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ORIGINAL PAPER

Habitat loss of floodplain meadows in north Germany since the 1950s

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Abstract Floodplain meadows are severely threatened by land use change and intensification in Central Europe. This study investigates quantitative and qualitative changes in the vegetation of wet and species-rich mesic meadows in the floodplains of north Germany since the 1950s, considering their spatial extent, fragmentation, and replacement by other land use types. Historical high-resolution vegetation maps were compared with recent vegetation surveys in seven study regions (six unprotected areas, one protected reference area) in former West and East Germany. The unprotected sites showed alarming losses in wet and species-rich mesic meadows in the past 50 years (>80%). Wet meadows were substituted by species-poor, intensively managed grasslands (26–60% of the former area), arable fields (0–47%) or set-asides (2–33%). Species-rich mesic meadows were transformed to arable fields (42–72%) or species-poor, intensively managed meadows (14–72%). Decreases in effective mesh size and patch size indicated increasing fragmentation of wet meadows, whilst changes in landscape structure were less consistent in mesic meadows. Only slight changes in the protected floodplain study area indicate that landscape change is mostly caused by local effects such as fertilisation and drainage, but not by general trends such as atmospheric N deposition or climate warming. Despite the contrasting political systems in West and East Germany with different agroeconomic frames, all unprotected study areas showed similar losses and increasing fragmentation of floodplain meadows, which may negatively influence the natural dynamics of, and the gene flow between, meadow plant populations. We conclude that floodplain meadows in north Germany urgently call for high-priority conservation measures.

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Abbreviations

PLAND	Percentage of landscape
NP	Number of patches
PD	Patch density
AM	Area-weighted mean of patch size
CA	Total class area
MESH	Effective mesh size

Introduction

Agricultural intensification is one of the most influential drivers of biodiversity loss all over Europe (e.g. Donald et al. 2001; Tscharntke et al. 2005; Ellenberg and Leuschner 2010). Since the 1950s, agriculture has been intensified through increasing application of fertilisers and pesticides, and the widespread drainage of groundwater-influenced habitats (Schmidt 1990; Ihse 1995; Treweek et al. 1997; Benton et al. 2003). In former West Germany, the European Union's Common Agricultural Policy (CAP) has led to large-scale land use changes in the past decades (Bignal and McCracken 2000; Henle et al. 2008). Intensification campaigns followed in East Germany with a delay of about one decade (Bauerkämper 2004). Despite the differences caused by the contrasting political systems, in both former German states, landscape composition and structure has changed tremendously as a result of intensification (Weiger 1990; Kienast 1993; Hundt 2001).

Grasslands are among the habitat types most severely affected by changes (Treweek et al. 1997; Joyce and Wade 1998; Norderhaug et al. 2000; Hundt 2001; Hodgson et al. 2005; Prach 2008). A considerable part of the managed grassland that was present in the 1950s, has been transformed to cropland, afforested or used for construction purposes (Riecken et al. 2006; Walz 2008). Even within the short time since 2003, the area of permanently managed grassland in Germany declined by 3.1%, and the remaining sites became increasingly fragmented (Lind et al. 2009). Consequently, species-rich wet and mesic meadows belong today to the most threatened grassland types in Central Europe (Bergmeier and Nowak 1988; Dierßen et al. 1988; Dierschke and Briemle 2002; Riecken et al. 2006). While drainage and subsequent lowering of the groundwater table are the main causes for the loss of wet meadows (Rosenthal and Hölzel 2009; Prajs and Antkowiak 2010), application of fertilisers and increasing mowing frequency are key drivers of biodiversity loss in both wet and mesic meadows (Grevilliot et al. 1998; Jannsens et al. 1998; Härdtle et al. 2006).

Habitat fragmentation is another consequence of agricultural intensification that has important implications for biodiversity (Jaeger 2000; Henle et al. 2004; Lindborg and Eriksson 2004; Piessens et al. 2005; Boschi and Baur 2008). Hence, documenting habitat fragmentation at historical time and comparing it with the recent situation may be important for understanding vegetation changes and can also help to determine best-practice restoration measures for grassland habitats.

Various authors have investigated changes in the extent of meadows on the landscape scale in Central Europe, but their studies were mostly limited to a single area (e.g.

Jeanneret et al. 2003; Prach 2008; Jansen et al. 2009), based on a relatively coarse spatial scale (Williams and Hall 1987; Ihse 1995; Soons et al. 2005), or they relied on the analysis of non-spatial data such as the comparison of vegetation relevés (Meisel and von Hübschmann 1976).

The lack of replicated studies at multiple locations, which include detailed spatial information, is a major shortcoming, given the formerly wide distribution of floodplain grasslands in Central Europe (Treweek et al. 1997; Jensen 1998; Joyce and Wade 1998). Especially long-term studies that refer to the time before agricultural intensification (>50 years ago) have not been conducted so far, mainly because historical spatially explicit vegetation data are rare (Prach 2008) forcing most authors to rely on the interpretation of aerial photographs (e.g. Ihse 1995; Weiers et al. 2004; Wozniak et al. 2009).

