Landscape change and impoverishment in North German grasslands since the 1950s

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General introduction

Landscape change in Central Europe

The world's natural vegetation cover has been widely replaced by man-made land covers. Central Europe would be almost entirely dominated by forests without the human influence (Bohn et al. 2000, 2003). During the last centuries increasing human populations created a cultural landscape that required large scale deforestation. The former forest areas were predominantly transformed into agriculture areas (cropland and grassland) used for food production (Ellenberg and Leuschner 2010). These human activities also led to the small-scaled and highly structured cultural landscape in Central Europe that could be found until large-scale intensifications started.

Since the 1950s agriculture has been rapidly intensified. The drainage of groundwater-influenced habitats as one consequence of meliorations occurred widespread (Schmidt 1990; Ihse 1995; Treweek et al. 1997; Benton et al. 2003). Many landscape structures were eliminated and landscape composition changed tremendously (Gustavsson et al. 2007; Krauss et al. 2010; Flohre et al. 2011). Species richness and composition of agro-ecosystems was additionally influenced by further aspects of management, such as mechanical disturbances, e.g. due to ploughing or mowing (Dupré et al. 2010; Morecroft et al. 2009; Smart et al. 2005). The application of fertilisers and pesticides accelerated since the advent of the Common Agricultural Policy (CAP) in Western Europe in the late 1950s. CAP was later identified as being responsible for increasing habitat degradation and biodiversity loss, and was reformed in several steps from the late 1980s to the European Union Agenda 2000 (Bignal and McCracken 2000, Henle et al. 2008). In Eastern Europe intensification campaigns followed 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 in land use (Weiger 1990; Kienast 1993; Hundt 2001). Finally, today's intensive agriculture 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). Land abandonment on mostly marginal sites can lead to an additional change in landscape, and thus to a shift in species composition but is only a regional phenomen (Henle et al. 2008).

Changes in quantity and quality of grasslands

Grasslands can harbour a large number of plant species in dependence of site conditions and management regime (intensity, grazing or mowing) (Dierschke and Briemle 2002). In Central Europe more than one thousand higher plant species are detected in grasslands and therefore this type of biotope harbours the communities richest in species number (Ellenberg and Leuschner 2010). During the last decades the management often changed and grasslands are among the most severely affected habitat types (Treweek et al. 1997; Joyce and Wade 1998; Norderhaug et al. 2000; Hundt 2001; Hodgson et al. 2005; Prach 2008). Depending on the local environmental and economic conditions, large fractions of former managed grassland in Central Europe have been transformed to cropland, afforested, abandoned or used as construction sites (Riecken et al. 2006; Walz 2008). Over the past 60 years the increasing trend towards more industrial agriculture has additionally led to significant increases in the amount of fertilizer applied, in mowing frequency and in increasing stocking densities on remaining grassland sites. As a consequence, the large group of threatened higher plants in Germany comprises taxa from extensively managed grasslands (Korneck et al. 1998; Korsch and Westhus 2004). Today extensively managed grasslands often remain only under marginal land conditions, e.g. steep slopes or sites with shallow or wet soil where the use of machinery is not feasible or inefficient. Wet or moist sites were often meliorated and so drainage and subsequent lowering of the groundwater table are the main causes for the loss of wet meadows (Rosenthal 2003; Rosenthal and Hölzel 2009; Prajs and Antkowiak 2010). Consequently, the application of fertilisers and an increasing mowing frequency become possible and act as key drivers of biodiversity loss in both wet and mesic meadows (Grevilliot et al. 1998; Jannsens et al. 1998; Härdtle et al. 2006). In contrast to the intensifications abandonment of grasslands is another threat that leads to slow deterioration in kind of succession. Even the type of grazing and the grazing frequency with heterogenous effects on species diversity and species composition changed during the last decades depending on region (Dierschke and Briemle 2002).

The tremendous decline of semi-natural relatively dry grasslands has been documented for many Northern and Central European landscapes (Hodgson et al. 2005; Pärtel et al. 2005; Strijker 2005; Cousins and Lindborg 2008). In the agriculturally dominated areas of Central Europe, moist and mesic grasslands are among the habitat types that have experienced the severest losses in area (Prach 2008). 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; Ellenberg and Leuschner 2010). Overall mesotrophic grasslands have suffered from an alarming species decline and habitat loss over the last few decades (Wittig et al. 2006; Rodwell et al. 2007). However, it has recently been recognized that grasslands generally show losses in plant species richness over time (Isselstein 2003). Deterioration of the quality and quantity of grasslands is not yet stopped. Even since 2003, the area of permanently managed grassland in Germany declined by 3.1% (Lind et al. 2009), with regional differences. Since the 1950s, in parallel to agricultural intensification in more productive areas, the area of grassland increased in marginal rural landscapes such as in the uplands of Germany and Britain (Peppler-Lisbach 2003; Hodgson et al. 2005; Wellstein et al. 2007; Waesch and Becker 2009).

Today grasslands have come under additional pressure through the increasing importance of renewable energy (Lind et al. 2009). Hence, the trend of declining grassland (predominantly by substitution with maize cultivation and intensifications in management on remaing grassland sites) is additionally amplified in some regions by the cultivation of energy crops.

Fragmentation

Habitat fragmentation is mainly caused by habitat loss. The term describes a landscape-level process in which a habitat type is subdivided in more scattered and isolated remnants that are smaller in size than the original habitat (Saunders et al. 1991). According to the theory of island biogeography (MacArthur and Wilson 1967) habitat fragmentation may affect biodiversity through decreased size of habitat patches and increased patch isolation (Debinski and Holt 2000; Fahrig 2003; Ewers and Didham 2006). Additional consequences are changes in landscape composition, structure and function. The underlying process could be natural, e.g. changes in the river course as a result of natural meandering or succession, but mainly occur as a result of human land use activities. In Central Europe habitat fragmentation is mainly a 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). The land consumption for infrastructure in Germany increased by ca. 120 ha every day from 1993-2007 (Schweppe-Kraft et al. 2008) and leads to increasing fragmentation in some regions. Changes in the fragmentation level depend on region, scale and the considered habitat type.

The exchange of genes between remaining populations and re-colonization after extinction is hampered with increasing patch-isolation in fragmented landscapes (Hanski 1999). If the distance to neighbouring areas does not exceed the dispersal range, pollen or seeds from plants in surrounding areas can increase the genetic diversity. The dispersal capability of plant seeds depends on their dispersal adaptations (e.g. Willson 1993; Hughes et al. 1994; Fischer et al. 1996; Danvind and Nilsson 1997 in Geertsema et al. 2002), but many grassland specialists have very limited dispersal ranges (Eriksson and Ehrlén 1992; Turnbull et al. 2000; Martin and Wilsey 2006; Cousins and Aggemyr 2008). Even plants with relatively long-distance wind dispersal are strongly negatively affected by fragmentation (Saar et al. 2012). A study of Winter et al. (2008) found negative effects through fragmentation on three typical floodplain plant species. Dauber et al. (2010) reported a negative effect on reproduction in small populations of flowering plant species due to lower pollination success. Due to usually positive correlations between the population size of a species and its habitat area (Honnay et al. 2006; Lennartsson 2000; Hanski 1999) there is a higher risk of extinction in smaller populations (Lande 1988, Matthies et al. 2004). Extinction is hence more likely in habitats affected by fragmentation. Habitat quality is also often lower in smaller patches as a result of an increased exposure to edge effects (Oostermeijer et al. 1994).

