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A re-visitation study (1948–2015) of wet grassland vegetation in the Stedinger Land near Bremen, North-western Germany

Veränderungen der Feuchtgrünland-Vegetation im Stedinger Land bei Bremen zwischen 1948 und 2015

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Abstract

Wet grasslands once covered a large area in the lowlands of northern Germany, but have declined since several decades as a result of land use intensification. Permanent plot data from such grasslands in the region that would allow to assess the extent of changes in species composition and richness are still rare. Here, we present a re-visitation study of 52 quasi-permanent plots from the *Stedinger Land* area in the basin of the river Weser near Bremen, comparing quadrat data between 1948 and 2015. In 1948, the grasslands were characterized by species typical of wet, moderately fertile grasslands belonging to the *Bromo-Senecionetum aquatici* (*Bromion racemosi*), including 15 species currently classified as threatened. Until 2015, the vegetation had changed strongly: almost all indicators of wet grasslands had either declined or completely vanished, whereas more nutrient-demanding species of less wet soils had increased, especially grasses. The cumulative number of species had declined by 50%, while mean plot species richness had decreased by 64.6%, mainly resulting from the pronounced loss of many herbs. A comparison of mean Ellenberg indicator values suggested that the plots had become drier, but also more base- and nutrient-rich, most likely triggered by the intensification of land use with drainage and fertilization as well as more frequent and earlier cutting. Our study reflects the dramatic loss of plant species diversity in wet grasslands over the past 60–70 years in areas not preserved and properly managed, and it documents the need for protecting remnants of these grasslands and for restoring wet grassland areas by re-wetting, nutrient removal and the transition to a less intensive land use.

Keywords: *Bromo-Senecionetum aquatici*, drainage, eutrophication, hay meadow, quasi-permanent plots, species richness, species turnover, wetlands

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The landscape of the lowlands of northern Germany has since long been characterized by grasslands, with forests and fields occupying only relatively small areas. Until the 1950s a large part of these grasslands consisted of wet meadows assigned to different communities

of the *Molinietalia caeruleae* Koch 1926 (MEISEL & VON HÜBSCHMANN 1976). Since then, the region has experienced a transformation of a small-scale rural agriculture to an intensive industrial production, associated with several processes having a strong impact on the vegetation: increasing fertilization and airborne deposition of nutrients, earlier and increased intensity of cutting, drainage, use of herbicides, soil compaction, plowing-up of the soil and sowing of new productive species (ELLENBERG & LEUSCHNER 2010). On a regional scale, evidence for changes in flora and vegetation comes mainly from floristic inventories and mapping projects showing that many species typical of wet grasslands and formerly common have drastically declined (e.g., CORDES et al. 2006) and are now part of the red list of threatened plant taxa for the region Niedersachsen and Bremen, for example *Bromus racemosus*, *Caltha palustris*, *Lathyrus palustris* and *Senecio aquaticus* (GARVE 2004). Analyses of vegetation maps have also shown the strong reduction in the distribution area of wet grasslands in the North German lowlands (MEISEL & VON HÜBSCHMANN 1976, ROSENTHAL et al. 1998, KRAUSE et al. 2011).

The extent of vegetation changes on a local scale is more difficult to assess. Although there are thousands of relevés available from periods prior to the land use change in the 1950s and 1960s, only few of these plots can be localized with such a high precision that a re-visitation is possible. Truly permanent plots in wet grasslands hardly exist owing to the difficulty of marking the plots, and to our knowledge there are only few studies from northern Germany based on semi-permanent plots (DIERSCHKE & WITTIG 1991, WITTIG et al. 2007, WESCHE et al. 2012). These, however, show concurring results: a considerable decrease in species richness and a change in species composition, associated with a change in the proportions of different functional groups of species (especially an increase in grasses at the expense of low-growing herbs). As no measurements of any site factors were available for the historical plots, the causal interpretation of the observed changes had to rely on the estimation of the values of environmental variables by means of Ellenberg indicator values. These suggest that the grasslands, apart from being managed in different ways, have become drier and more nutrient-rich.

In this study, we aimed to analyse the long-term change in the species composition and richness of wet grasslands based on an old inventory from 1948 and a re-sampling in 2015 in the *Stedinger Land* near Bremen, representing a typical example for agricultural land not being situated in a conservation area. Specifically, we wanted to (1) quantify the extent of change in species richness and diversity, (2) examine the winner and loser species, (3) analyse the changes in species composition and calculate the floristic similarity between old and new plots, and finally (4) compare our results with those obtained in other re-visitation studies from wet grasslands in northern Germany.

2. Material and methods

2.1 Study area

The study area *Stedinger Land* is located between the cities of Bremen and Delmenhorst in the district “Wesermarsch” in the North-west German lowlands as part of the “coastal area”. It has an approximate size of 96 km² and is bounded by the rivers Weser, Ochtum and Hunte. In the vegetation survey from 1948 the area was divided into two parts, *Brookseite* and *Lechterseite*, separated by the river Ollen and differing in their soil conditions as well as in the predominating vegetation (PLATE 1949). The *Lechterseite* consisted of mineral wet soil and was mainly covered by pastures of the *Lolio-Cynosuretum cristati* Br.-Bl. et De Leeuw 1936 (EGGERSMANN 1939). In contrast, the *Brookseite* was

composed of peat soil with thick, coarse- or fine-grained clay over peaty deposits. Here, the soil was relatively wet and hard to cultivate, and therefore the grasslands were used extensively for haymaking and characterized mainly by meadows assigned to the *Bromo-Senecionetum aquatici* Lenski 1953 (PLATE 1949). The former management of these meadows was abandoned in the 1960s, as the wet soil did not allow the usage of heavy machinery. The grasslands were drained by ditches and fertilized to allow a more intensified land use with two or often more mowing events each year beginning in some parts of the study area already in May. The former gradients in management intensity resulting from the varying distances between grassland and farm gradually disappeared, leading to a homogenization of the landscape. Between 1963 and 1996 nearly 80% of the smaller farms vanished, still about 98% of the agricultural land in the *Stedinger Land* is currently managed as grassland (VONDERACH 2002).

2.2 Methods

Based on Helmut Plate's map from 1948, 70 plots of former *Bromo-Senecionetum aquatici* meadows (*Bromion racemosi* Tx. in Tx. et Preising ex de Foucault 2009) were relocated as exactly as possible and registered with their geographic coordinates using Google Earth to be able to find the exact position in the field via Google MyMaps and a GPS-device. Most plots were located in the central part of the *Stedinger Land* with some km distance from the river Weser (Supplement E1, E2). Some of these plots had either been transformed to fields, were not accessible (grazed by bulls) or had given way to buildings of the growing city of Lemwerder. Therefore, only 52 plots could be re-visited. The re-sampling most likely did not take place at the exact location of the original plot; however, as the grassland parcels were highly homogeneous in terms of topography and land use, we assumed that any deviation in the location between new and old plots did not systematically distort the analyses. Thus, we consider the plots as quasi-permanent (semi-permanent) (KOPECKÝ & MACEK 2015). The plot size used in 1948 was unknown to us and probably not held constant, and for the re-sampling we decided to apply a standard size of 20 m² which is in the range of plot sizes usually recommended for vegetation analyses in grasslands. In 5 selected plots we collected additional species richness data for varying plot sizes (1, 2, 4, 8, 16, 32, 64 and 100 m²) and constructed species-area curves, which helped us to assess how much of the change in species richness between old and new inventories might be attributed to methodological differences.

The vegetation of the plots was sampled according to the Braun-Blanquet method (BRAUN-BLANQUET 1964) that was also used for the sampling in 1948. The field work was carried out between the beginning of May and the end of July 2015. The nomenclature follows the species list provided by NETZWERK PHYTODIVERSITÄT DEUTSCHLAND & BUNDESAMT FÜR NATURSCHUTZ (2013). The old species list by Plate was carefully checked for synonyms. For some species it was not clear which species concept had been applied in the old study, these had to be merged to aggregates, such as *Luzula campestris* agg. (including *L. campestris* and *L. multiflora*). Red-listed species were classified based on GARVE (2004), the syntaxonomy follows DIERSCHKE & BRIEMLE (2002), BURKART et al. (2004) and MUCINA et al. (2016).