Here, we studied two floodplain meadow habitat types, i.e. wet meadows and species-rich mesic meadows, at several locations in the lowlands of northern Germany and analysed changes in habitat extent and landscape structure in the time interval from the 1950/1960s to recent time (2008), i.e. over a period of 50 years. One of the investigated sites is a protected area according to the EU Habitats Directive (FFH, 92/43/EEC; European Commission 2007), which experienced only minor changes in the management regime and is thus used as a reference site for distinguishing between local and large-scale over-regional drivers of vegetation and landscape change (air-borne nutrient input, climate change etc.). The aim of our study was to document and analyse changes in these two formerly widespread floodplain grassland types in terms of spatial extent, temporal continuity or replacement, and fragmentation of habitats. We hypothesized that (1) both floodplain meadow types have significantly declined in their extent, but wet meadows are expected to have experienced more severe habitat losses due to their higher sensitivity to drainage, (2) both grassland types have largely been replaced by other land use types, but species-rich mesic meadows have mainly been transformed to habitat types subjected to enhanced land use intensity (such as arable fields and intensively managed grasslands), (3) the present extent of the two meadow types is partly determined by the historical floodplain meadow landscape structure, and (4) landscape change and habitat loss occurred at a much slower path at the protected floodplain site.

Methods

Study region

Landscape analysis and vegetation mapping were conducted in seven floodplain areas in the lowlands of northern Germany between the rivers Ems in the west and Havel in the east (Fig. 1). Historical (1950/1960) and recent (2008) vegetation maps covering a total area of 1961 ha each formed the basis of the analysis, the latter being compiled by the authors. In the 1950/1960s, wet and semi-wet meadow communities of the order *Molinietalia caeruleae* (including the main alliances *Calthion palustris*, *Molinion caeruleae* and *Cnidion dubii,* Appendix Table 5) and the species-rich mesic meadows of the order *Arrhenatheretalia elatioris* (comprising moist variances of *Cynosurion* and *Arrhenatherion*) were the most abundant grassland communities.

All study areas were situated in lowland regions with elevations ranging from 3 to 155 m a.s.l. in the seven regions (Table 1). While mean annual temperature varied only little (annual means of 8.5–9.5°C in the seven regions), precipitation ranged from

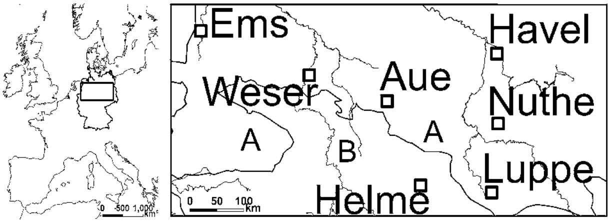

Fig. 1 Study region in north Germany and location of the seven study areas (*squares*) in the north German pleistocene lowlands (*A*), and in the Thuringian basin at the margin of the German uplands (*B*) (WGS 1984 PDC Mercator projection)

757 mm year^{-1} at the Ems river in the west (oceanic climate) to 484 mm year^{-1} at the Helme river in southeast Central Germany (subcontinental climate).

Four of the seven study areas were situated on the former territory of the German Democratic Republic (Helme, Luppe, Havel and Nuthe), the other three were located in western Germany (Ems, Weser, Aue). The Havel region has been protected since 1967, and became part of the Natura 2000 network. Furthermore, a small part of the Weser floodplain study area has been part of a nature reserve since 1961. All other study areas were not covered by nature protection measures.

Study area selection

We searched the relevant libraries and archives for the few existing high-quality historical vegetation maps that clearly distinguished between wet and species-rich mesic meadows. The historical maps of the study areas in West Germany (Ems, Weser and Aue) dated from 1946–1956, long before major land use changes occurred as a consequence of the agricultural policy of the EU. The East German vegetation maps were compiled in the period 1953–1969. The later maps were considered to be comparable to those from West Germany, because the intensification of agriculture started in East Germany only in the late 1960s (Hundt 2001; Bauerkämper 2004). In the case of the protected reference area (Havel), the oldest vegetation map dated from 1980; it was backdated by using monochromatic aerial photographs of 1953. This was based on the assumption that the composition of plant communities did not change much because the whole area has been protected during the time of interest here. The Havel study area was treated only as a reference and was not included in the statistical analyses.