As such, patch size and habitat isolation are likely to increase the risk of local extinctions occurring in more isolated patches of grassland. These factors, along with the substantial decline in overall grassland area, have been associated with the progressive fragmentation of the remaining meadows and pastures in a matrix of arable land and other land-use types (Treweek et al. 1997; Joyce and Wade 1998; Norderhaug et al. 2000; Hodgson et al. 2005). Documenting habitat fragmentation at historical and recent time is important for understanding vegetation changes and can also help to determine best-practice restoration measures for grassland habitats. As long as a species that is predicted to become extinct still persists, conservation measures for improving the habitat conditions can be performed (Kuussaari et al. 2009). It is easier to preserve and restore habitats with remaining species than creating new habitats and re-establishing vanished species. Hence the detection of the causes of extinction debt through fragmentation processes is important for nature conservation.

Extinction debt

Biodiversity patterns are the result of combined environmental conditions of the past and today (Lunt and Spooner 2005). Recent studies indicate that, besides the type and intensity of present-day management, land use history and habitat continuity play a crucial role in the explanation of grassland diversity (Lindborg 2006; Gustavsson et al. 2007; Aavik et al. 2008; Cousins and Lindborg 2008; Waesch and Becker 2009). The vast majority of temperate grassland species are perennials and many of these species can survive extended periods of unfavourable conditions following land-use change (Eriksson 1996; Eriksson and Ehrlen 2001). Therefore, local extinction of grassland specialists can occur with a substantial time delay following habitat loss (Kuussaari et al. 2009). This time delay between changing habitat conditions or habitat extent and species response in kind of extinction is called extinction debt (Tilman et al. 1994). Today’s plant species composition can be threatened by changes that happened years or decades before and extinction of species is already sealed. As a consequence, land use history may, to a considerable extent, explain present-day species diversity and distribution patterns (Tilman et al. 1994; Eriksson and Ehrlén 2001). In addition to a decrease in area and the resulting fragmentation, an extinction debt of species on remaining areas is either increased from a qualitative influence e.g. by anthropogenic nutrient enrichment (Pykälä 2000) or abandonment (Pärtel et al. 1999). The functional traits and the ecological margins of the grassland species determine the risk of extinction (Fischer and Stöcklin 1997; Piqueray et al. 2011). The effects of fragmentation on grassland species has been mainly analysed for semi-natural dry grasslands (e.g. Bruun 2000; Öster et al. 2007; Rusterholz and Baur 2010) but effects on grassland diversity in floodplain meadows were not observed.

Slow responses of plant species richness to fragmentation and habitat loss in grasslands were observed by Eriksson et al. (2002), Helm et al. (2006) and Rusterholz and Baur (2010). These studies describe lag periods of up to 50-100 years before a species eventually becomes extinct after habitat deterioration (Lindborg and Eriksson 2004). Gustavsson et al. (2007) obtained corresponding results for Swedish grasslands, where pastures abandoned between the late 19th century and 1961 did not differ significantly from sites abandoned between 1961 and 2003-2005. In their study, the existing grassland diversity was mainly explained by management practices that have been emplaced over 200 years ago.

Time lags in species responses often hinder the detection of fragmentation effects (Kuussaari et al. 2009). Consequently, a number of recently published studies found no or only little influence of past landscape patterns on present-day plant species richness in grasslands (Adriaens et al. 2006; Bruun 2000; Cousins et al. 2007; Öster et al. 2007).

As a result of the tremendous decline in grassland area, in the most ‘ordinary’ (i.e. highly transformed) landscapes, the influence of management history was absent or of minor importance, because many grassland specialists became already extinct (Adriaens et al. 2006; Cousins et al. 2007; Cousins and Eriksson 2008; Cousins 2009).

Functional diversity

Various taxa and ecosystems show different qualitative and quantitative trends in taxonomic and functional diversity. A high functional trait diversity can act as a buffer against environmental changes and can have a positive impact on the number of ecosystem services (e.g. Tilman and Downing 1994; Hector and Bagchi 2007; Maes et al. 2012; Temperli et al. 2012). In parallel to the widespread decline in species numbers, functional diversity also shows a declining trend. Both can have negative effects on ecosystem functioning (Bernhardt-Römermann et al. 2008; Fried et al. 2009; Laliberté et al. 2010). Losses in functional diversity are often lower than those in taxonomic diversity (Flynn et al. 2009), pointing to functional redundancy (Mayfield et al. 2010; Sasaki et al. 2009). Results from recent grassland and arable field studies confirm these statements (Flynn et al. 2009; Vandewalle et al. 2010). The intensification in grasslands leads to decreasing portions of flowering herbs and grasslands dominated by wind-pollinated grasses. Additionally, flowering species which are mainly dependent on insect pollination are most negatively affected by habitat fragmentation and isolation (Aguilar et al. 2006; Winter et al. 2008; Cranmer et al. 2012). Hence, insect-pollinated plants and associated pollinators are especially endangered and can be seen as prime example for losses in functional groups and associated losses at higher trophic levels (Biesmeijer et al. 2006; Öckinger and Smith 2007; Weiner et al. 2011). The success of pollination and dispersal is highly dependent on a combination of species characteristics and landscape composition (Dauber et al. 2010). Furthermore, Waesch and Becker (2009) found that the age of grasslands largely determines the composition of plant species traits. Due to the high diversity potential of plants and animals in temperate grasslands (Ellenberg and Leuschner 2010; Wallis de Vries et al. 2002) the observed trends are of a great concern to nature conservation.

General study aims and chapter outline

The management practices in agriculture and their distribution in the landscape has changed dramatically over time. However, since World War II, the speed and extent of such changes increased rapidly. The main changes of grassland management commenced in Central Europe five or six decades ago (Joyce and Wade 1998; van Dijk 1991). In some regions, grasslands were drained, intensified and ploughed, in other regions, grasslands were abandoned or cropland on marginal lands was transformed into grassland (Waesch and Becker 2009). Overall, intensifications dominated in Central European crop- and grasslands during the last decades. The focus of this study was to detect and quantify changes in Central European grasslands, which belongs to one of the most species-rich habitats (Ellenberg and Leuschner 2010) harbouring a large number of endangered plant species.

General study aims were:

(1) to detect changes in the extent of floodplain grasslands since the 1950/60s through agricultural land use change,

(2) to analyse shifts in plant species richness, species composition and corresponding functional traits of floodplain grasslands,

(3) to investigate the effects of fragmentation and management (indicated by Ellenberg Inicator Values (EIV)) at the landscape- and the plot-level on the diversity of characteristic meadow species and

(4) to test for effects of habitat continuity and present-day management on species diversity, species composition and the composition of pollination traits in upland grasslands.