Soil samples were taken to examine the impact of edaphic factors on the current vegetation. In each plot, a mixed sample from the four corners of the plot was collected with a core from the upper 5 cm. The soil was air dried, grounded and sieved (2 mm) for further analysis. For the determination of pH 10 g of soil was mixed with 0.01 M calciumchloride (CaCl₂) solution in small plastic bottles. Depending on the amount of the humus content either 25 or 50 ml of calciumchloride solution was used. The bottles were placed on a shaker for at least 1.5 hours after which the pH in the supernatant was determined with pH-meter. Prior to the determination of carbon (C) and nitrogen (N), the grinded and sieved soil was milled. Then 5 mg of the milled soil were weighted into small plastic cups and analysed via gas chromatography with an elemental C/N analyzer EuroEA (Hekatech). The contents of calcium (Ca), potassium (K) and Mg (Magnesium) were measured via Atomic Absorption Spectroscopy (AAS, Philips) based on a flame emission spectroscopy. For this, 5 g of grinded soil were mixed with 100 ml acetate-lactate solution and put on a shaker for at least 4 hours. In the next step the solution was filtrate-

ed to obtain a clear supernatant, which was partly diluted and then injected into the measuring device. The content of plant available phosphate (P) was determined with flow injection analysis (FIA), also based on an acetate-lactate solution. All soil analyses were carried out according to SUCHOPAR (2014).

2.3 Statistical analysis

All statistical analyses were carried out with R, version 3.3.2 (R DEVELOPMENT CORE TEAM 2016). The relative frequencies of all species (number of occurrences / total number of plots) were calculated separately for the two time periods. To visualize and examine the changes in species composition from 1948 to 2015, a vegetation table with all 2 x 52 plots was constructed. We carried out an indirect gradient analysis on this joint vegetation table, using the transformed cover-abundance values of species and running Detrended Correspondence Analysis (DCA; gradient length of the first axis > 4) with default options. A DCA on presence-absence values gave very similar results, and also a downweighting of rare species did not alter the results to a large extent. To quantify the similarity between old and new plots, Jaccard coefficients were calculated using the *vegdist* function in the *vegan* package.

Mean plot species richness was compared between 1948 and 2015 using Wilcoxon signed rank test for paired data. For each plot we also calculated the Shannon diversity index H' ($= - \sum P_i * \ln P_i$; P_i is the proportion of the cover-abundance value of species i in a plot) and the Evenness index J ($= H' / \ln S$; S represents the total number of species) (MAGURRAN 2004). These two diversity indices were again compared between study years with the Wilcoxon signed rank test.

As no soil measurements were available from 1948, the environmental conditions in the plots were evaluated with the help of Ellenberg indicator values (ELLENBERG et al. 1992), focusing on light (L), soil moisture (M), soil reaction (R) and soil nitrogen (N, often regarded as soil nutrients). Values for the species' sensitivity to cutting (cut resistance) were obtained from BRIEMLE & ELLENBERG (1994). For each plot, the mean Ellenberg values (mL, mM, mR, and mN) and mean cut resistance values (mCut) were calculated based on the cover-abundance values of the species. The differences of these weighted means (all being normally distributed) between the years were examined with paired *t*-test. Furthermore, the mean Ellenberg values of the plots were *post hoc* fitted to the results of the DCA ordination, and the significance of the effects of the variables was tested with Monte Carlo permutation (with 9999 permutations) separately for each variable. We tested whether the mean Ellenberg values for the plots from 2015 were related to the corresponding measurements of soil variables from that year, applying Spearman rank order correlation, which was also applied for examining the inter-correlation between the mean Ellenberg values.

3. Results

3.1 Changes in species composition

In 1948 the grasslands in the *Stedinger Land* were characterized by indicators of mesic and wet, oligotrophic to mesotrophic grasslands (meadows): across the 52 plots, many of these species reached a relative abundance higher than 80%, mainly herbs (*Lychnis flos-cuculi*, *Rumex acetosa*, *Trifolium repens*), but also some grasses (*Anthoxanthum odoratum*, *Deschampsia cespitosa*, *Festuca pratensis*) (Table 1; for a full vegetation table, see Supplement E3). The character species of the association, *Senecio aquaticus*, was present in 63.5% of the plots, and also *Bromus racemosus* (also eponymous to the association) reached a high frequency. The relatively wet soil conditions are reflected also in the occurrence of several sedge species (*Carex acuta*, *C. disticha*, *C. nigra*).

Until 2015, the vegetation had changed dramatically: almost all indicators of wet grasslands had disappeared completely (Table 1). Only few species with a relative frequency of 50% or more in 1948 remained frequent (*Taraxacum officinale*, *Holcus lanatus*, *Cerastium*

Table 1. Relative frequency of vascular plant species in 52 quasi-permanent grassland plots in the *Stedinger Land* near Bremen (Germany) sampled in 1948 and re-sampled in 2015. Only species occurring in at least 10% of the plots in one of the two years are shown. Species are ordered according to their extent of decrease or increase.

Tabelle 1. Relative Häufigkeit von Pflanzenarten in 52 quasi-permanenten Grünland-Dauerflächen im Stedinger Land bei Bremen im Vergleich der Jahre 1948 und 2015. Nur Arten mit einer Mindesthäufigkeit von > 10 % in einem der beiden Jahre sind aufgeführt. Die Arten sind nach dem absoluten Ausmaß ihrer Ab- oder Zunahme geordnet.

Species (Art)	Grass [G] or herb [K]	Relative frequency in 1948 in %	Relative frequency in 2015 in %	Decrease [-] or increase [+]
<i>Lychnis flos-cuculi</i>	K	88.5	0.0	-88.5
<i>Persicaria amphibia</i>	K	76.9	0.0	-76.9
<i>Scorzoneroide autumnalis</i>	K	76.9	0.0	-76.9
<i>Trifolium repens</i>	K	92.3	17.3	-75.0
<i>Anthoxanthum odoratum</i>	G	82.7	9.6	-73.1
<i>Ranunculus repens</i>	K	90.4	19.2	-71.2
<i>Rhinanthus minor & angustifolius</i>	K	67.3	0.0	-67.3
<i>Agrostis canina</i>	G	67.3	1.9	-65.4
<i>Carex acuta</i>	K	65.4	1.9	-63.5
<i>Deschampsia cespitosa</i>	K	80.8	17.3	-63.5
<i>Senecio aquaticus</i>	K	63.5	0.0	-63.5
<i>Caltha palustris</i>	K	59.6	0.0	-59.6
<i>Ranunculus flammula</i>	K	59.6	0.0	-59.6
<i>Cirsium palustre</i>	K	59.6	1.9	-57.7
<i>Achillea ptarmica</i>	K	55.8	0.0	-55.8
<i>Trifolium pratense</i>	K	76.9	21.2	-55.7
<i>Festuca pratensis</i>	G	82.7	28.8	-53.9
<i>Galium palustre</i>	K	53.8	0.0	-53.8
<i>Bromus racemosus</i>	G	50.0	0.0	-50.0
<i>Equisetum fluviatile</i>	K	50.0	0.0	-50.0
<i>Ranunculus acris</i>	K	75.0	26.9	-48.1
<i>Prunella vulgaris</i>	K	50.0	1.9	-48.1
<i>Mentha aquatica</i>	K	48.1	0.0	-48.1
<i>Rumex acetosa</i>	K	80.8	32.7	-48.1
<i>Festuca rubra</i>	G	50.0	3.8	-46.2
<i>Lotus pedunculatus</i>	K	42.3	0.0	-42.3
<i>Juncus effusus</i>	K	48.1	7.7	-40.4
<i>Vicia cracca</i>	K	40.4	1.9	-38.5
<i>Galium uliginosum</i>	K	38.5	0.0	-38.5
<i>Trifolium dubium</i>	K	38.5	0.0	-38.5
<i>Carex nigra</i>	K	38.5	1.9	-36.6
<i>Glyceria fluitans</i>	G	36.5	0.0	-36.5
<i>Cardamine pratensis</i>	K	51.9	19.2	-32.7
<i>Cynosurus cristatus</i>	G	32.7	0.0	-32.7
<i>Myosotis laxa</i>	K	32.7	0.0	-32.7
<i>Potentilla anserina</i>	K	32.7	0.0	-32.7
<i>Agrostis stolonifera</i>	G	50.0	21.2	-28.8
<i>Filipendula ulmaria</i>	K	28.8	0.0	-28.8
<i>Holcus lanatus</i>	G	78.8	51.9	-26.9
<i>Carex panicea</i>	K	26.9	0.0	-26.9