Map standardisation and resurveying procedure

All selected historical vegetation maps were based on phytosociological units, which were in most cases accompanied by tables of phytosociological relevés. Because the phytosociological system has experienced major changes over the past decades and different underlying classification schemes had been applied in the seven areas, we decided to standardise the habitat categories identified in the historical maps using a widely applied key for habitat surveys developed by nature protection agencies in Germany (von Drachenfels 2004). This key is based on structural properties of the vegetation, indicator species, species richness data and abiotic habitat characteristics such as nutrient and water availability. The habitat key was used in the historical maps and was also applied in the 2008 resurvey. Two broad floodplain meadow habitat classes were defined based on

Table 1 Location and characteristics of the seven floodplain study areas (six unprotected areas plus the Havel protected reference area) in north Germany named after main rivers

Study area	Historical inventory (year)	Area covered by historical vegetation map (ha)	Size of protected area (ha)	Mean annual precipitation (mm $year^{-1}$)	Mean annual temperature (°C)	Elevation (m a.s.l)	Coordinates (GC-WGS 1984)	Historical source
Ems	1954	390	0	757	8.8	3	N 52°56′54″ E 07°17′32″	Ernsting et al. (unpublished)
Weser	1956	155	19	654	9.1	27	N 52°30′58″ E 09°05′52″	Hübschmann et al. (unpublished)
Aue	1946	264	0	620	8.9	67	N 52°16′20″ E 10°22′48″	Ellenberg (unpublished)
Nuthe	1958	376	0	560	8.8	115	N 52°02′44″ E 12°14′40″	Hundt 1958
Luppe	1967	186	0	500	9.5	90	N 51°21′43″ E 12°07′57″	Gräfe (unpublished)
Helme	1969	1081	0	484	8.5	155	N 51°26′33″ E 10°57′02″	Hundt 1969
Havel	1953	293	293	526	8.7	22	N 52°43′44″ E 12°13′00″	Fischer 1980

Climate data from German National Meteorological Service, DWD, based on the reference period 1961–1990 moisture conditions and species richness: wet meadows (including 98–100% of *Calthion* communities) and species-rich mesic meadows that have lower groundwater tables than the former and are in most cases not subject to inundation. Habitat type definitions and corresponding phytosociological units are summarised in Table 5 and Fig. 3 in the Appendix. Phytosociological relevés that further document the historical and recent meadow vegetation of the study areas have been registered under GIVD-EU-DE-009 (GIVD 2010).

The current vegetation was mapped during field-surveys between mid-May and mid-September 2008 using digital geo-referenced aerial ortho-photos from 2005–2007 with a ground resolution of 20–40 cm as basic maps. In cases where historical meadow sites had been transformed to other habitat types, the type of replacement habitat was recorded using a categorization system of six classes: (1) species-poor, intensively managed grasslands; (2) abandoned floodplain marshes and grassland fallows; (3) woodland and scrubland; (4) arable fields; (5) water-bodies, and (6) settlements and industrial areas.

Geo-statistical analysis

The historical and actual vegetation maps were digitised in a vector framework using corresponding map resolutions (scale c. 1:10 000) and were geo-statistically analysed using ArcGIS-ArcInfo software, v. 9.2 (ESRI 2006–2009) and the program Fragstats 3.0 (McGarigal et al. 2002).

Intersecting the two vector layers allowed demarcating areas where historically-old meadows persisted, new meadows had been created, and historical meadows had been replaced by other habitat types.

Habitat fragmentation analysis examined the area covered by the target meadow types in historical and recent times. For each study area and time period, individual grid maps (4 m $\times$ 4 m resolution) were produced illustrating the spatial distribution of (1) wet meadows, (2) species-rich mesic meadows, and (3) the combined area of the two meadow types. The grids were imported to Fragstats 3.0 and the following class-level landscape metrics were calculated: percentage of the landscape (PLAND) covered by a given habitat type, number of patches (NP), patch density (PD), area-weighted mean of patch size (AM), total class area (CA) and effective mesh size (MESH) equalling the sum of patch area squared, summed across all patches of the corresponding patch type and divided by the total landscape area. For MESH, AM and total extent, the significance of changes between the two time periods was tested by a Wilcoxon-test for pair-wise differences using R-software (R Development Core Team 2010).

Results

Changes in the extent of floodplain meadows

In the six unprotected study areas, wet and species-rich mesic meadows declined enormously between the 1950/1960s and 2008 (differences significant at $p \leq 0.05$; Fig. 2, Table 2). On average, wet meadows lost 85.2% of their former area, and species-rich mesic meadows decreased by 83.6%. Wet meadows were nearly completely lost at the Weser and the Luppe with <5 ha remaining, while species-rich mesic meadows were reduced to about 8 ha. In the largest study area (Helme), a 83% loss led to a remaining wet meadow area of 100.3 ha, of which 77.5 ha were historically old and 22.8 ha were newly created after