In chapter two, “Habitat loss of floodplain meadows in North Germany since the 1950s”, landscape changes in seven floodplain areas, which were dominated by wet and moist meadows in the 1950/60s, are analysed. 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 during the last decades. It is thus used as a reference site for distinguishing between local and large-scale over-regional drivers of vegetation and landscape change (nutrient input from deposition, climate change etc.). The study sites are located in the lowlands of northern Germany and were investigated with a focus on changes in habitat extent and landscape structure between the 1950/60s and today (2008), i.e. over a period of 50-60 years. The main objective was to quantify and analyse changes in these two formerly widespread floodplain grassland types in terms of spatial extent, temporal continuity or replacement, and fragmentation of habitats based on historical vegetations maps and own recent field surveys.

Chapter three “Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants” focuses on how management intensification and increased nutrient input since the 1950/60s has altered grassland plant community composition, species diversity and functional trait composition using comprehensive datasets from five floodplain regions (plus one protected reference region) in northern Germany. Sites with available historical relevés and vegetation maps (1950/60s, 1990s) were resampled in 2008 to facilitate the analysis of a period spanning four to five decades.

In chapter four “Historical and recent fragmentation of temperate floodplain grasslands: Do patch size and distance affect plant species richness of wet meadows?” changing structures at local and landscape scales are analysed on how they affect grassland species that are adapted to wet and moist conditions. Again, historical as well as recent vegetation maps and vegetation relevés are taken into account. The studied recent and historical grasslands were divided in two groups: (a) habitats which still harbour formerly common wet or moist grassland communities (hereafter referred to as ‘optimal habitats’), and (b) habitats where grassland communities have been modified due to melioration or fallowing (subsequently termed ‘suboptimal habitats’).

The main objective was to examine whether effects of fragmentation, legacies of past land use patterns or recent habitat conditions (Ellenberg Indicator Values for nutrients and moisture) have had an influence on the present-day diversity and composition of typical floodplain meadow communities in seven representative floodplain areas in northern Germany (six and one protected reference site).

Chapter five “The significance of habitat continuity and current management on the compositional and functional diversity of grasslands in the uplands of Lower Saxony, Germany” presents a case study located in the Solling Forelands, an escarpment landscape east of the Solling highlands and 15 km west of the City of Göttingen in southern Lower Saxony, Germany. This study aimed at identifying the environmental factors that control grassland diversity (plant community composition, species richness, and pollination trait composition). The study area could act as a model region for most of the Central European uplands which have seen an extension of grassland area in the course of land use change since the 1950s.

Study sites

All study areas are located in the northern and central parts of Germany, in the federal states of Lower Saxony, North Rhine-Westphalia, Brandenburg, Saxony-Anhalt and Thuringia (Tab.1; Fig. 1). Seven study sites (six and one protected) are situated in the lowlands of Germany between the rivers Ems in the west and Havel in the east, for analysing landscape structure and vegetation change of floodplain meadows. The study site of chapter five (Mühlenberg) is located in the uplands 15 km west of Göttingen (Tab. 1). Overall, the covered conditions should be representative for the northern part of Central Europe.

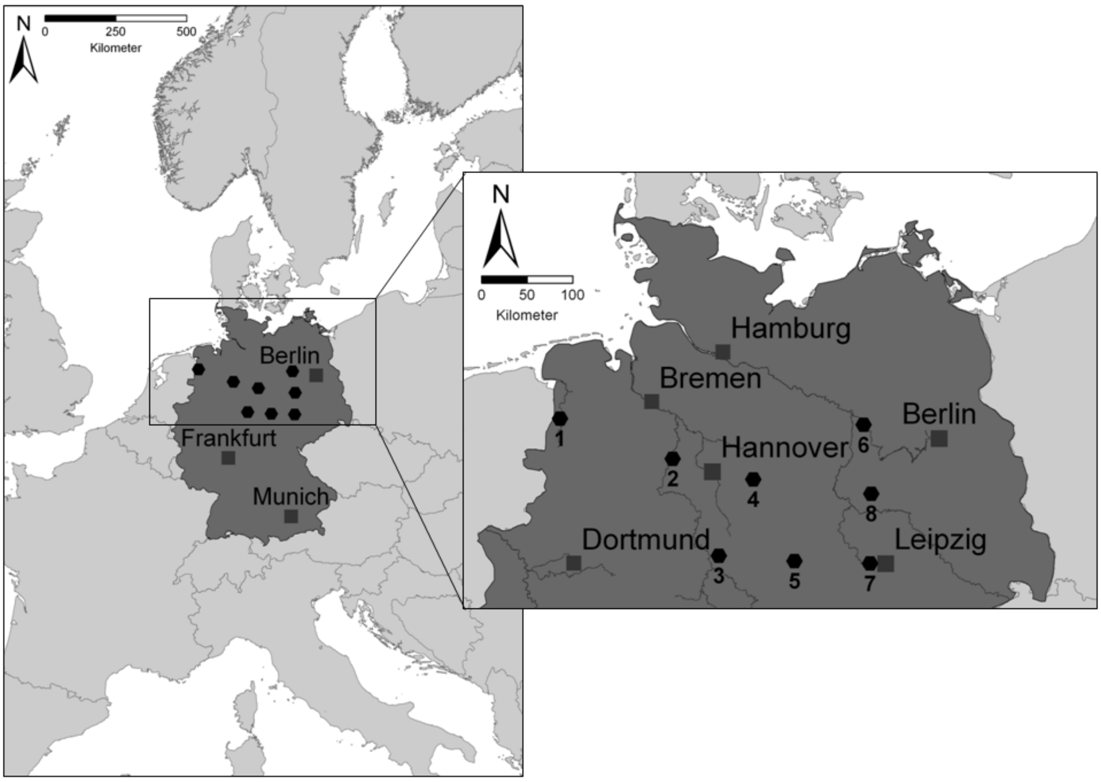

Fig. 1 The study region in Germany and location of the eight study areas (black dots) with characteristics explained in Tab. 1.

Table 1 Location and characteristics of the study areas in Northern and Central Germany (climate data from German National Meteorological Service, DWD, based on the reference period 1961—1990).

