mit beta = -0.25) angewendet. *Indicator Species Analysis* wurde angewendet um spezifische Ökotonarten zu identifizieren. Als Generalisten wurden Arten mit indifferentem Verhalten (Zeigerwert „×“ nach ELLENBERG et al. 1992) hinsichtlich Bodenfeuchte, Reaktion und Nährstoffreichtums eingestuft.

Ergebnisse – Die Breite des Ökotons variierte zwischen 1,8 bis 8 m. Die mittlere Transektlänge, Breite des Ökotons und Länge der DCA-Gradienten unterschieden sich signifikant zwischen den beiden Gebieten (Tab. 1). Mit Ausnahme der N-Zeigerwerte im feuchten Grasland zeigten die Ellenberg-Zeigerwerte in beiden Gebieten sehr ähnliche edaphische Bedingungen an (Tab. 2). Die α-Diversität des feuchten Graslands war in dem heterogenen Gebiet signifikant höher als in dem homogenen Gebiet, während sich der Übergangsbereich und auch das trockene Grasland in ihrer α-Diversität zwischen den beiden Gebieten nicht unterschieden (Tab. 3). Die γ-Diversität des Feuchtgraslands war in dem heterogenen Gebiet doppelt so hoch wie in dem homogenen Gebiet. Weder der Übergangsbereich noch der trockene Bereich unterschied sich signifikant zwischen den beiden Gebieten.

In dem heterogenen Gebiet lag die β-Diversität des Ökoton-Graslands lediglich tendenziell höher als im angrenzenden trockenen oder feuchten Grasland. In dem homogenen Gebiet war die β-Diversität im Ökoton-Grasland dagegen signifikant niedriger als im Feuchtgrasland und tendenziell niedriger als im trockenen Grasland. Die Klassifikation der Aufnahmeflächen des heterogenen Gebiets war weniger stabil und die Vegetationsgradienten waren hier gradueller (Tab. 4). Im trockenen Grasland wurden die meisten Zeigerarten festgestellt, die zweitmeisten im feuchten Grasland (Anhang 1). In beiden Gebieten wurden im Übergangsgrasland jeweils die wenigsten Zeigerarten beobachtet, obwohl dort die Gesamtartenzahl zumindest im Vergleich zum Feuchtgrasland höher lag. Der Anteil der Generalisten lag im Übergangsgrasland im intermediären (zwischen dem trockenen und feuchten) Bereich (Abb. 5).

Diskussion – Wahrscheinlich wird der Artenreichtum im Übergangsbereich verschiedener Graslandgesellschaften nicht allein durch spezielle Ökotoneffekte, wie z. B. die *patchiness* der Gesellschaften, den Vizinismus sowie die Umweltstochastizität determiniert. Vielmehr könnten die im halbnatürlichen Grasland allgemein wichtigen Umweltfaktoren Feuchte, Nährstoffversorgung und Bewirtschaftungsart für den Artenreichtum des Ökotons maßgebend sein. Wir hatten vermutetet, dass der Ökoton zwischen trockenem und feuchtem Grasland stärker durch spezifische Übergangsarten und generalistische Arten als durch die Arten des trockenen und feuchten Graslands gekennzeichnet ist. Ein solches Muster war jedoch nicht zu erkennen. Daher vermuten wir, dass sich die an den Ökoton angrenzende Matrix-Vegetation hinsichtlich Störungsintensität und Umweltstochastizität nicht von dem Ökoton unterscheidet. Es kann gefolgert werden, dass die untersuchten Ökotone zu der Hierarchie von Übergängen in einem Flussökosystem gehören, in dem das feuchte und trockene Grasland mitsamt dem Ökoton als Teil eines hierarchischen Ökoton-Ökosystems zwischen der (semi-)aquatischen Umwelt des Flusses und der terrestrischen Umwelt wirken (DÉCAMPS et al. 2004, VERRY et al. 2004). Diese Interpretation wird durch die Tatsache der im hier untersuchten Grasland überdurchschnittlich hohen Gesamtartenzahl an Generalisten gestützt, die auch erheblich höher als in entsprechenden Vegetationstypen Lettlands außerhalb von Flussauen lag.

Weiterhin hatten wir im Ökoton eine höhere β-Diversität erwartet. Dies traf lediglich für das heterogene Gebiet, aber nicht für das homogene Gebiet zu, für das die Partitionierung der Artendiversität und auch die Clusteranalyse eine geringe β-Diversität zeigte. Da sich die Übergangsbereiche in beiden Gebieten in ihrer Hangneigung, Meereshöhe und ihren Ellenberg-Zeigerwerten nicht signifikant unterschieden, liegt der Grund für die beobachteten Muster wahrscheinlich in der unterschiedlichen Landschaftsheterogenität und der Bewirtschaftungsart der Gebiete.