Species (Art)	Grass [G] or herb [K]	Relative frequency in 1948 in %	Relative frequency in 2015 in %	Decrease [-] or increase [+]
<i>Centaurea jacea</i>	K	26.9	0.0	-26.9
<i>Lysimachia nummularia</i>	K	25.0	0.0	-25.0
<i>Plantago lanceolata</i>	K	25.0	0.0	-25.0
<i>Eriophorum angustifolium</i>	K	23.1	0.0	-23.1
<i>Thalictrum flavum</i>	K	23.1	0.0	-23.1
<i>Plantago major</i>	K	28.8	5.8	-23.0
<i>Glyceria maxima</i>	G	21.2	0.0	-21.2
<i>Leucanthemum vulgare</i>	K	21.2	0.0	-21.2
<i>Glechoma hederacea</i>	K	28.8	9.6	-19.2
<i>Carex disticha</i>	K	19.2	0.0	-19.2
<i>Lathyrus pratensis</i>	K	19.2	0.0	-19.2
<i>Luzula campestris</i> agg.	K	19.2	0.0	-19.2
<i>Lysimachia vulgaris</i>	K	15.4	0.0	-15.4
<i>Stellaria palustris</i>	K	15.4	0.0	-15.4
<i>Iris pseudacorus</i>	K	13.5	0.0	-13.5
<i>Juncus articulatus</i>	K	13.5	0.0	-13.5
<i>Comarum palustre</i>	K	13.5	0.0	-13.5
<i>Succisa pratensis</i>	K	13.5	0.0	-13.5
<i>Cerastium holosteoides</i>	K	61.5	50.0	-11.5
<i>Lathyrus palustris</i>	K	11.5	0.0	-11.5
<i>Triglochin palustris</i>	K	11.5	0.0	-11.5
<i>Achillea millefolium</i>	K	21.2	11.5	-9.7
<i>Alopecurus geniculatus</i>	G	36.5	26.9	-9.6
<i>Bellis perennis</i>	K	11.5	3.8	-7.7
<i>Rumex crispus</i>	K	17.3	13.5	-3.8
<i>Taraxacum officinale</i>	K	53.8	53.8	0.0
<i>Phleum pratense</i>	G	38.5	44.2	5.7
<i>Phalaris arundinacea</i>	G	19.2	26.9	7.7
<i>Cerastium glomeratum</i>	K	0.0	13.5	13.5
<i>Poa trivialis</i>	G	48.1	69.2	21.1
<i>Poa pratensis</i>	G	48.1	73.1	25.0
<i>Bromus hordeaceus</i>	G	9.6	36.5	26.9
<i>Dactylis glomerata</i>	G	0.0	26.9	26.9
<i>Lolium multiflorum</i>	G	1.9	28.8	26.9
<i>Rumex obtusifolius</i>	K	0.0	28.8	28.8
<i>Elymus repens</i>	G	1.9	46.2	44.3
<i>Poa annua</i>	G	0.0	50.0	50.0
<i>Alopecurus pratensis</i>	G	21.2	82.7	61.5
<i>Lolium perenne</i>	G	13.5	90.4	76.9

holosteoides). None of the 15 species found in 1948 that now are included in the Red List was re-sampled in 2015, even species having a former abundance higher than 50% such as *Bromus racemosus*, *Caltha palustris*, *Rhinanthus minor* & *angustifolius* and *Senecio aquaticus* (Table 1). Further endangered species were *Carex echinata*, *C. panicea*, *C. vulpina*, *Cirsium dissectum*, *Juncus filiformis*, *Lathyrus palustris*, *Menyanthes trifoliata*, *Pedicularis palustris*, *Succisa pratensis*, *Thalictrum flavum* and *Triglochin palustre*. Among the 79 spe-



Fig. 1. a) Intensiv managed sow meadow (plot no. 58) for haymaking, dominated by *Lolium multiflorum* and *L. perenne*, **b)** Intensiv managed hay meadow (plot no. 60) dominated by *Alopecurus pratensis* (Photo: A. Immoor, June 2015).

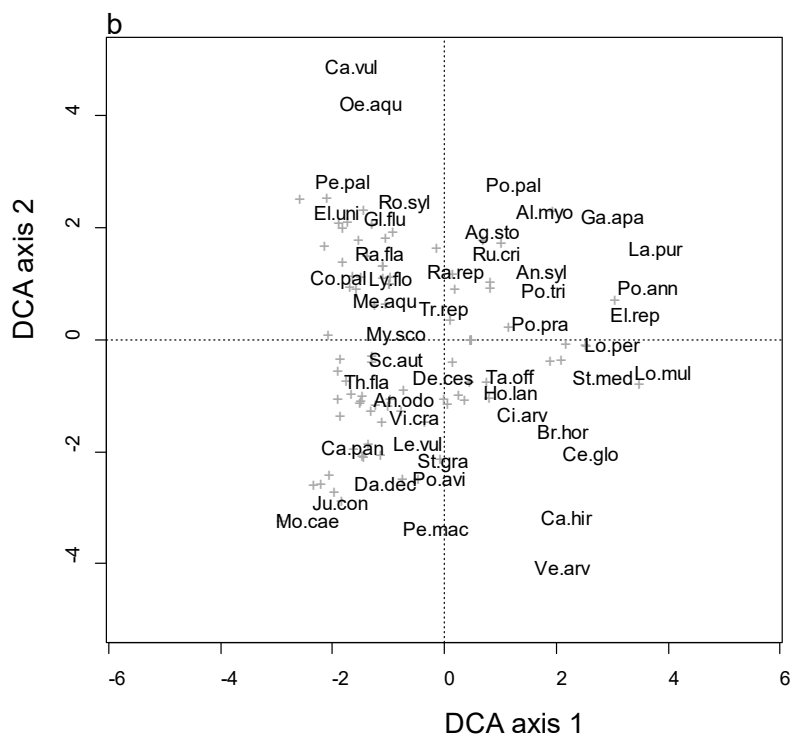
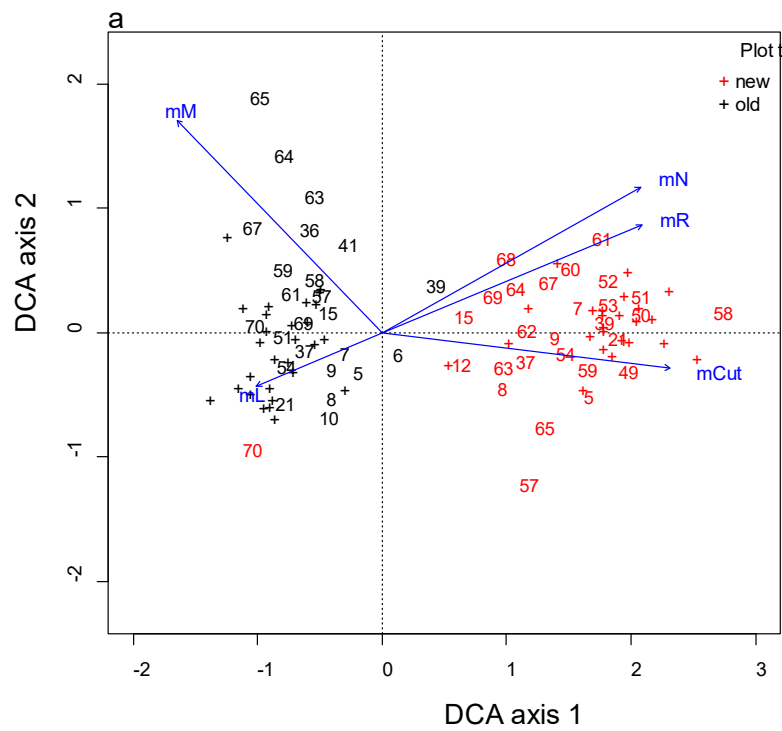
Abb. 1. a) Intensiv bewirtschafteter 'Grasacker' (Plot 58), dominiert von *Lolium multiflorum* und *L. perenne*, **b)** Intensiv bewirtschaftete Mähwiese (Plot 60) dominiert von *Alopecurus pratensis* (Foto: A. Immoor, Juni 2015).

cies occurring in at least 10% of the plots in one of the study years, only 13 increased in frequency, 11 of which were grasses and only 2 herbs. Most notable was the increase in *Lolium perenne* (Fig. 1a), *Alopecurus pratensis* (Fig. 1b) and several *Poa* species.

The drastic change in species composition is also reflected in the DCA ordination diagram of plots (Fig. 2a) showing a complete (except plot 70) separation of plots from the two study years, with the old plots situated at the left and the re-sampled plots at the right. The ordination diagram of species underlines the change in species composition from wetland indicators of extensively grazed pastures and hay meadows in the left-hand side of the graph to a grass-dominated vegetation being cut-resistant and typical for fertilized grassland with high pH and nitrogen availability to the right (Fig. 2a). Mean Jaccard similarity between old and new plots was 0.089, with a maximum of 0.312 and a minimum of 0 for plot 70, meaning that the old and new plot did not have a single species in common!