Number	Name of the study area	Chapter	Federal state	Historical inventory (first yr)	Study area size (ha)	Size of protected area (ha)	Mean annual precipitation (mm yr^{-1})	Mean annual temperature (°C)	Elevation (m a.s.l)	Geographical coordinates
1	Ems	2, 4	Lower Saxony	1954	390	0	757	8.8	3	N 52°56’54’’ E 07°17’32’’
2	Weser	2, 3, 4	Lower Saxony and North Rhine-Westphalia	1956	155	19	654	9.1	27	N 52°30’58’’ E 09°05’52’’
3	Mühlenberg	5	Lower Saxony	1786	2500	484	645	8.7	255	N 51°32’26’’ E 09°45’49’’
4	Aue	2, 3, 4	Lower Saxony	1946	264	0	620	8.9	67	N 52°16’20’’ E 10°22’48’’
5	Helme	2, 3, 4	Thuringia	1969	1081	0	484	8.5	155	N 51°26’33’’ E 10°57’02’’
6	Havel	2, 3, 4	Brandenburg	1953	293	293	526	8.7	22	N 52°43’44’’ E 12°13’00’’
7	Luppe	2, 3, 4	Saxony-Anhalt	1967	186	0	500	9.5	90	N 51°21’43’’ E 12°07’57’’
8	Nuthe	2, 3, 4	Brandenburg	1958	376	0	560	8.8	115	N 52°02’44’’ E 12°14’40’’

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CHAPTER

2

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 7 study regions (6 unprotected areas, 1 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.

Keywords: agricultural intensification; landscape fragmentation; land use change; land use history; nature conservation; vegetation mapping

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 und 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 1950/60s 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.

Materials and 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 (1950/60) 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 1950/60s, 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.

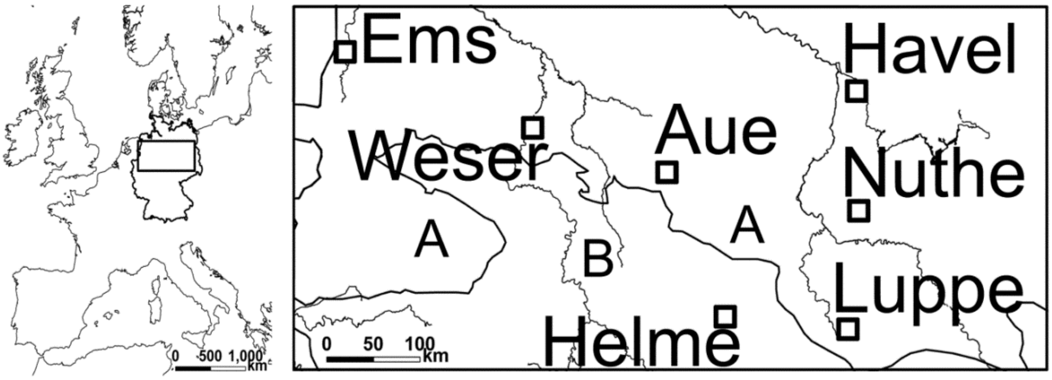

Fig. 1 Study region in North Germany and location of the seven study areas (squares) in the north German pleistocene lowlands (A), and in the Thuringian basin at the margin of the German uplands (B) (WGS_1984 PDC Mercator projection).

All study areas were situated in lowland regions with elevations ranging from 3 to 155 m a.s.l. in the seven regions (Tab. 1). While mean annual temperature varied only little (annual means of 8.5 to 9.5 °C in the seven regions), precipitation ranged from 757 mm yr^{-1} at the Ems river in the west (oceanic climate) to 484 mm yr^{-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.

Table 1 Location and characteristics of the seven floodplain study areas (six unprotected areas plus the Havel protected reference area) in northern Germany named after main rivers (climate data from German National Meteorological Service, DWD, based on the reference period 1961—1990).

Study area	**Historical inventory (yr)**	**Area covered by historical vegetation map (ha)**	**Size of protected area (ha)**	**Mean annual precipitation (mm yr^{-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. (unpubl.)
Weser	1956	155	19	654	9.1	27	N 52°30’58’’ E 09°05’52’’	Hübschmann et al. (unpubl.)
Aue	1946	264	0	620	8.9	67	N 52°16’20’’ E 10°22’48’’	Ellenberg (unpubl.)
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 (unpubl.)
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

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 re-surveying 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 (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 re-survey. Two broad floodplain meadow habitat classes were defined based on 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 × 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 covered by a given habitat type (PLAND), 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 1950/60s and 2008 (differences significant at $p \leq 0.05$; Fig. 2, Tab. 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 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%).

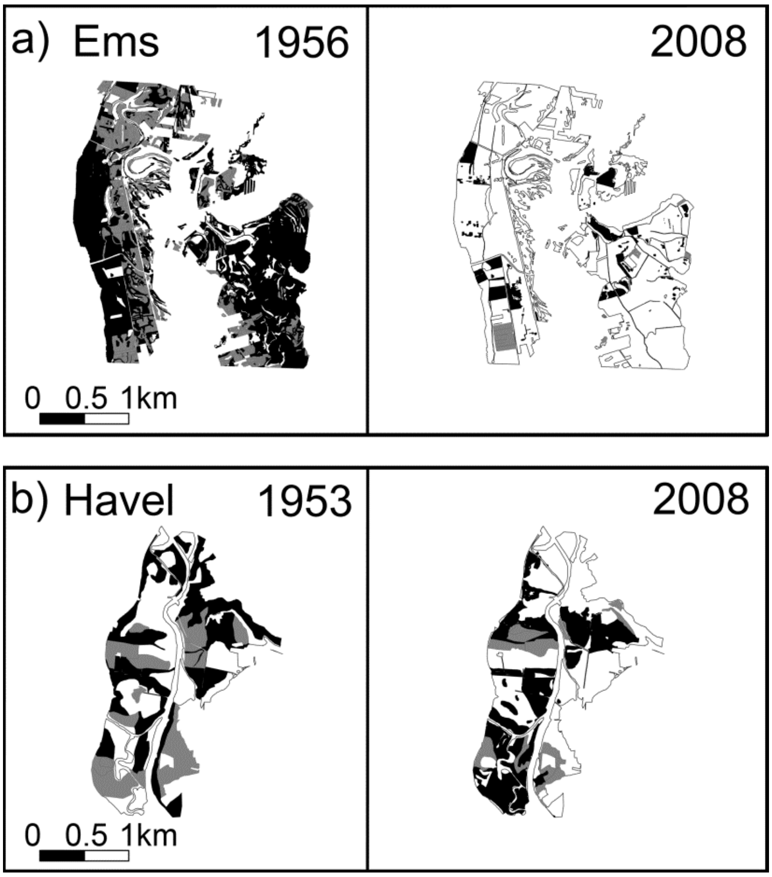

Fig. 2 Areas of wet meadows (black) and species-rich mesic meadows (grey) in two of the seven study areas (a) Ems, (b) Havel, in the 1950/60s and in 2008. Other habitat types: white areas.

Table 2 Changes in the area of wet and species-rich mesic floodplain meadows between the 1950/60s and 2008.

Study area	Historical area in the 1950/60s (ha)	Current area in 2008 (ha)	Historically old area remaining in 2008 (ha)	New area in 2008 (ha)	Total area loss 1950/60s - 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

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 (Tab. 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 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 (Tab. 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.

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.

Table 3 Transformation of historical species-rich mesic meadows (MM) and wet meadows (WM) into other land use types (1950/60s to 2008), and remaining area of historically old meadows (italics) in the seven study areas, expressed as percentage of the area in the 1950/60s. The mean refers to the average of the six unprotected study areas; the protected Havel area is presented as a reference.