Die in dem heterogenen Gebiet höhere β-Diversität des Übergangsbereichs könnte durch die höhere Dichte an verschiedenen Habitaten in Kombination mit Beweidung entstanden sein. Beweidung kann zu einer höheren β-Diversität führen, da die Vegetation von Weiden vertikal und horizontal komplexer strukturiert ist, was eine kleinräumige Habitat-Heterogenität bewirkt, die wiederum mit der β-Diversität der Vegetation positiv korreliert. Der Vizinismus nach HOBOHM & HÄRDTLE (1997) könnte in dem heterogenen Gebiet wegen der hier stärker ausgeprägten Mikrotopographie und der damit verbundenen höheren Dichte an Habitaten stärker ausgeprägt gewesen sein. Die zwischen den Gebieten unterschiedliche β-Diversität des Feuchtgraslands und unterschiedliche α-, β- und γ-Diversität des trockenen Graslands konnte nicht auf die erst seit relativ kurzer Zeit stattfindende Beweidung des heterogenen Gebiets zurückgeführt werden.

Obwohl unsere Forschung nicht vorranging auf die Analyse des Vizinismus abzielte, deuten unsere Ergebnisse darauf hin, dass Ökotone sowohl als Empfänger als auch als Spender von pflanzlichen Ausbreitungseinheiten dienen können und damit die Artendiversität sowohl im Übergangsbereich als auch in der angrenzenden Vegetation steigern könnten. Eine andere wichtige Funktion von Ökotonen in Flussauen kann die Erhaltung des dynamischen Gleichgewichts der Flussaue über Jahrzehnte sein.

Unsere Untersuchung zeigt, dass Ökotone in extrem trockenen oder feuchten Perioden die Existenz der Arten im trockenen und feuchten Bereich gewährleisten können, da etwa 50% der Arten des feuchten Graslands und 45–65% der Arten des trockenen Graslands im Ökoton wachsen. Weiterhin zeigen unsere Ergebnisse, dass Ökotone im Auengrünland wichtiger für die β-Diversität, und damit wichtiger für die Vielfalt an Gesellschaften sind als für die γ-Diversität. Im Auengrasland bedingen Ökotone spezielle Pflanzengesellschaften, enthalten aber nahezu keine eigenen Pflanzenarten. Die Bedeutung von Ökotonen für die γ-Diversität der Grasländer war in dem homogenen Gebiet höher, da das feuchte Grasland hier artenarm war und feuchtigkeitsliebende Arten zumeist im Ökoton wuchsen. Bezüglich der Hierarchie von Ökotonen in Flusslandschaften vermuten wir, dass eine abnehmende Heterogenität auf der unteren Stufe, z. B. durch die Zerstörung des Ökotons zwischen trockenem und feuchtem Grasland infolge von Regulierungen des Grundwasserspiegels oder auch infolge von Nutzungsaufgabe, zur Abnahme der Ökotonprozesse in der gesamten Flussaue führen kann. Daher sollten weitere Studien über die Bedeutung von kleinräumigen Ökotonen für die Biodiversität des Auengraslands und deren ökologische Wiederherstellung durchgeführt werden.

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Supplements and Appendices

Appendix 1. Indicator species of *wet*, transitional (*tra*) and *dry* sections of the heterogeneous and the homogeneous floodplain grassland site and their constancy (in %) in each section. Underlined constancy values show sections for which the species is classed as indicator species with the indicator value (IndVal) and *P* value shown in the respective data set. For each site the indicator species with the highest indicator values of a given section are printed in bold type. Only five indicator species with highest indicator values are shown for wet and dry sections, whereas all indicator species are shown for transitional sections.

Anhang 1. Zeigerarten für das feuchte (wet), trockene (dry) und Übergangsgrasland (tra) in einem heterogenen und einem homogenen Auengebiet. Stetigkeiten (in %) sind dargestellt. Unterstrichene Stetigkeitswerte zeigen den betreffenden Transektbereich, den eine Art nach einer *Indicator Species Analysis* anzeigt. Die Spalte *IndVal* zeigt die entsprechenden Zeigerwerte und die Spalte *p* die entsprechenden *P*-Werte. Die stärksten Zeigerarten für einen Transektbereich innerhalb eines Gebiets sind fett dargestellt. Für das feuchte und trockene Grasland sind jeweils nur die fünf stärksten Zeigerarten dargestellt. Für den Übergangsbereich sind alle Zeigerarten dargestellt.