3.2 Changes in species richness

The cumulative number of species in the plots from 1948 (116) was twice as high as that of the plots from 2015 (58). As many as 75 species found in 1948 had disappeared, whereas only 17 new species arrived between the two study periods. The species loss is also reflected in the change in plot species richness: all 52 plots had more species in 1948 (range from 20 to 45, mean 32.8, standard deviation [sd] 6.6) than in 2015 (range from 5 to 23, mean 11.6, sd = 4.2), the differences between time periods varying between 2 and 38 ($V = 1378$, $p < 0.001$, $n = 52$; Fig. 3). On average 64.6% of the species in the plots were lost. This loss is mainly attributed to the disappearance of herbs: while these made up on average 78.9% of the species in 1948, their share declined to 30.2% in 2015. In seven of the re-sampled plots, exclusively grasses were found. These dramatic changes in species richness cannot be attributed only to possible differences in the plot sizes used in the two study periods: when increasing plot size from 16 m² to 100 m² in five selected plots - assuming that plot sizes in 1948 were chosen to be unusually high - species richness on average increased by only 10.3%.



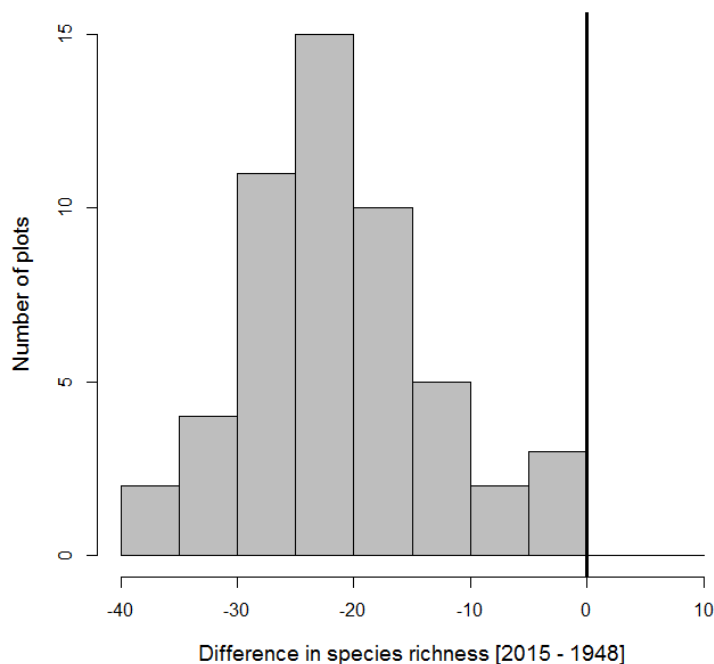


Fig. 3. Change in total species richness from 1948 to 2015 in 52 quasi-permanent grassland plots in the *Stedinger Land* near Bremen (Germany), shown as histogram of the pairwise differences in the number of species. The black line indicates the 0 value of no change in species richness.

Abb. 3. Veränderung der Gesamtartenzahl von 1948 bis 2015 in 52 quasi-permanenten Grünland-Dauerflächen im Stedinger Land bei Bremen, dargestellt als Häufigkeitsverteilung der Differenzen in der Artenzahl. Die schwarze Linie gibt den 0-Wert (keine Veränderung in der Artenzahl) wieder.

Previous page (vorherige Seite):

Fig. 2. Detrended Correspondence Analysis (DCA) of 52 quasi-permanent plots in the *Stedinger Land* near Bremen. **a)** Diagram of plots sampled in 1948 (marked in black) and re-sampled in 2015 (marked in red). Mean Ellenberg values were fitted *post hoc* to the ordination and displayed if they had a significant effect on the variation in species composition at $p < 0.0001$; mM = soil moisture, mN = soil nitrogen, mR = soil reaction, mL = light, and mCut = cut resistance. Some plots were not given by their number (but with +) for reasons of clarity. Eigenvalues: axis 1 = 0.593, axis 2 = 0.170; gradient lengths: axis 1 = 4.086, axis 2 = 3.107. **b)** Species diagram. Some species were not displayed by their number (but with +) for reasons of clarity. Full species names are given in Supplement E3.

Abb. 2. Detrended Correspondence Analysis (DCA) von 52 quasi-permanenten Grünland-Dauerflächen im Stedinger Land bei Bremen. **a)** Diagramm der Probeflächen aus den Jahren 1948 (in schwarz) und 2015 (in rot). Gewichtete mittlere Ellenberg-Werte wurden *post hoc* zur Ordination in Beziehung gesetzt und sind abgebildet, wenn sie einen signifikanten Einfluss ($p < 0,0001$) auf die Artenzusammensetzung der Plots zeigten; mM = Bodenfeuchtigkeit, mN = Bodennstickstoff, mR = Bodenreaktion, mL = Licht, und mCut = Schnittfestigkeit. Zur besseren Lesbarkeit werden einige Plots nicht mit ihren Nummern (sondern mit +) dargestellt. Eigenvalues: Achse 1 = 0,593; Achse 2 = 0,170; Gradientenlängen: Achse 1 = 4,086; Achse 2 = 3,107. **b)** Diagramm der Arten. Zur besseren Lesbarkeit wurden einige Arten nicht mit ihren Abkürzungen, sondern mit + dargestellt. Die vollständigen Pflanzennamen finden sich in Anhang E3.

The mean Shannon-Wiener index declined from 3.03 (sd 0.26) in 1948 to 1.82 (sd 0.38) between 1948 and 2015 ($V = 0$, $p < 0.001$, $n = 52$), while evenness decreased from 0.87 (sd 0.04) to 0.79 (sd 0.09) ($V = 49$, $p < 0.001$, $n = 52$).

3.3 Vegetation and environment

All of the five tested variables mM, mL, mN, mR and mCut had a significant impact on the variation in species composition when *post hoc*-fitted to the DCA (Fig. 2a). The first axis was highly positively correlated with mN ($r_s = 0.92$), mR ($r_s = 0.89$) and mCut ($r_s = 0.93$), and negatively correlated with mM ($r_s = -0.9$) and mL ($r_s = -0.36$, all $p < 0.0001$ and $n = 104$). In other words, the mean indicator values suggested high values of soil nutrients and pH as well as high cut resistance in the plots from 2015, in contrast to low values for light and soil moisture in the new plots (and the opposite in the old plots). This is corroborated in a comparison of the mean indicator values of plots between 1948 and 2015 (Fig. 4): Whereas the mean mM had decreased by on average about 1.5 units, the averages for mN, mR and mCut had increased over the years by between 1 and 2 units. The average mL values had only slightly declined. Most of the environmental variables were less important for the second axis, but still significant for mM ($r_s = 0.31$, $p < 0.01$). Both mM and mL were negatively correlated with mN, mR and mCut (all $p < 0.001$).

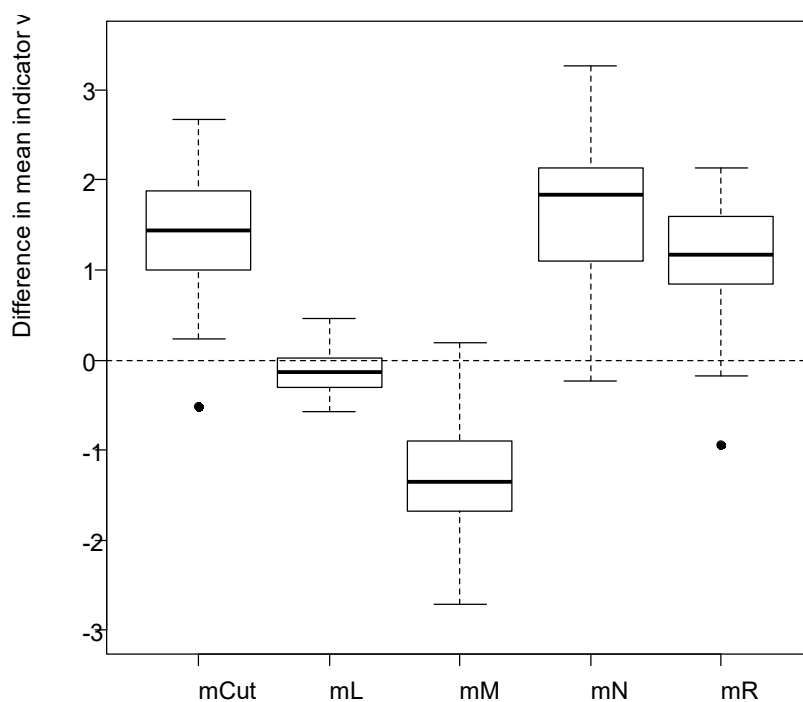


Fig. 4. Boxplots of changes in weighted mean Ellenberg values from 1948 to 2015 in 52 quasi-permanent plots in the *Stedinger Land* near Bremen. mM = soil moisture, mN = soil nitrogen, mR = soil reaction, mL = light, and mCut = cut resistance.