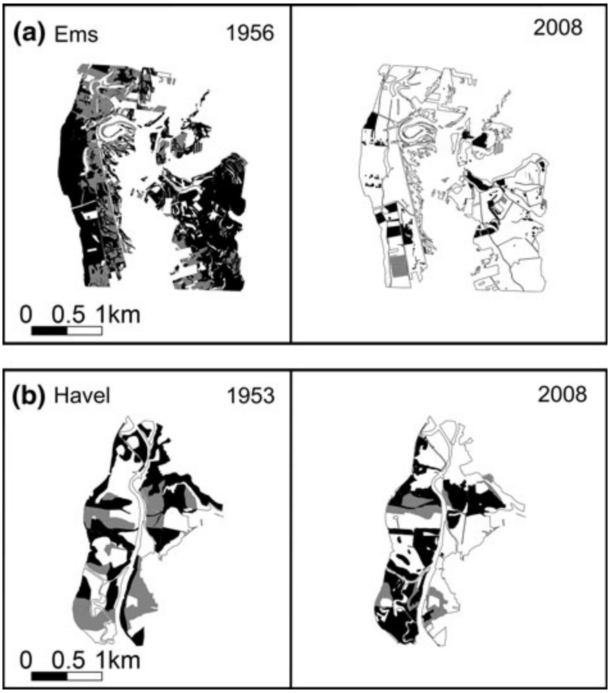

Fig. 2 Areas of wet meadows (*black*) and species-rich mesic meadows (*grey*) in two of the seven study areas **a** Ems, **b** Havel, in the 1950/1960s and in 2008. Other habitat types: *white* areas

1969. The Helme floodplain also harbours at present the largest area of species-rich mesic meadows (12.3 ha), of which 8.3 ha were newly created. The current extent of wet meadows in the Havel protected area was comparatively large (100.8 ha), but only about a third was historically old. While wet meadows at the Havel declined only slightly during the past decades (by 7.4%), the loss of species-rich mesic meadows was substantial (54.3%).

Replacement of historical floodplain meadows by other habitat types

Landscape conversion was large in all unprotected study areas, with historically-old wet meadows being nowadays present on only 9.1% (±5.5 SD) of their former area, and only 3.1% (±4.3 SD) of species-rich mesic meadows persisting (Table 3). Wet meadows were mainly substituted by species-poor, intensively managed grasslands. In the Ems, Aue and Nuthe areas, 45–60% of the meadows were converted into species-poor grasslands. At the Luppe, most meadows were converted to arable fields (47%) followed by the proportion of grasslands transformed to species-poor, intensively used grasslands (26%). In the Weser area, species-poor grasslands, fallows and arable fields were established, replacing former meadows. At the Helme, a dam was constructed in 1969, resulting in the conversion of much of the meadow area to a lake. The formerly widespread species-rich mesic meadows at the Ems, Weser, Aue and Luppe were largely substituted by arable fields (42–72%), followed by transformation to species-poor, intensively used meadows. In the Nuthe and

Table 2 Changes in the area of wet and species-rich mesic floodplain meadows between the 1950/1960s and 2008

Study area	Historical area in the 1950/1960s (ha)	Current area in 2008 (ha)	Historically old area remaining in 2008 (ha)	New area in 2008 (ha)	Total area loss 1950/1960s – 2008 (%)
Wet meadows					
Ems	242.6	28.7	20.8	7.9	−88.2
Weser	100.4	4.1	2.8	1.3	−95.9
Aue	28.1	7.9	3.8	4.1	−71.9
Helme	575.8	100.3	77.5	22.8	−82.6
Luppe	22.2	3.0	0.5	2.5	−86.5
Nuthe	343.8	48.7	48.0	0.7	−85.8
Mean (±SD)	218.8 (±196.9)	32.1 (±34.5)	25.6 (±28.4)	6.6 (±7.6)	−85.2 (±7.2)
Havel	108.8	100.8	32.9	67.9	−7.4
Species-rich mesic meadows					
Ems	109.6	8.9	3.2	5.7	−91.9
Weser	45.0	7.1	0.3	6.8	−84.2
Aue	158.6	4.6	0.3	4.3	−97.1
Helme	34.5	12.3	4.0	8.3	−64.3
Luppe	92.6	8.2	2.8	5.4	−91.1
Nuthe	27.2	7.3	0.1	7.2	−73.2
Mean (±SD)	77.9 (±47.0)	8.1 (±2.3)	1.8 (±1.6)	6.3 (±1.3)	−83.6 (±11.5)
Havel	71.7	32.8	12.9	19.9	−54.3

Helme areas, formerly species-rich mesic meadows were to >50% replaced by species-poor meadows.

The situation was completely different in the Havel area. Here, wet meadows remained the most abundant habitat type (30% of the area). More than 90% of the former species-rich mesic meadows remained grasslands, even though a large proportion was transformed to species-poor, intensively managed grassland (37%). Another 40% of the study area referred to newly established wet meadows.

Habitat fragmentation

The various investigated measures of landscape structure indicated similarly large changes over the 50-year period for wet and species-rich mesic meadows, except for the protected Havel area where only very small changes occurred (Table 4). The remaining wet meadows of the unprotected floodplains experienced increasing fragmentation, as indicated by the patch size (area-weighted mean, AM) which decreased from 33.6 ha in the first census period to 2.8 ha in 2008 (difference significant at $p \leq 0.05$). However, trends in the number of patches per study area were not consistent. Effective mesh size (MESH), which gives the degree of fragmentation, dramatically decreased in the wet meadow area from a mean of 24.14 to 0.25 ha ($p \leq 0.05$). In contrast, in the protected Havel area, AM and MESH remained more or less constant, indicating constancy in the degree of habitat fragmentation during the past decades.