	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

Table 4 Landscape metrics for wet meadows, species-rich mesic meadows and their combined areas in the 7 studied floodplain study areas. Significant differences between the 1950/60s and 2008 are marked by asterisks (*). Floodplain meadows (total) are the sum of wet and species-rich mesic meadows.

Study area	**Year of first inventory**	**Number of patches 1950/60**	**Number of patches 2008**	**Remaining number of patches (%)**	**Patch density 1950/60 (*n* 100 ha^{-1})**	**Patch density 2008 (*n* 100 ha^{-1})**	**Mean patch size 1950/60 (ha)**	**Mean patch size 2008 (ha)**	**Effective mesh size 1950/60 (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
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

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 1950/60s, 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 Tab. 2-4. 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 20th 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 1950/60s 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.

Conclusion

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 1950/60s. 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 over 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:

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

	Species-rich mesic meadows	**Wet meadows**
Habitat code (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 (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* (*alopecuretosum 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*

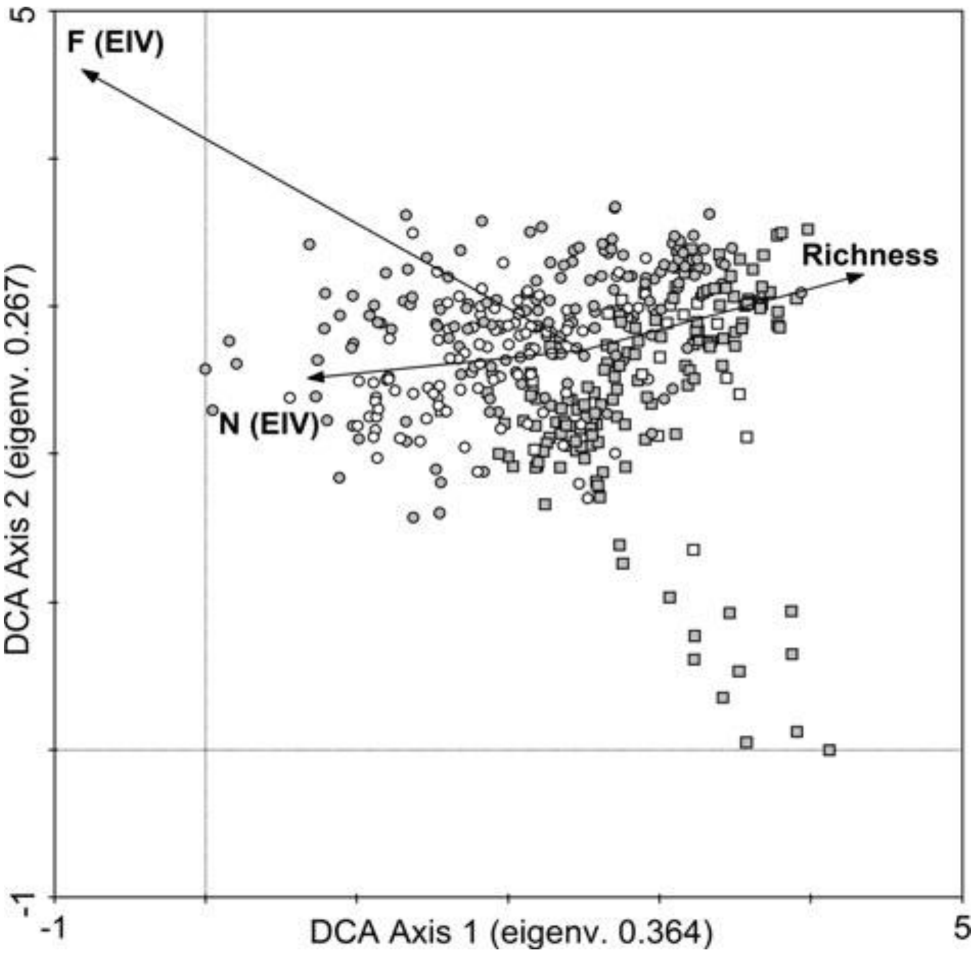

Fig. 3 Detrended Correspondance Analysis (DCA) of wet and mesic meadow relevés from the 1950/60s and 2008 (423 relevés). The samples are coded according to main habitat classes: circles, wet meadows; squares, mesic meadows; filled symbols, historical relevés (1950/60s); open symbols, current relevés (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).

CHAPTER

3

Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants

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Abstract

There is growing concern that biodiversity loss in European agricultural landscapes is having negative effects on functional trait diversity. Long-term studies examining vegetation changes from the period before agricultural industrialisation are however rare. Here, we ask how management intensification and increased nutrient input initiated in the 1950/60s have altered grassland plant community composition, species diversity and functional trait composition using comprehensive datasets from five floodplain regions (plus one protected reference region) in northern Germany. Sites with available historical relevés and vegetation maps (1950s/1960s, 1990s) were resampled in 2008 to facilitate the analysis of a period spanning four to five decades.

Plant community composition changed tremendously in all study regions during the 50 year period, which was related to increasing Ellenberg indicator values for nutrient availability. Species richness at the plot-level fell by 30-50% over the period, and losses in functional diversity were equally large. A non-formal comparison with the results from the protected reference study region indicates that the changes may mostly be attributable to local nutrient input rather than to supra-regional climate change. Our results indicate a consistent trend toward much more species-poor communities dominated by mow-tolerant, N-demanding competitive grasses, whereas species with more ruderal strategies, species flowering early in the season and, in particular, insect-pollinated herbs have all decreased. The substantial loss of nectar-producing grassland herbs is likely to have negative effects on the abundance of pollinating insects, with consequences for the grassland animal communities. This highlights the growing need for adequate grassland management schemes with low N input to preserve high-nature-value grassland.

Keywords: managed grasslands; Germany, historical comparison; land-use intensification; N fertilisation; plant functional traits; zoogamous plants

Introduction

The rapid intensification and industrialisation of agriculture in the second half of the 20th century has severely affected the structure and functioning of grasslands and arable fields in the industrialised regions of the world (Dallimer et al. 2009; Fried et al. 2009b). In the agricultural landscapes of Central Europe, moist and mesic grasslands count among the habitat types that have experienced the severest losses (Prach 2008), and they have currently come under additional pressure through the growing interest in energy from biomass initiatives and fibrous crops (Lind et al. 2009). As a consequence, the largest group of threatened higher plants in Germany comprises taxa from extensively managed grasslands (Korneck et al. 1998; Korsch and Westhus 2004).

Species richness and composition in agro-ecosystems can be influenced by several aspects of management including mechanical disturbance, such as ploughing or mowing, and the use of agrochemicals (Smart et al. 2005; Morecroft et al. 2009; Dupré et al. 2010). Perhaps the most persistent effect is caused by nitrogen (N) input, which facilitates the increasing dominance of a limited number of strongly competitive plants leading to floristic homogenisation, decreasing species richness and changes in functional trait composition (Kahmen et al. 2002; Smart et al. 2006; Walker et al. 2009). Communities on infertile soils (such as acidic grasslands on Leptosols) are already threatened by relatively low N inputs from aerial sources while agro-ecosystems on richer soils (such as moist meadows on Gleysols) are characterised by higher critical N loads, and have thus been found to respond only to higher levels of N deposition and to fertilisation (Bobbink et al. 2010, Stevens et al. 2010).