Abb. 4. Boxplots der Veränderung der gewichteten mittleren Ellenberg-Werte von 1948 bis 2015 in 52 quasi-permanenten Grünland-Dauerflächen im Stedinger Land bei Bremen. mM = Bodenfeuchtigkeit, mN = Bodenstickstoff, mR = Bodenreaktion, mL = Licht, und mCut = Schnittfestigkeit.

Table 2. Values (minimum (Min), maximum (Max) and median) of soil variables in 52 quasi-permanent grassland plots in the *Stedinger Land* near Bremen (Germany) sampled in 2015. For comparison, median values for the same set of soil variables are given for three other extensively managed grassland areas in North-western Germany obtained with the same analytical methods in the same laboratory: (a) mesotrophic meadows and pastures on fresh and moist soils in the nature reserve "Westliches Hollerland" in Bremen, sampled in 2011 (unpubl. data); (b) mesotrophic meadows on moist soils with remnant populations of some rare plant species (*Cirsium dissectum*, *Pedicularis palustris*, *Serratula tinctoria*, *Viola persicifolia*) sampled across the Weser-Elbe region in 2009 (WOLTERINK 2010); (c) restored wet grasslands in the Ochsenmoor nature reserve at Lake Dümmer collected in 2008 and 2009 (BLÜML 2011).

Tabelle 2. Werte (Minimum und Maximum sowie der Median) von Bodenfaktoren in 52 quasi-permanenten Grünland-Dauerflächen im Stedinger Land bei Bremen aus dem Jahr 2015. Zum Vergleich werden Medianwerte derselben Bodenfaktoren für drei andere, extensiv genutzte Grünlandregionen Nordwest-Deutschlands angegeben, die mit identischen Analyseverfahren in demselben Bodennlabor ermittelt wurden: (a) mesotrophe Wiesen und Weiden auf frischen bis feuchten Böden im Naturschutzgebiet "Westliches Hollerland" in Bremen von 2011 (unveröff. Daten); (b) mesotrophe Wiesen auf Feuchtböden mit Restpopulationen der seltenen Pflanzenarten *Cirsium dissectum*, *Pedicularis palustris*, *Serratula tinctoria* und *Viola persicifolia* aus der Weser-Elbe-Region von 2009 (WOLTERINK 2010); (c) renaturiertes Feuchtgrünland im Naturschutzgebiet Ochsenmoor am Dümmer aus den Jahren 2008 und 2009 (BLÜML 2011).

Soil variable	Stedinger Land			Hollerland	Weser-Elbe region	Dümmer
	Min	Max	Median (n = 52)	Median (n = 51)	Median (n = 36)	Median (n = 91)
pH	3.6	6.7	4.8	4.3	4.1	5.2
Ca [mg / 100 g soil]	53.5	711.3	225.6	354.0	253.2	998.7
K [mg / 100 g soil]	9.6	107.3	27.4	29.2	18.7	12.7
Mg [mg / 100 g soil]	17.5	128.0	52.8	37.4	34.0	12.9
P [mg / 100 g soil]	1.3	34.2	5.5	1.4	1.9	2.8
C [%]	2.6	31.5	11.1	13.5	21.5	35.1
N [%]	0.2	2.4	0.9	1.2	1.7	2.5
C/N ratio	10.1	23.1	13.9	11.8	13.0	13.9

The values of the soil variables from 2015 (Table 2, Supplement E4) show a considerable variation in all measured factors. Soil pH values were uncorrelated to the mR from the same year ($r_s = 0.133$, $p = 0.348$, $n = 52$), and also the measures for nutrient availability did not show significant correlations with mN (phosphorus: $r_s = 0.193$, $p = 0.170$; C/N ratio: $r_s = -0.062$, $p = 0.664$; N: $r_s = 0.062$, $p = 0.661$, all $n = 52$). An ordination of the 2015 vegetation data with a subsequent *post hoc* fit of measured soil values revealed that none of the variables was significantly related to the species composition at $p < 0.01$, and only potassium was related to DCA axis 2 at $p = 0.011$.

4. Discussion

Extensively managed meadows on wet and more or less acidic soils assigned to the alliance *Bromion racemosi* have existed only since about 100 years. They have usually developed from *Molinion* meadows after moderate fertilization or from (often *Carex*-dominated)

mires following slight drainage (ELLENBERG & LEUSCHNER 2010). Despite their young age they once covered large areas in the lowlands of Central Europe, especially in river valleys (MEISEL & VON HÜBSCHMANN 1976, KRAUSE et al. 2011). Compared to meadows on more base-rich soils and in more continental areas, *Bromion* communities are often considered as relatively species-poor, but across the 52 plots studied in 1948 mean plot species richness was as high as about 33.

When the land use became more intensive in the 1950s and 1960s, species composition began to change and the number of species to decline. Large areas of wet grasslands were either converted to species-poor, intensively managed grasslands, abandoned or replaced by arable fields (for data for North Germany in KRAUSE et al. 2011). Previous studies in wet grasslands using quasi-permanent plots documented a decrease in species richness of up to 60% (WITTIG et al. 2007, WESCHE et al. 2012). In our study, we found a mean decline in plot species richness of about 65%, meaning that almost 2/3 of all species had disappeared. Among the grassland communities in Central Europe, such a dramatic decline is unprecedented, although for example *Nardion* grasslands have also suffered from a considerable species loss over the past decades (DUPRÉ et al. 2010). It is unlikely that this dramatic decline in species richness is largely attributed to an imprecise re-location of plots or to the possible use of smaller plot sizes in the re-visitation compared to the original study (see also WESCHE et al. 2012), because the vegetation in the grassland parcels is highly homogeneous and the increase in the number of species with increasing plot size was weak. In the Holutumer Moor region not far from our study area (but also in other parts of the North German lowlands, see MEISEL & HÜBSCHMANN 1976, ROSENTHAL & MÜLLER 1988), most species already got lost from the wet grasslands during an early phase of land use intensification up to the end of the 1980s (DIERSCHKE & WITTIG 1991), but the negative trend has continued since then (WITTIG et al. 2007). Only where wet grasslands are preserved and continuously managed under stable habitat conditions as in parts of the Havel region, species richness can be kept at a high level (WESCHE et al. 2012). Species losses from wet grasslands were also reported from other parts of North-western Central Europe, especially the Netherlands (GROOTJANS et al. 1996, 2004, JANSSENS et al. 1998).

In fact, even more species than 63% have been lost as also new species have arrived; in one plot, all species had disappeared and were replaced by few other species. This and the ordination diagram reflect the link between the decline in species richness and the dramatic change in species composition, away from - nowadays often rare and red-listed - indicators of wet grasslands to more common species typical for more mesic and fertile soils. This and previous temporal studies on wet grasslands (WITTIG et al. 2007, WESCHE et al. 2012) show some consistent shifts in species composition: (1) a strong decline of often insect-pollinated, relatively short-lived herbs and grasses, among them those species regarded as character species of wet grasslands, such as *Bromus racemosus* and *Senecio aquaticus*; (2) an increase in the cover degree of grasses and in the frequency of many graminees, such as *Lolium perenne*, *L. multiflorum*, *Poa spec.*, *Elymus repens* and *Dactylis glomerata*. Especially conspicuous is the widespread dominance of *Alopecurus pratensis* (see also DIERSCHKE 1997). However, other grasses show declining trends, including *Anthoxanthum odoratum*, *Cynosurus cristatus* and *Festuca spec.*; (3) an increase in ruderal species such as *Rumex obtusifolius* and *Stellaria media*. These vegetation changes are similar to those observed in other grassland types, such as *Nardetalia* (DUPRÉ et al. 2010) and *Arrhenatheretalia* (ROSENTHAL & MÜLLER 1988). This makes it likely that these consistent changes are at least partly caused by the same set of environmental factors and processes.

A main trigger for the vegetation changes in wet grasslands is drainage. The systematic construction of ditches found all over the lowlands of North-western Europe resulted in a lowering of the water table that in turn made it possible to manage the land with a heavier machinery. Drainage goes along with the intensification of microbial activity and the release of mineral nitrogen, narrowing the C/N ratio. This is accompanied by an increased fertilization (along with increasing atmospheric nitrogen deposition) and liming and a change of land use: more frequent and earlier cutting, grazing or a mixture of both. Old-growth grassland was replaced by a widespread sowing of more productive grass species (e.g., *Alopecurus pratensis*, *Lolium multiflorum*) (see also KRAUSE et al. 2014). All these trends together are reflected in the ordination diagram indicating an increase in more base- and nutrient-demanding, cut-resistant species at the expense of more undemanding species typical for traditionally managed grasslands, especially hay meadows cut once or twice a year (DRACHENFELS 2012).