Table 3 Transformation of historical species-rich mesic meadows (MM) and wet meadows (WM) into other land use types (1950/1960s to 2008), and remaining area of historically old meadows (*italics*) in the seven study areas, expressed as percentage of the area in the 1950/1960s

	Species-rich mesic meadows		Wet meadows		Species-poor, intensively managed grasslands		Marshes, fens, watersides and fallows		Woodlands and shrublands		Arable fields		Water-bodies		Settlements, industrial areas	
Original habitat type	MM	WM	MM	WM	MM	WM	MM	WM	MM	WM	MM	WM	MM	WM	MM	WM
Ems	*2.9*	2.0	4.2	*8.6*	36.4	44.4	4.0	7.1	2.1	4.5	49.6	32.3	0.5	0.7	0.3	0.6
Weser	*0.6*	7.0	2.9	*2.8*	27.9	18.3	9.3	32.6	3.6	21.5	50.1	16.0	1.5	0.4	4.1	1.4
Aue	*0.2*	6.5	2.9	*13.5*	37.9	51.3	6.1	11.7	7.0	13.4	42.8	1.8	0.5	1.4	2.8	0.4
Nuthe	*11.6*	1.2	9.1	*13.5*	72.2	59.8	0.5	2.0	1.9	7.7	3.7	14.7	0.9	0.9	0.1	0.2
Luppe	*3.0*	11.6	0.1	*2.1*	14.1	26.1	2.8	2.1	7.7	9.6	71.5	46.6	0.5	1.0	0.2	0.8
Helme	*0.2*	0.8	0.8	*14.0*	50.7	30.3	10.6	9.5	0.1	0.5	0.2	0.1	37.0	44.5	0.3	0.4
Mean	*3.1*	4.8	3.3	*9.1*	39.9	38.4	5.6	10.8	3.7	9.5	36.3	18.6	6.8	8.2	1.3	0.6
Havel	*18.1*	11.7	40.1	*30.3*	37.3	26.5	3.1	10.5	0.9	2.7	0.5	0.0	0.0	18.0	0.0	0.4

The mean refers to the average of the six unprotected study areas; the protected Havel area is presented as a reference

Table 4 Landscape metrics for wet meadows, species-rich mesic meadows and their combined areas in the seven floodplain study areas

Study area	Year of first inventory	Number of patches 1950/1960s	Number of patches 2008	Remaining number of patches (%)	Patch density 1950/1960s (n 100 ha^{-1})	Patch density 2008 (n 100 ha^{-1})	Mean patch size 1950/1960s (ha)	Mean patch size 2008 (ha)	Effective mesh size 1950/1960s (ha)	Effective mesh size 2008 (ha)
Wet meadows										
Ems	1956	231	111	48.1	59.2	28.5	60.1	1.6	37.36	0.12
Weser	1954	48	13	27.1	30.9	8.4	17.9	0.8	11.54	0.02
Aue	1946	26	40	153.8	9.8	15.2	3.3	1.0	0.36	0.03
Helme	1969	203	32	15.8	18.8	3.0	30.2	9.3	16.08	0.86
Luppe	1967	10	8	80.0	5.4	4.3	3.8	0.9	0.45	0.01
Nuthe	1958	29	45	155.2	7.7	12.0	86.3	3.3	79.04	0.43
Mean (±SD)		91.2 (±90.0)	41.5 (±33.8)	80.0 (±56.3)	22.0 (±18.7)	11.9 (±8.5)	33.6* (±30.4)	2.8* (±3.0)	24.1* (±27.5)	0.25* (±0.3)
Havel	1953	18	37	205.6	6.2	12.6	11.5	12.3	4.29	4.22
Species-rich mesic meadows										
Ems	1956	230	19	8.3	59.0	4.9	4.2	2.4	1.19	0.05
Weser	1954	61	11	18.0	39.3	7.1	2.0	2.4	0.57	0.11
Aue	1946	88	6	6.8	33.3	2.3	6.5	2.2	3.89	0.04
Helme	1969	86	16	18.6	8.0	1.5	1.6	2.2	0.05	0.02
Luppe	1967	16	16	100.0	8.6	8.6	16.2	1.1	8.08	0.04
Nuthe	1958	51	14	27.5	13.6	3.7	1.2	1.0.	0.09	0.02
Mean (±SD)		88.7 (±67.6)	13.7 (±4.2)	29.9 (±32.1)	27.0 (±18.7)	4.7 (±2.5)	5.3 (±5.2)	2.1 (±0.5)	2.3* (±2.9)	0.05* (±0.03)
Havel	1953	13	12	92.3	4.4	4.1	11.7	8.9	2.86	1.00
Floodplain meadows (total)										
Ems	1956	110	120	109.1	28.2	30.8	65.7	1.8	59.33	0.17
Weser	1954	67	22	32.8	43.1	14.2	17.0	1.8	15.95	0.13
Aue	1946	65	43	66.2	24.6	16.3	7.4	2.6	5.22	0.12