Concern has been growing that functional diversity is declining as well and that this will have an effect on ecosystem functioning (Bernhardt-Römermann et al. 2008; Fried et al. 2009a; Laliberté et al. 2010). Recent evidence from grassland and arable field studies supports this assumption (Flynn et al. 2009; Vandewalle et al. 2010). The loss of insect-pollinated plants and associated pollinators serves as a prime example for losses in functional groups and associated losses at higher trophic levels (Biesmeijer et al. 2006; Weiner et al. 2011). Such trends are of great concern to nature conservation, as temperate grasslands can harbour a high diversity of plants and animals as long as they are not managed too intensively (Wallis de Vries et al. 2002; Ellenberg and Leuschner 2010).

Qualitative and quantitative trends in taxonomic and functional diversity differ between taxa and ecosystems. In vascular plants, functional diversity rarely shows disproportionately greater declines than taxonomic diversity (Flynn et al. 2009), and losses in functional diversity are often even lower than in taxonomic diversity, pointing to functional redundancy (Sasaki et al. 2009; Mayfield et al. 2010). However, patterns of change over time are not sufficiently understood because most studies on the effects of land-use change on biodiversity are based on the comparison of sites along land-use gradients (space-for-time substitution; Flynn et al. 2009; Laliberté et al. 2010). The few true ‘before and after’ comparisons either cover limited time scales or concentrate mainly on changes in taxonomic diversity (Tamis et al. 2005; Britton et al. 2009), because suitable historic data are rare.

In Central Europe, land-use changes in the 1950s to 1970s had a particularly notable effect on the current structure of the agricultural landscapes (Bender et al. 2005; Prach 2008; Pancer-Koteja et al. 2009). Raster surveys and local floras provide data for the time before the 1950/60s (Tamis et al. 2005; Pompe et al. 2008; Knapp et al. 2010), but they mostly indicate only species presence in a given region rather than giving information on species abundance in local communities. Moreover, raster surveys tend to be over-optimistic from an ecosystem service and nature conservation perspective because species that are currently present with low numbers or at only a few specific sites, may be irrelevant for ecosystem functioning. In vegetation science, a number of excellent long-term studies are available covering the last three decades, but only a few permanent plots were established in the 1960s or earlier (Bennie et al. 2006; Wittig et al. 2007; Kuiters et al. 2009; Walker et al. 2009). Indeed, the importance of permanent stand-level monitoring was not widely realised until the late 1960s or 1970s, when most of the current monitoring schemes were implemented (Lengyel et al. 2008). This renders the development of any general conclusions on the effects of land-use change on plant diversity since the 1950/60s difficult.

Phytosociologists were among the first to describe profound changes in plant community composition in the agricultural landscape (Tüxen 1955; Meisel 1970; Meisel and v. Hübschmann 1976), although their conclusions were not based on statistically reliable analyses of larger datasets. Mining of the increasingly available vegetation databases (Bruelheide and Chytrý 2000; Schaminée et al. 2007) allows for a more extensive temporal and spatial coverage, but problems arise from inconsistent sampling methodologies and non-random sampling in the past, which requires careful statistical processing and interpretation of time-series data (Palmer 1993; Knollová et al. 2004; Smart et al. 2005; Haveman and Janssen 2008). Moreover, supplementary information is limited, and even crude locality data are often absent. It may therefore be difficult to disentangle spatial effects from temporal trends in vegetation composition.

Here, we adopt a strategy that is intermediate between the re-sampling of fixed sites and the mining of large historical databases. Older publications were searched to find case studies where both vegetation relevés and vegetation maps were available, thereby ensuring that new relevés were taken for similar communities and in a comparable landscape context. We chose five study regions along a west-east gradient in the northern German lowlands that were located in floodplain areas and had been under a non-intensive mowing and grazing regime that was typical for moist grasslands before the onset of agricultural intensification. Historical data were also available for one particularly well preserved region in the Havel floodplain that had been protected by national and European law since 1967. Here, land-use remained essentially similar over the observation period and thus allowed for a non-formal assessment of whether potential supra-regional drivers of vegetation change, such as shifts in climate or nitrogen deposition, are relevant influencing factors (Stevens et al. 2011).

We tested the following hypotheses:

i) Since the 1950s, floodplain meadows have undergone major changes in community composition and associated reductions in species diversity.

ii) The main drivers of shifts in species composition and of diversity losses are nutrient (mainly nitrogen) input and grassland drainage, i.e. management-related factors.

iii) Increased fertilisation and mowing frequency have led to substantial losses of functional diversity with insect-pollinated species being especially affected.

The data analysis concentrated on the five main study regions that underwent pronounced land-use intensification in the past 50 years; the data from the protected reference site are used only for comparison.

Materials and Methods

Study areas

All five sites (plus the reference site) are situated in floodplains built by alluvial sediments with soils varying from anhydromorphic Cambisols to groundwater-influenced Gleysols. Grassland communities range from mesic meadows (mainly of the alliance *Arrhenatherion*) to moist meadows (of the *Molinion, Cnidion* and *Calthion* alliances). Over the past 50 years, not only have land-use systems and landscape structures been altered in the study regions, but changes in the hydrodynamic regime and river morphology have taken place as well (Tab. 1 and supporting information / electronic appendix S1). The total area covered by grassland in the study regions decreased from a mean proportion of 91% in the 1950/60s to 46% in 2008 (Krause et al. 2011). Former grasslands were replaced by arable fields (2008: 21%), artificially created water bodies (mainly in the Helme region: 22%) and forest/scrub (4%). In species-rich mesic grasslands, 98% of the previous area was lost, while moist species-rich meadows were reduced by 88%. Intensive pastures (alliance *Cynosurion*) or sown grass fields greatly increased in size. The conversion of grassland to other agro-ecosystem types is a widespread trend in Central Europe (Prach 2008; Lind et al. 2009), and the resulting effects on community composition are tremendous. Here, we concentrate on the more subtle changes in community composition that took place on sites that are still covered by grassland, i.e. persistent meadow and pasture sites with more or less altered species composition.

Sampling approach

For the 1950/60s, 385 phytosociological relevés were available for the five main study regions and 174 relevés for the protected Havel region (Tab. 1). Since the exact location of the historical vegetation relevés was not known, we digitised vegetation maps from the 1950/60s and developed a set of stratified randomly selected sampling points for the former grasslands using GIS-Hawth's Tools (Beyer 2004). In 2008, the chosen coordinates were visited in the field using standard handheld GPS (Garmin, Olathe, Kansas). Relevés were sampled where sites were still covered by grassland or related successional communities such as forb-rich fallows, but not arable fields or closed shrub/forest communities. In addition, particularly species-rich meadow stands were selected in a similar manner as had been practised in historical surveys (Chytrý 2001). Our relevé sample thus included both average and particularly well-developed (species-richer) grassland stands, ensuring that observed effects were not solely caused by artefacts introduced by concentrating on extreme samples alone (Palmer 1993). The two datasets showed qualitatively similar trends, and we thus report results from both randomly and deliberately positioned relevés together.