The ordination results based on Ellenberg indicator values are indirectly supported by the measurements of soil variables. While no data for the 1948 plots were available, the values for 2015 can be compared with recent measurements from other, more species-rich grasslands areas and habitats based on exactly the same analytical procedures (Table 2). Soil pH values in the *Stedinger Land* showed a wide range of more than 3 units, but were on average higher than in the Hollerland area in Bremen (with moist to mesic, mesotrophic meadows and pastures) and in other mesotrophic grasslands and mires in the Weser-Elbe region. Restored grasslands in the Ochsenmoor area at Lake Dümmer had on average slightly higher pH values. The base cation contents in the *Stedinger Land* were not consistently higher or lower compared to the other regions: whereas calcium contents were relatively low, potassium (K) and especially magnesium contents were relatively high. The most pronounced differences between the *Stedinger Land* and the other regions was observed for total nitrogen (N, low values) and phosphorus (P), the latter ranging between 1.3 and 34.2 (median 5.5) mg / 100 g dry soil. P availability (along with N and K, OLDE VENTERINK et al. 2003) is a key factor for productivity and species richness in grassland vegetation, and our results coincide with those from JANSSENS et al. (1998) showing that 5 mg P / 100 g dry soil is a threshold above which productivity is no longer P-limited and species richness drops. The importance of P limitation for floodplain grasslands has also been demonstrated by HÄRDTLE et al. (2006). In contrast, potassium - with relatively high average values of ca 27 mg / 100 g dry soil - is probably not the main driver of the decline of most species, as the ranges governing high productivity and high species richness do not differ much (JANSSENS et al. 1998). The importance of P and K availabilities and their ratio for the productivity and species richness in wet grasslands and for their restoration potential are discussed in detail by OELMANN et al. (2009) and POPTCHEVA et al. (2009).

5. Conclusions

Although the widespread decline of wet grasslands from the Central European lowlands has been repeatedly stressed (ELLENBERG & LEUSCHNER 2010), quantifications of the extent of the changes in species richness and composition are still rare. In our study, we show that intensification of land use with drainage, fertilization and transition of old-growth grasslands have led to a dramatic loss of plant species diversity over the past 60–70 years. Abandonment of land use affects all types of grassland and finally results in their complete disappearance, often even in protected areas. Among the grasslands still managed, however, wet

grasslands have faced the strongest changes due to the combination of processes acting on the vegetation: whereas other grassland types - for example mesic *Arrhenatherion* grasslands - also suffer from a more intensive management, artificial fertilization and airborne nitrogen deposition, the altered water regime of the formerly wet grasslands has profoundly changed the basic habitat conditions. The *Stedinger Land* represents an example of agricultural land that is not suitable for being used as arable field (because of the wetness of the soil) but in use as large-scale grassland, and which is not part of a nature conservation area. The documented loss of plant species diversity especially with regard to elements of the historic landscape reveals the urgent need for protecting remnants of species-rich grasslands as preserved areas in combination with a suitable management. The restoration of species-poor, intensively used wet grasslands cannot be achieved by solely stopping fertilization and removing nutrients by harvesting or sod-cutting, but depends on additional re-wetting. Even then the current rarity of many plant species typical for wet grasslands and the strong fragmentation of the remaining habitats (KRAUSE et al. 2015) will slow down the biotic recovery of the grasslands. Only where nutrient depletion and re-wetting are implemented over a long time and on a large spatial scale, such in the Ochsenmoor area at Lake Dümmer, species richness can be re-stored and many rare plant taxa be retrieved (BLÜML et al. 2012).

Erweiterte deutsche Zusammenfassung

Einleitung – Feuchtgrünland bedeckte über viele Jahrzehnte große Teile des Norddeutschen Flachlands, vor allem in den Marschen entlang der großen Flüsse. Mit der Nutzungsintensivierung seit den 60er Jahren des letzten Jahrhunderts hat sich das Erscheinungsbild des Feuchtgrünlands indes stark gewandelt und floristische Daten belegen den starken Rückgang vieler einst häufiger Pflanzenarten aus der Region. Da trotz des Vorhandenseins Tausender alter Vegetationsaufnahmen von Feuchtwiesen nur wenige Dauerquadrate aus Norddeutschland vorliegen, ist das Ausmaß der Veränderungen der Vegetation und des Artenreichtums der Feuchtwiesen des Gebiets nur unzureichend dokumentiert. Die hier vorgestellte Untersuchung basiert auf 52, in ihrer geographischen Lage auf einer alten Karte festgehaltenen Vegetationsaufnahmen von 1948 aus dem Stedinger Land in der Weseraue nahe Bremen, einem nicht unter Schutz stehenden Marschengebiet. Im Jahr 2015 wurden diese "Quasi-Dauerflächen" wieder aufgenommen, um den Wandel der Feuchtgrünlandvegetation zu beschreiben.

Methoden – Die Wiederaufnahme der Dauerflächen erfolgte nach der Braun-Blanquet-Methode und entsprach der Vorgehensweise der früheren Vegetationserfassung. Die Größe der Aufnahmeflächen von 1948 ist nicht dokumentiert, in 2015 wurde für die Plots eine einheitliche Größe von 20 m² festgelegt. Zusätzlich wurden in fünf Probeflächen Arten-Areal-Kurven (1, 2, 4, 8, 16, 32, 64 und 100 m²) erhoben, um festzustellen, inwieweit Unterschiede in der Artenzahl zwischen alten und neuen Plots auf unterschiedlich große Aufnahmeflächen zurückzuführen sind. Aus allen Flächen wurden Bodenproben entnommen und Standardmethoden folgend im Hinblick auf verschiedene Variablen (pH, pflanzenverfügbare Gehalte an Kalium, Magnesium, Calcium und Phosphor, Gehalte an Kohlenstoff und Stickstoff) analysiert. Da keine Vergleichswerte von 1948 vorlagen, wurden sowohl für alte als auch neue Aufnahmeflächen mittlere Ellenberg-Zeigerwerte für die Faktoren Licht, Boden-Feuchtigkeit, -pH und -Stickstoff (Nährstoffe) sowie Schnittfestigkeit berechnet. Veränderungen in der Artenzusammensetzung zwischen den Jahren wurden mittels *Detrended Correspondence Analysis* analysiert, der Vergleich der Artenzahlen zwischen den Perioden erfolgte mit dem nicht-parametrischen Wilcoxon-Test für gepaarte Daten.

Ergebnisse – Die Aufnahmeflächen aus dem Jahr 1948 zeichneten sich durch eine hohe Dominanz von Arten aus, die für nasse, mesotrophe Feuchtwiesen der Gesellschaft *Bromo-Senecionetum aquatici* (*Bromion racemosi*) typisch sind. Insgesamt 15 der damals beobachteten Arten gelten heute im Naturraum der Küste als gefährdet. Die Vegetation der Flächen hatte sich bis zum Jahr 2015 drastisch verän-

dert: während die in Bezug auf die Nährstoffversorgung eher anspruchslosen Feuchtezeiger (inklusive aller heute seltenen Arten) vollständig oder weitgehend verschwunden waren, hatten Indikatoren nährstoffreicherer und trockenerer Standorte stark zugenommen, vor allem - teilweise eingesäte - Gräser. Diese Veränderungen werden auch bei einem Vergleich der mittleren Ellenberg-Zeigerwerte deutlich, die darauf hindeuten, dass die Böden trockener, aber gleichzeitig basischer und nährstoffreicher geworden sind. In einer Fläche vollzog sich ein vollständiger Artenwechsel, d. h., die im Jahr 1948 vorgefundenen Arten wurden bis 2015 komplett von anderen Arten abgelöst. Die kumulative Artenzahl sank um 50 % von 116 in 1948 auf 58 in 2015, und die Artenzahl in den Probeflächen ging im gleichen Zeitraum um durchschnittlich 64,6 % (von 32,8 auf 11,6) zurück. Die Messwerte verschiedener Bodenfaktoren im Stedinger Land im Vergleich zu anderen Grünlandgebieten im Bremer Raum legen nahe, dass die heutige Dominanz weniger produktiver Gräser und Kräuter und die damit einhergehende Artenarmut in erster Linie mit der hohen Phosphat-Verfügbarkeit der Böden zusammenhängen.