Table 4 continued

Study area	Year of first inventory	Number of patches 1950/1960s	Number of patches 2008	Remaining number of patches (%)	Patch density 1950/1960s (n 100 ha^{-1})	Patch density 2008 (n 100 ha^{-1})	Mean patch size 1950/1960s (ha)	Mean patch size 2008 (ha)	Effective mesh size 1950/1960s (ha)	Effective mesh size 2008 (ha)
Helme	1969	262	45	17.2	24.2	4.2	29.0	9.1	16.35	0.95
Luppe	1967	18	21	116.7	9.7	11.3	22.2	1.2	13.70	0.07
Nuthe	1958	17	57	335.3	4.5	15.2	99.8	3.1	98.55	0.46
Mean (±SD)		89.8 (±83.3)	51.3 (±33.3)	112.9 (±105.9)	22.4 (±12.6)	15.3 (±8.0)	40.2* (±32.3)	3.3* (±2.7)	34.9* (±33.4)	0.3* (±0.3)
Havel	1953	12	35	291.7	4.1	12.0	41.7	18.9	25.73	8.65

Significant differences between the 1950/1960s and 2008 are marked by asterisks (*). Floodplain meadows (total) are the sum of wet and species-rich mesic meadows

In contrast to the wet meadows, the landscape metrics analysis for the species-rich mesic meadows showed few consistent trends over the 50 years, even if the protected area is excluded. Only MESH showed a uniform and significant decline for all unprotected study areas with a decrease from a mean of 2.31 to 0.05 ha ($p \leq 0.05$). In comparison, AM of the species-rich mesic meadows in the Havel area decreased only slightly and this parameter remained several times larger than at the other study sites (8.9 ha). The mean MESH value at the Havel decreased from 2.86 to 1.00.

Pooling the data of the two meadow types confirmed the trends shown in the separate analyses with significant decreases in both AM and MESH ($p \leq 0.05$) in the unprotected area. At the Havel, this overarching analysis also showed a decline in AM and MESH ($p \leq 0.05$). However, the landscape structure parameters in this area were not only 50 years ago, but also in 2008 several times larger than those from the unprotected study areas demonstrating a relatively low degree of grassland fragmentation.

Discussion

Habitat loss of wet and species-rich mesic meadows in unprotected areas

Despite the different political histories of East and West Germany from 1945 to 1989 and corresponding differences in the agricultural development, the six unprotected study areas showed similar trends of grassland development with severe losses in the spatial extent of wet and species-rich mesic meadows (total losses >80%). Similarly high losses of wet meadows were detected by several other case studies in European countries. In a study from the U.K., the extent of lowland floodplain grasslands was reduced by >80% and much of the remaining wet meadows had been intensified from the 1930s until the 1980s (Treweek et al. 1997). In Hungary, the area of wet meadows decreased by two-third, which was mainly related to intensification (Joyce and Wade 1998). Soons et al. (2005) described the almost complete disappearance of wet and moist grasslands over the last 100 years for three studied landscapes in the Pleistocene lowlands of the Netherlands. In our study, we found evidence for a general decline in area in both meadow types, but we had to reject the hypothesis that wet meadows have experienced significantly larger losses because of their higher sensitivity to drainage.

For their present extent, site history seems to play an important role: in the few study sites where a relatively large proportion of historically-old meadows persisted until 2008, the absolute extent of meadows in the past was generally larger than elsewhere. However, while the percentage of remaining historical area in wet meadows was higher than in mesic meadows, the establishment of new grasslands was more important in mesic than in wet meadows. Large parts of the current wet and species-rich meadows are not historically old. Recently established wet meadows are generally less species rich and more uniform in their species composition than old ones (Bissels et al. 2004). Klimkowska et al. (2007) found that the restoration success of wet meadows in western Europe is rather limited, and is more successful in cases where the remaining meadows still hold more target species. This emphasizes the outstanding importance of extensively used, historically-old grasslands for nature conservation.

Transformation of meadows in the course of agricultural intensification

We found that a large part of the former wet and mesic grasslands (about 40%) had been substituted by species-poor, intensively used grasslands. Agricultural intensification which includes the application of chemical fertilisers, drainage, re-sowing often combined with ploughing, and a shift from hay-making to silage, in fact represents the most serious threat to north-western and central European lowland meadows (Hodgson et al. 2005; Wittig et al. 2006; Rodwell et al. 2007).

A considerable part of the grassland area has been transformed to arable fields during the past 50 years, which should have been associated with a large loss of soil organic carbon to the atmosphere (Guo and Gifford 2002). Drainage of meadow areas typically enhances C and N mineralization (Wassen and Olde Venterink 2006), resulting in internal eutrophication of the grasslands.