Plot size in 2008 was 16-20 m², a common relevé size used in Central European grassland surveys (Bruelheide and Chytrý 2000). Since the plot size of the historical relevés was more variable (median 25 m^2, inter-quartile range 25-35 m^2), we additionally collected species richness data for a subset of 321 plots, where we also extended the sampling area to 50 m².

For three regions, additional relevés from the 1990s were available that had preferentially taken samples with known spatial positions (accuracy < 10 m). These plots were re-sampled in 2008.

At each plot, all vascular plant species, their cover (Londo scale) and supplementary information were recorded. Bryophytes and lichens were omitted as historical records were far from complete in this respect.

Table 1 Overview of sampling sites, geographical coordinates, size, historical/current extent of grasslands, and the number of vegetation samples available for the three censuses ('pref' = preferentially chosen; 'rand.' = randomly chosen); data sources for historical samples are indicated below the table.

	Locality	Size	Grassland Area		No. relevés				
					1950/60	1990	2008		
	°E/°N	(ha)	1950s	2008	pref.	pref.	pref.	rand.	∑
1 Weser[a]	9.1/52.5	156	145	44	131			25	**156**
2 Aue[b]	10.4/52.3	265	240	113	51		3	37	**91**
3 Helme[c]	10.9/51.5	1081	971	427	60		18	43	**121**
4 Elster[d]	12.1/51.4	188	121	43	108	77	29	38	**252**
5 Nuthe[e]	12.3/52.0	374	371	284	35	48	37	48	**168**
reference									
6 Havel[f*]	12.1/52.4	293	193	221	174	26	25	21	**246**
∑		**(2357)**			**559**	**151**	**112**	**212**	**1034**

References: [a]v. Hübschmann et al. 1954; [b]Ellenberg 1952a, b; [c]Hundt 1969; [d]Abdank 1995; Gräfe 1967; Täglich 1956; [e]Hundt 1958; Schnelle 1992; Umwelt 1996; [f]Burkart 1998; Fischer 1980, 1990.

*Data from the 1980s only, no older samples available but historical aerial photographs indicate limited changes.

Data processing

All data were stored in a Turboveg database (Hennekens and Schaminee 2001). The R package vegdata was used to access the data, amend the species' taxonomy based on a standard list (GermanSL, Jansen and Dengler 2008), and convert values from various cover abundance scales to % cover (class mean). Subspecies were aggregated to species rank. The few taxa that were only identified to the genus level were included as separate taxa in the analyses of species richness, but were skipped in all other analyses.

Information on Ellenberg Indicator Values (EIV), phytosociological affinities (see supporting information S2) and Red List statuses of the species (see supporting information S2) were also retrieved from the GermanSL package. We used cover (square-root)-weighted Ellenberg Indicator values as proxies for site conditions, but unweighted (presence/absence) values yielded essentially similar results (in all cases $r^2_{\text{weighted/unweighted}} > 0.8$). We selected morphological and functional plant traits that are considered important in grassland communities and that were available for all our species (Dierschke and Briemle 2002; Klotz and Briemle 2002): Raunkiaer life form; plant longevity; propagule type and weight; indicator values for tolerance to mowing and grazing; fodder value; pollination type; phenological group; form of clonal growth, and plant life strategy (CSR system). To meet the requirements of the different analytical steps, the raw data (Tab. 1) were split into different sub-sets:

- SET_{main} - 779 relevés with 436 species: Derived from the raw data by excluding relevés of the unprotected Havel area and 9 relevés with markedly different community compositions (meadows on saline soils; Sörensen similarity to the other samples >2.5 standard deviations of average among-sample distance, McCune et al. 2002).

- $\text{SET}_{\text{mulva}}$ - 779 relevés, 286 species: Derived from SET_{main} by excluding species that occurred in less than three relevés and the few unidentified taxa. This reduced the influence of poorly represented species in multivariate analysis, but had no influence on the species diversity patterns (correlation between richness in SET_{main} and $\text{SET}_{\text{mulva}}$ $r^2= 0.999$).
- $\text{SET}_{\text{funct}}$ - 654 relevés, 281 species: Derived from $\text{SET}_{\text{mulva}}$ by excluding data from the 1990s that were not in the focus of the functional analysis.

Statistical analysis

Since our database consists partly of non-random vegetation samples (historical relevés), statistical analysis is, in the strictest sense, not allowed (Lájer 2007). We consequently focused our analysis on the description of patterns and used the results of statistical tests as supplementary information. We believe that such a procedure can still provide valuable information in cases where qualitatively better datasets are not available and cannot be generated (see also Oksanen 2001 for a similar argument).

We found a weak but significant positive correlation between plot size and species richness in the complete dataset (both for untransformed and log-transformed data, $r^2 < 0.05$, $p < 0.001$). This association was even weaker ($r^2 < 0.01$, ns) when only the historical data were analysed, even though the range of plot sizes was larger than in the recent samples. In the 2008 samples, the median species richness of the smaller 16 m^2 plots was 19 (inter-quartile range 14 to 25, 19.9±7.9), while the median for the larger 50m^2 plots was 20 (IQR 15 – 27, 21.3±8.5). Although effects of plot size on species richness were significant (Wilcoxon test $p < 0.001$), they were nonetheless too small to introduce a major confounding effect in the subsequent analysis.

Univariate analyses of diversity patterns in the historical and recent data were based on linear mixed models with plot size as a covariate and region as a random factor; the residuals were graphically checked for deviations from model assumptions. We used Indicator Species Analysis to detect species that showed strong frequency changes in the 50-year period; significances were obtained by permutating samples 999 times within a given region (Bakker 2008). Species Accumulation Curves (100 permutations) were used to compare different sampling periods at a standardised sampling density (200 samples). In Detrended Correspondence Analysis, supplementary variables were correlated *post hoc* with the ordination axes. An initial correlation matrix PCA on the pooled species trait values for each vegetation sample (tool functcomp in R-package FD) revealed that the first 10 significant axes captured only 57% of the total variance in trait space, suggesting that redundancy among traits did exist but was not very pronounced. We thus kept all traits for further analysis. Functional diversity (FD) was calculated based on the length of the branches of a cluster dendrogram for species, which was based on the Gower dissimilarity of the traits (UPGMA, Petchey and Gaston 2002; Podani and Schmera 2006, 2007). FD and measures such as functional richness have been shown to be sensitive to changes in alpha-diversity (Poos et al.2009; Pakeman 2011), so we also calculated the conceptually different RAO's quadratic entropy and functional dispersion (Botta-Dukát 2005; Laliberté and Legendre 2010) in a cover-weighted form, again based on Gower dissimilarity. Values for RAO and functional dispersion correlated closely (r=0.97), so we only reported RAO values. Responses of specific traits over time were analysed using fourth-corner statistics, as modified by Dray & Legendre (2008, univariate approach, permutations under model 1).