Diskussion – Die Untersuchung aus dem Stedinger Land spiegelt den drastischen Verlust an Arten und den ausgeprägten Vegetationswandel auch in anderen Feuchtgrünländern über die vergangenen Jahrzehnte wider. Diese Veränderungen sind das Resultat eines umfangreichen Landnutzungswandels, geprägt durch Entwässerung, Düngung, häufigerem und früherem Schnitt der Wiesen, die Anwendung von Herbiziden und die Einsaat produktiver Grassorten. Dies ist überall dort geschehen, wo die Wiesen nicht unter Naturschutz gestellt und durch ein auf standortspezifische und hohe Biodiversität ausgerichtetes Management gepflegt wurden. Angesichts der Gefährdung vieler früher typischer Feuchtgrünlandarten ist es dringend notwendig, die noch bestehenden Restflächen zu schützen und angemessen zu pflegen bzw. genutzte Flächen in geeigneten Gebieten durch Wiedervernässung, Nährstoffentzug und Extensivierung der Landnutzung zu renaturieren.

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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. The study area *Stedinger Land* in the district Wesermarsch near Bremen, North-west Germany. Marked in red are 52 out of originally 70 plots recorded by Helmut Plate between 1936 and 1948 that were re-sampled in 2015.

Anhang E1. Das Untersuchungsgebiet *Stedinger Land* im Landkreis Wesermarsch bei Bremen, Nordwestdeutschland. Rot markiert sind die 52 von ursprünglich 70 zwischen 1936 und 1948 von Helmut Plate bearbeiteten Probeflächen, die 2015 wieder aufgenommen wurden.

Supplement E2. Coordinates of 52 quasi-permanent plots in the *Stedinger Land* near Bremen that were sampled by Helmut Plate in 1948 and re-sampled in 2015.

Anhang E2. Koordinaten der 52 quasi-permanenten Probeflächen im *Stedinger Land* bei Bremen, die zwischen 1936 und 1948 von Helmut Plate bearbeitet und 2015 wieder aufgenommen wurden.

Supplement E3. Vegetation table of 52 quasi-permanent plots in the *Stedinger Land* near Bremen, sampled in 1948 (plot numbers with 'a') and re-sampled in 2015 (plot numbers with 'n'). Species shown in Fig. 2b are given with their abbreviated names.

Anhang E3. Vegetationstabelle von 52 quasi-permanenten Probeflächen im *Stedinger Land* bei Bremen, bearbeitet 1948 (Aufnahmenummern mit 'a') und wieder aufgenommen 2015 (Vegetationsaufnahmen mit 'n').

Supplement E4. Values of soil variables measured in 52 quasi-permanent plots in the *Stedinger Land* near Bremen sampled in 2015.

Anhang E4. Werte von im Jahr 2015 gemessenen Bodenvariablen in 52 Probeflächen im *Stedinger Land* bei Bremen.

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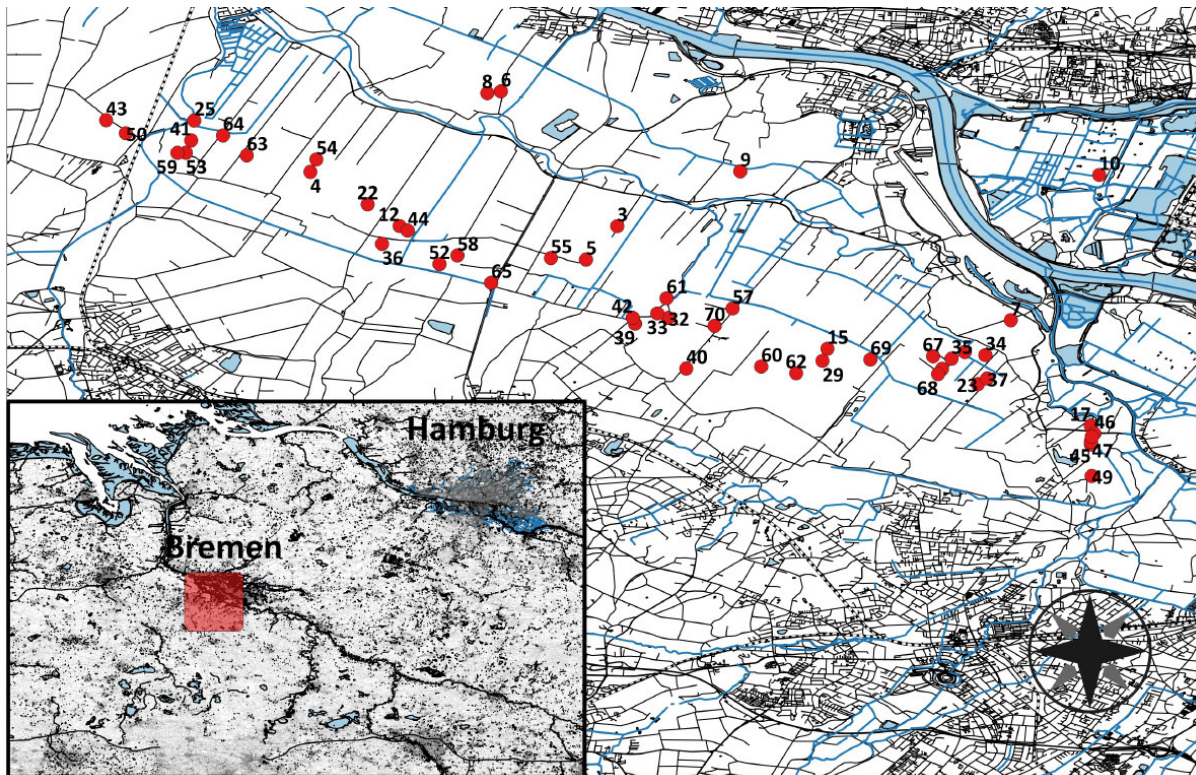
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Anhang E1. The study area *Stedinger Land* in the district Wesermarsch near Bremen, North-west Germany. Marked in red are 52 out of originally 70 plots recorded by Helmut Plate between 1936 and 1948 that were re-sampled in 2015. Copyright: Open Street Map (<http://download.geofabrik.de/europe.html>).

Supplement E1. Das Untersuchungsgebiet *Stedinger Land* im Landkreis Wesermarsch bei Bremen, Nordwestdeutschland. Rot markiert sind die 52 von ursprünglich 70 zwischen 1936 und 1948 von Helmut Plate bearbeiteten Probestellen, die 2015 wieder aufgenommen wurden. Copyright: Open Street Map (<http://download.geofabrik.de/europe.html>).



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Supplement E2. Coordinates of 52 quasi-permanent plots in the *Stedinger Land* near Bremen that were sampled by Helmut Plate in 1948 and re-sampled in 2015. North = Coordinates for the latitude, East = coordinates for the longitude. Additionally, coordinates are given in decimal numbers.

Anhang E2. Koordinaten der 52 quasi-permanenten Probeflächen im *Stedinger Land* bei Bremen, die zwischen 1936 und 1948 von Helmut Plate bearbeitet und 2015 wieder aufgenommen wurden. North = Koordinaten für die geographische Breite, East = Koordinaten für die geographische Länge. Die Koordinaten sind außerdem in Dezimazahlen angegeben.