Patterns of conversion strongly depend on the soil moisture regime. Mesic grassland areas were twice as often converted into arable fields than wet meadows, mainly due to the high costs of draining wet grasslands. In contrast, former wet meadows were twice as often abandoned than mesic meadows and thus were frequently invaded by scrub, or converted to forest plantations (mostly poplar). Abandoned meadows may soon be dominated by *Phragmites australis* or tall sedges with negative effects on plant diversity (Marschalek et al. 2008).

Fragmentation of floodplain meadows

Agricultural intensification is typically linked to a re-organization of the production landscape, shifting to larger arable fields and homogeneously structured, intensively used grassland patches. For typical floodplain meadow habitats, which are linked to extensive land use practises, we found the opposite trend. Since the 1950/1960s, floodplain meadows became highly fragmented as reflected by significant decreases in the structural parameters AM and MESH (an exception is the AM value of species-rich mesic meadows). Clearly, both measures are sensitive to artefacts introduced by digitising and rastering of maps. However, the 50-year differences are so large and occurred so uniformly in all six study areas, that a misinterpretation of trends can be excluded. Moreover, the direct comparison of historical and current maps (see Fig. 2) supports the data presented in Tables 2, 3 and 4. Soons et al. (2005), who investigated changes in Dutch moist and wet grasslands since 1900, came to similar conclusions. They found the largest reduction in patch size (AM) during the first half of the twentieth century, with an average reduction by 0.2 ha per year over the last 100 years. Two of our study areas (Helme and Nuthe) showed a larger effective mesh size (MESH) in 2008 than the other areas. At these sites, wet meadows covered a particularly large area in the 1950/1960s which seems to have retarded fragmentation in the past 50 years.

Large patches of meadow vegetation generally harbour a larger proportion of the species pool since edge effects are reduced (Kiviniemi and Eriksson 2002). A high connectivity of meadow localities in historical time may also have a positive effect on the species richness of temperate grasslands in recent time (Lindborg and Eriksson 2004). In addition, many typical wet meadow species are adapted to seed dispersal by flooding (Gerard et al. 2008). Given that Central European river floodplains nowadays are less frequently flooded than in the past, the probability of natural seed input from abroad is most likely smaller in remnant areas that are small and isolated than in large patches. In addition, isolated meadow patches of small size will expose their plant populations to the increased risks of genetic drift and the harmful consequences of stochastic population fluctuations that may eventually lead to their extinction.

Local and continent-wide drivers of vegetation change

Substantial area losses were also recorded in the protected Havel floodplains, in particular in the species-rich mesic meadows, which demonstrates that the existing legislative tools for nature protection are not sufficient in the agricultural landscape, because they allowed a certain degree of agricultural intensification, at least in the years before 1990. In most nature reserves dedicated to protect species-rich meadows, it is nowadays prohibited to intensify agricultural management, but this does not exclude effects of atmospheric N deposition, nutrient input through sedimentation processes (Gulati and van Donk 2002), and climatic changes, which act as additional large-scale drivers of vegetation change in both unprotected and protected meadow areas. Despite these overarching threats, the Havel example demonstrates that protection efforts were successful in preserving a large patch of species-rich wet and mesic meadows with sufficient connectivity of the localities in the landscape. In most parts of north Germany and also in the Netherlands (Soons et al. 2005), valuable mesic and wet meadows are nowadays restricted to such conservation areas.

Conclusions

The extent and habitat quality of north German lowland floodplain grasslands has dramatically decreased since the 1950s, and the loss of endangered grassland habitats is an ongoing process in Germany (Ammermann 2008; Lind et al. 2009). Our representative sample of lowland floodplain areas shows that in most cases only isolated patches of the formerly widespread floodplain meadows persisted until today. Larger meadow patches (>3 ha) were conserved only in the Helme and Nuthe areas which had the largest grassland areas in the 1950/1960s. A low degree of fragmentation may facilitate future restoration and nature conservation efforts, because the dispersal of many grassland species is low (Soons et al. 2005; Bischoff et al. 2009), and the restoration of typical grassland habitats is difficult (Bakker and Berendse 1999). Thus, enhancing or at least maintaining the connectivity of remaining grassland patches is a prerequisite to increase population sizes and prevent local extinction of endangered species.

Our study provides evidence that the current extent and structure of floodplain meadows is also influenced by the site history. In areas where the historical extent of floodplain meadows was highest and historical fragmentation lowest, are the percental losses in species-rich mesic grasslands smaller and the present-day fragmentation lower. We conclude that the losses in wet and mesic grasslands with high conservation value are dramatic in north Germany calling for large-scale floodplain meadow sanctuaries in areas where remnants of historically old grasslands still persist.

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Appendix

See Table 5 and Fig. 3.