Site	Heterogeneous site					Homogeneous site				
Transect section	wet	tra	dry	IndVal	*P*	wet	tra	dry	IndVal	*P*
Number of species per section	48	69	84			32	60	73		
Species restricted to a section	6	6	28			9	4	22		
Number of indicator species	16	10	35			4	10	41		
Ranunculus repens	**100**	**3**	**0**	**99.9**	**<0.001**	–	–	–	–	–
Carex vulpina	**94**	**47**	**6**	**67.2**	**<0.001**	22	0	0	21.7	0.021
Galium palustre	**75**	**34**	**0**	**65.7**	**<0.001**	17	13	0	9.8	0.432
Veronica scutellata	**56**	**0**	**0**	**56.2**	**<0.001**	–	–	–	–	–
Ranunculus flammula	**44**	**0**	**0**	**43.7**	**<0.001**	–	–	–	–	–
Carex acuta	9	38	0	36.2	<0.001	**57**	**13**	**0**	**54.0**	**<0.001**
Phalaris arundinacea	44	69	6	33.0	0.011	**65**	**20**	**0**	**64.6**	**<0.001**
Elytrigia repens	0	13	0	12.5	0.025	**57**	**20**	**0**	**49.2**	**<0.001**
Carex vulpina	94	47	6	67.2	<0.001	**22**	**0**	**0**	**21.7**	**0.021**
Filipendula ulmaria	**50**	**94**	**34**	**85.4**	**<0.001**	26	60	5	45.3	0.001
Veronica longifolia	**25**	**75**	**9**	**58.5**	**<0.001**	4	0	0	4.3	1.000
Inula salicina	**0**	**41**	**4**	**40.0**	**0.001**	0	0	5	4.5	0.612
Galium boreale	**38**	**81**	**81**	**57.1**	**0.001**	26	73	91	30.2	0.530
Thalictrum flavum	**0**	**25**	**0**	**25.0**	**0.001**	–	–	–	–	–
Lychnis flos-cuculi	**25**	**34**	**0**	**28.1**	**0.006**	9	0	0	8.7	0.325
Lysimachia vulgaris	**0**	**13**	**0**	**12.5**	**0.025**	0	0	27	27.3	0.004
Juncus filiformis	**0**	**13**	**0**	**12.5**	**0.026**	–	–	–	–	–
Ranunculus auricomus	**75**	**72**	**30**	**31.4**	**0.047**	48	67	55	25.6	0.435
Festuca pratensis	22	25	87	56.3	<0.001	**4**	**93**	**91**	**67.6**	**<0.001**
Alopecurus pratensis	–	–	–	–	–	**74**	**93**	**41**	**57.0**	**<0.001**
Deschampsia cespitosa	56	69	64	26.9	0.583	**17**	**67**	**5**	**47.1**	**<0.001**
Festuca arundinaea	28	6	30	15.3	0.355	**9**	**73**	**36**	**46.1**	**0.001**
Phleum pratense	16	6	60	48.0	0.001	**4**	**73**	**77**	**53.8**	**0.002**
Carec cespitosa	69	56	34	33.9	0.052	**30**	**53**	**18**	**38.9**	**0.005**
Lathyrus pratensis	53	25	79	39.3	0.006	**17**	**67**	**77**	**52.8**	**0.007**
Poa palustris	50	88	11	32.8	0.013	**30**	**53**	**5**	**38.2**	**0.007**
Anthriscus sylvestris	0	0	4	4.3	0.540	**0**	**20**	**0**	**20.0**	**0.014**
Agrostis tenuis	**31**	**25**	**98**	**90.5**	**<0.001**	0	47	95	66.8	<0.001
Alchemilla vulgaris	**0**	**13**	**85**	**82.9**	**<0.001**	0	27	77	68.4	<0.001
Festuca rubra	**6**	**31**	**89**	**76.4**	**<0.001**	0	67	77	48.4	0.002
Anthoxanthum odoratum	**0**	**6**	**66**	**65.0**	**<0.001**	0	33	95	72.7	<0.001
Filipendula vulgaris	6	28	96	64.6	<0.001	**13**	**53**	**95**	**78.9**	**<0.001**
Trifolium montanum	0	0	49	48.9	<0.001	**0**	**20**	**86**	**71.1**	**<0.001**
Helictrotrichon pratense	6	0	60	57.6	<0.001	**0**	**20**	**73**	**69.3**	**<0.001**
Primula veris	0	0	2	2.1	1.000	**0**	**0**	**64**	**63.6**	**<0.001**
Festuca ovina	0	0	13	12.8	0.074	**0**	**0**	**55**	**54.5**	**<0.001**

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