Plot	North	North Decimal	East	East Decimal
3	53°08'12.61" N	53.13683611	8°33'37.41" E	8.560391667
4	53°08'52.1"N	53.14780556	8°29'53.5"E	8.498194444
5	53°07'48.3"N	53.13008333	8°33'14.6"E	8.554055556
6	53°09'50.65" N	53.16406944	8°32'12.44" E	8.536788889
7	53° 7'4.14"N	53.11781667	8°38'24.49"E	8.640136111
8	53°09'49.40" N	53.16372222	8°32'02.57" E	8.534047222
9	53°08'52.5"N	53.14791667	8°35'07.1"E	8.585305556
10	53° 8'49.83"N	53.147175	8°39'29.01"E	8.658058333
12	53°08'12.68" N	53.13685556	8°30'58.61" E	8.516280556
15	53°06'43.4"N	53.11205556	8°36'10.7"E	8.602972222
17	53°05'47.3"N	53.09647222	8°39'22.9"E	8.656361111
21	53°05'33.70" N	53.09269444	8°39'22.99" E	8.656386111
22	53°08'28.47" N	53.14124167	8°30'35.32" E	8.509811111
23	53°06'17.6"N	53.10488889	8°38'00.4"E	8.633444444
25	53°09'29.5"N	53.15819444	8°28'28.8"E	8.474666667
29	53° 6'34.55"N	53.10959722	8°36'7.09"E	8.601969444
32	53°07'05.78" N	53.11827222	8°34'14.59" E	8.570719444
33	53°07'09.09" N	53.11919167	8°34'06.61" E	8.568502778
34	53°06'38.74" N	53.11076111	8°38'05.88" E	8.634966667
35	53° 6'36.13"N	53.11003611	8°37'41.20"E	8.628111111
36	53° 7'59.68"N	53.13324444	8°30'45.77"E	8.512713889
37	53°06'21.7"N	53.10602778	8°38'07.2"E	8.635333333
39	53°07'01.60" N	53.11711111	8°33'50.33" E	8.563980556
40	53°06'28.94" N	53.10803889	8°34'27.73" E	8.574369444
41	53°09'14.98" N	53.15416111	8°28'26.57" E	8.474047222
42	53° 7'5.85"N	53.11829167	8°33'48.69"E	8.563525
43	53°09'29.7"N	53.15825	8°27'24.5"E	8.456805556
44	53°08'09.36" N	53.13593333	8°31'04.53" E	8.517925
45	53°05'35.66" N	53.09323889	8°39'22.94" E	8.656372222
46	53°05'41.58" N	53.09488333	8°39'25.39" E	8.657052778
47	53°05'39.38" N	53.09427222	8°39'23.59" E	8.656527778
49	53°05'10.8"N	53.08633333	8°39'23.5"E	8.656527778
50	53°09'20.2"N	53.15561111	8°27'39.0"E	8.460833333
51	53°06'41.05" N	53.11140278	8°37'50.87" E	8.630797222
52	53° 7'45.05"N	53.12918056	8°31'27.74"E	8.524372222
53	53°09'05.97" N	53.15165833	8°28'22.74" E	8.472983333
54	53° 9'1.17"N	53.150325	8°29'57.91"E	8.499419444
55	53°07'49.4"N	53.13038889	8°32'49.0"E	8.546944444
57	53°07'12.7"N	53.12019444	8°35'01.5"E	8.58375
58	53°07'51.26" N	53.13090556	8°31'40.78" E	8.527994444
59	53°09'05.93" N	53.15164722	8°28'16.56" E	8.471266667
60	53° 6'30.42"N	53.10845	8°35'22.38"E	8.58955
61	53°07'20.1"N	53.12225	8°34'13.3"E	8.570361111
62	53°06'25.6"N	53.10711111	8°35'47.9"E	8.596638889
63	53°09'04.1"N	53.15113889	8°29'07.1"E	8.485305556
64	53°09'18.6"N	53.15516667	8°28'49.8"E	8.4805
65	53°07'31.4"N	53.12538889	8°32'05.4"E	8.534833333
66	53° 6'28.68"N	53.10796667	8°37'34.33"E	8.626202778
67	53° 6'37.94"N	53.11053889	8°37'27.76"E	8.624377778
68	53°06'24.9"N	53.10691667	8°37'31.4"E	8.625388889
69	53° 6'35.50"N	53.10986111	8°36'42.03"E	8.611675
70	53° 7'0.05"N	53.11668056	8°34'48.42"E	8.580116667

Anhang E3. Vegetationstabelle von 52 quasi-permanenten Probestellen im *Stedinger Land* bei Bremen, bearbeitet 1948 (Aufnahmenummern mit 'a') und wieder aufgenommen 2015 (Vegetationsaufnahmen mit 'n').

	<i>Scheuchzeria-Caricetea</i> species also occurring in Molinietales communities
	<i>Phragmitetea</i> species also occurring in Molinietales communities
	<i>Molinietales</i> species
	Frequent companions of wet meadow communities

[illegible]

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Supplement E4. Values of soil variables measured in 52 quasi-permanent plots in the *Stedinger Land* near Bremen sampled in 2015.

Anhang E4. Werte von im Jahr 2015 gemessenen Bodenvariablen in 52 Probeflächen im *Stedinger Land* bei Bremen.

Plot no.	P [mg / 100 g dry soil]	Mg [mg / 100 g dry soil]	Ca [mg / 100 g dry soil]	K [mg / 100 g dry soil]	pH	N [%]	C [%]	C/N ratio
3n	2.68	46.78	191.06	17.48	4.36	1.00	10.04	10.08
4n	3.94	29.91	120.32	29.13	3.85	1.11	13.87	12.54
5n	6.09	81.87	301.34	20.37	4.81	1.42	16.58	11.65
6n	1.98	49.65	167.36	19.59	4.74	0.37	5.15	13.87
7n	9.63	82.59	261.16	107.30	5.31	0.95	11.31	11.93
8n	17.27	60.84	711.33	65.83	6.69	0.62	9.42	15.30
9n	23.01	91.69	317.23	13.32	4.79	1.03	21.79	21.20
10n	34.21	55.79	291.37	33.26	4.89	0.89	11.69	13.11
12n	3.91	44.88	252.83	53.68	4.64	0.70	10.18	14.61
15n	6.40	59.72	196.10	93.08	4.47	1.00	13.54	13.54
17n	2.85	24.48	90.48	12.99	4.19	0.29	5.33	18.25
21n	11.52	36.63	117.02	60.60	4.54	0.35	6.56	18.74
22n	1.25	59.68	250.73	10.86	4.19	0.75	9.07	12.11
23n	6.12	103.18	350.22	35.36	5.50	0.91	10.36	11.45
25n	3.20	52.68	195.13	11.41	5.38	0.32	5.11	15.96
29n	16.44	103.76	406.70	92.21	5.27	1.29	16.01	12.42
32n	5.61	37.63	225.25	60.01	4.94	0.48	6.95	14.63
33n	5.83	51.12	198.40	85.23	4.49	1.29	17.80	13.85
34n	11.14	49.65	234.13	70.93	4.96	0.66	9.30	14.15
35n	2.76	58.68	307.13	17.70	5.01	0.48	7.71	15.97
36n	3.89	64.34	218.95	97.94	4.51	2.10	29.25	13.91
37n	6.04	77.24	364.48	17.87	5.49	0.82	10.29	12.61
39n	1.29	55.34	222.28	21.37	4.71	0.73	9.31	12.70
40n	20.69	44.70	179.18	26.67	4.46	0.81	13.53	16.81
41n	2.34	38.48	148.49	82.10	4.31	1.38	19.57	14.15
42n	20.39	52.89	292.84	21.76	4.80	0.99	13.37	13.52
43n	2.58	41.81	290.24	19.59	4.48	1.13	16.18	14.36
44n	20.66	56.73	218.47	20.08	4.58	1.42	18.43	12.99
45n	6.41	31.81	171.54	22.47	5.57	0.24	4.74	19.65
46n	6.54	17.49	153.28	9.96	5.73	0.22	5.03	23.09
47n	6.38	30.20	133.93	13.82	4.88	0.20	4.34	21.72
49n	2.90	92.67	53.46	9.78	4.24	0.17	2.55	15.20
50n	1.31	53.94	349.79	14.60	4.89	0.89	10.70	12.04
51n	10.69	58.22	265.35	82.97	4.90	0.78	8.78	11.20
52n	15.28	19.53	171.98	14.99	3.60	2.35	30.13	12.80
53n	3.02	48.43	245.53	33.66	4.48	1.64	21.21	12.97
54n	15.66	28.67	142.96	80.49	4.58	0.32	4.05	12.57
55n	6.88	34.87	195.55	15.20	5.25	0.53	8.74	16.59
57n	5.34	27.09	164.08	27.45	5.61	0.27	5.04	18.59
58n	3.69	26.58	255.28	12.43	4.20	2.44	31.50	12.93
59n	4.01	35.64	174.89	37.73	4.40	1.06	13.04	12.29
60n	5.36	50.55	224.71	96.85	4.95	0.88	12.76	14.48
61n	2.48	49.24	201.54	20.19	4.48	0.99	14.71	14.81
62n	3.01	70.50	284.50	31.71	4.58	1.58	19.61	12.38
63n	4.16	55.58	249.23	52.54	4.85	0.98	13.90	14.17
64n	5.12	64.90	225.94	38.08	4.40	1.67	19.70	11.81
65n	15.14	22.85	195.09	9.60	5.31	0.29	6.11	21.35
66n	10.26	74.34	343.25	34.12	5.43	1.02	13.53	13.29
67n	18.90	128.02	708.87	38.85	6.52	0.82	10.98	13.37
68n	3.34	69.02	271.95	17.92	4.64	1.09	13.31	12.23
69n	3.83	70.07	336.79	27.32	4.79	0.63	10.17	16.15
70n	4.28	62.15	266.54	29.44	4.87	1.00	13.86	13.87

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