Table 5 Criteria applied for classifying meadows during current vegetation mapping and on historical vegetation maps and relevés in the two main meadow habitat classes

	Species-rich mesic meadows	Wet meadows
Habitat code (von Drachenfels 2004)	9.1.1, 9.1.3, 9.1.5: Mesophilous grasslands	9.3: Wet meadows dominated by sedges or forbs; 9.4: Other wet meadows
Moisture conditions	Moderately dry to moderately wet	Permanently or temporarily wet, either caused by high levels of groundwater or by temporary flooding
General habitat description (von Drachenfels 2004)	Rich to moderately rich in typical meadow species, structure of grassland or fallow with a still reasonably high number of typical grassland species, usually mown (1–)2(–3) times per year, characteristic mixture of tall and low grasses, usually rich in herbs.	Grassland on wet or periodically wet sites with either high cover of sedges and/or rushes, or of herbs indicating wet conditions. Usually low-intensity mown or grazed grassland, if fallow then wet meadow indicators still present.
Characteristic phytosociological units included in meadow groups after von Drachenfels (2004)	Mesic to moist variants of the *Cynosurion* or the *Arrhenatherion* s.l.: e.g. *Lolio perennis-Cynosuretum cristati (lotetosum, luzuletosum, plantaginetosum mediae, typicum)*; *Arrhenatheretum alopecuretosum*; *Dauco-Arrhenatheretum eliatoris, Anthoxanthum odoratum-Holcus lanatus* grassland	*Molinietalia caeruleae and Potentillo-Polygonetalia* communities: e.g. *Junco Molinietum*; *Molinietum caeruleae; Angelico-Cirsietum oleracei* (incl. *caricetosum fuscae*); *Bromo-Senecionetum* (incl. *agrostietosum caninae);* *Polygono-Cirsietum oleracei*; *Ranunculo-Alopecuretum geniculati*
Phytosociological units as assigned on the historical vegetation maps (cp. Table 1)	*Galio molluginis-Alopecuretum pratensis*; *Angelica sylvestris-Arrhenatherum elatius* community; *Dactylis glomerata-Cirsium oleraceum* community, *Lolio perennis-Cynosuretum cristati (lotetosum, luzuletosum,* typicum); *Arrhenatheretum elatioris* (a*lopecuretosum pratensis*, d*eschampsietosum cespitosae*, *sanguisorbetosum officinalis*); *Alopecuretum pratensis*; *Dauco-Arrhenatheretum eliatoris*; *Filipendulo-Ranunculetum polyanthemi*	*Molinietalia caeruleae and Potentillo-Polygonetalia* communities: *Angelico-Cirsietum; Polygono-Cirsietum*; *Carex-Cirsium oleraceum* community; *Bromo-Senecionetum*; *Scirpietum sylvatici*; *Junco-Molinietum*; *Rumici crispi-Alopecuretum geniculati*; *Ranunculo-Alopecuretum geniculati*; *Sanguisorbo officinalis-Silaetum silai;* *Carex acuta* meadows; *Poa palustris-Carex acuta* community; *Phalaridetum arundinaceae*; *Glycerietum maximae*; *Pediculari palustris-Juncetum filiformis*; *Cnidio-Deschampsietum*

Nomenclature of plant communities (syntaxa and their synonyms) and of habitats follows Rennwald (2000) and von Drachenfels (2004)

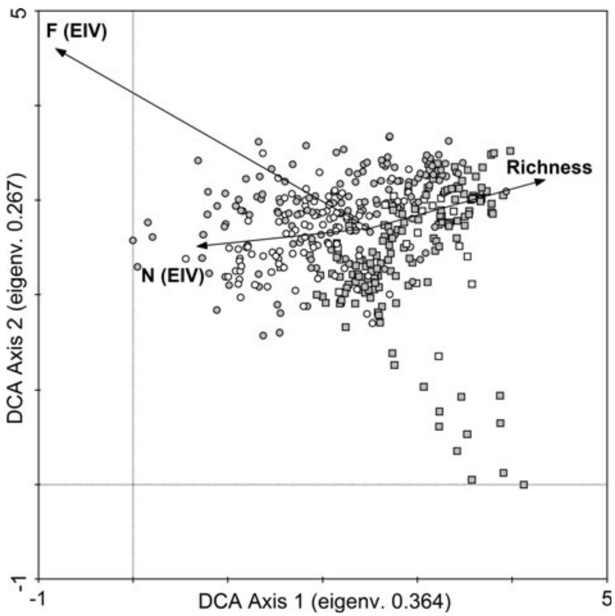

Fig. 3 Detrended correspondance analysis (DCA) of wet and mesic meadow relevés from the 1950/1960s and 2008 (423 relevés). The samples are coded according to main habitat classes: *circles* wet meadows, *squares* mesic meadows, *filled symbols* historical relevés (1950/1960s), *open symbols* current relevés (2008). Cover values are log-transformed (downweighting of rare species, eigenvalues/length of gradient *axis 1*: 0.364/4.124; *axis 2*: 0.267/3.672). Secondary variables were correlated with DCA axis in a post hoc manner (mean Ellenberg indicator values (*EIV*) for moisture (*F*) and nutrients (*N*); species richness)

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