The statistical analyses were conducted with the software R 2.10.1(R Core Development Team 2004, packages vegdata, vegan, ade4, cluster, lme4, FD, see supporting information S3), PC-ORD (McCune and Mefford 2006) and CANOCO (ter Braak and Šmilauer 2002).

Results

Changes in species composition and diversity

In the five main study regions, we found a total of 289 vascular plant species in 2008 (277 relevés), while 299 species were recorded in the historical relevés from the 1950/60s (377 relevés). Only 189 species were observed in both censuses. Compared against a standardised number of 200 samples (species accumulation curves), mean species numbers were 260 (±7) in the 2008 census and 264 (±6) in the 1950/60s census.

Indicator Species Analysis revealed that more species had decreased than increased over time (Tab. 2, dataset $\mathrm{SET}_{\mathrm{funct}}$). Taxa with a decrease in frequency included species of mesic grasslands such as *Rumex acetosa*, *Ranunculus acris*, *Anthoxanthum odoratum* and *Festuca rubra*. The increasing species were typical of intensively-used and fertilised grasslands such as *Cirsium arvense*, *Phleum pratense*, *Urtica dioica* and *Lolium perenne*.

While the median species richness per plot differed between areas, trends over time were always negative, except for that of the Havel region (Table 3a). A similar pattern was found when only relevés taken in true grasslands were considered (Table 3b). Between the 1990s and 2008, the Nuthe and Havel regions showed only small changes in species richness and species composition, while in the third study region (Elster), pronounced losses equivalent to those observed between the 1950/60s and the 1990s were found.

Averaged over the five main regions, plot-level diversity decreased from a median of 27 species in the 1950/60s to a median of 19 in 2008. This reduction was also apparent when only the residuals of a plot size vs. richness regression were inspected (Fig. 1a). The linear mixed model for the effects of census period and plot size (with region as random effect and plots size as a covariate) indicated that the differences in species richness between the two census intervals were significant ($p_{period} < 0.01$).

The frequency of phytosociologically diagnostic species for moist grasslands (phytosociological order Molinietalia, see list S2a – supporting information) was already small in the 1950/60s, and the median declined to two in the relevés from 2008 (Fig.1b, $p_{period} < 0.05$). The number of species indicating high moisture (German “Feuchte” – F) but low nutrient levels (Ellenberg IV F >5 and EIV N < 6) showed a non-significant decreasing trend over time. Species that are currently considered to be threatened on a nation-wide scale, such as *Dactylorhiza majalis* or *Cnidium dubium* (see list S2b – supporting information), were already rare in the historical relevés. Taxa that are red-listed on a regional scale only, i.e. on the level of the respective federal states, showed pronounced losses (Fig.1c, $p_{period} < 0.05$).

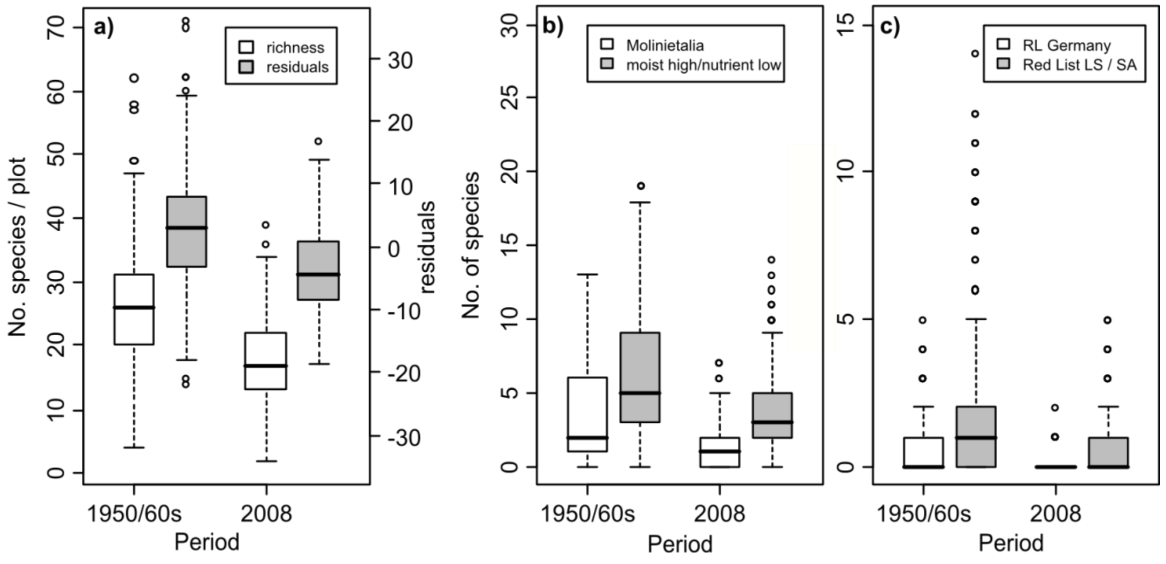

Fig. 1 Changes in species richness between the 1950/60s and 2008 (654 samples as SET_{funct}, but all species given including those identified to genus level only). a) Raw data and residuals from the regression of richness against plot size. b) Numbers of species typical of the Molinietalia, and species

with a mean Ellenberg IV for M >5, and N <6. c) Species currently red-listed on the federal level and in Lower Saxony (LS) / Saxony-Anhalt (SA) only.

Changes in community composition and site conditions

The ordination (including relevés from forb-rich meadow fallows or dry grasslands, dataset $\mathrm{SET}_{\mathrm{mulva}}$) revealed a main gradient along the 1st axis that was mainly related to soil moisture, as inferred from mean Ellenberg IVs (Fig. 2). The second axis differentiated plots from the 1950/60s and 2008, with plots from the 1990s taking intermediate positions. The mean EIVs for nutrients and, to a lesser extent, soil reaction (pH) increased along axis 2, while the vectors for species richness, evenness and Shannon diversity negatively correlated with axis 2. The median plot-level Ellenberg IV for moisture was very similar for the two censuses (median = 6.2 in the 1950/60s and in 2008; inter-quartile ranges 5.7-9.0 and 5.6 – 8.0, respectively), the EIV for soil reaction showed an increase ($\mathrm{median}_{1950/60s}$ 6.1 / IQR 5.7-6.7; median_{2008} 6.8 / IQR 6.5-7.0), as did the EIV for nutrients (mainly nitrogen, $\mathrm{median}_{1950/60s}$ 5.5 / IQR 5.0-7.1; median_{2008} 6.2 / IQR 5.7-8.1).

In agreement with the results of the ordination, species richness correlated negatively with the Ellenberg IV for nutrients (Spearman rho = -0.69, $p < 0.001$) while the relationships of species richness to the EIVs for soil moisture (rho = -0.20, $p < 0.001$) and soil reaction were less pronounced (Pearson $r_{adj} = -0.40$, $p < 0.001$).

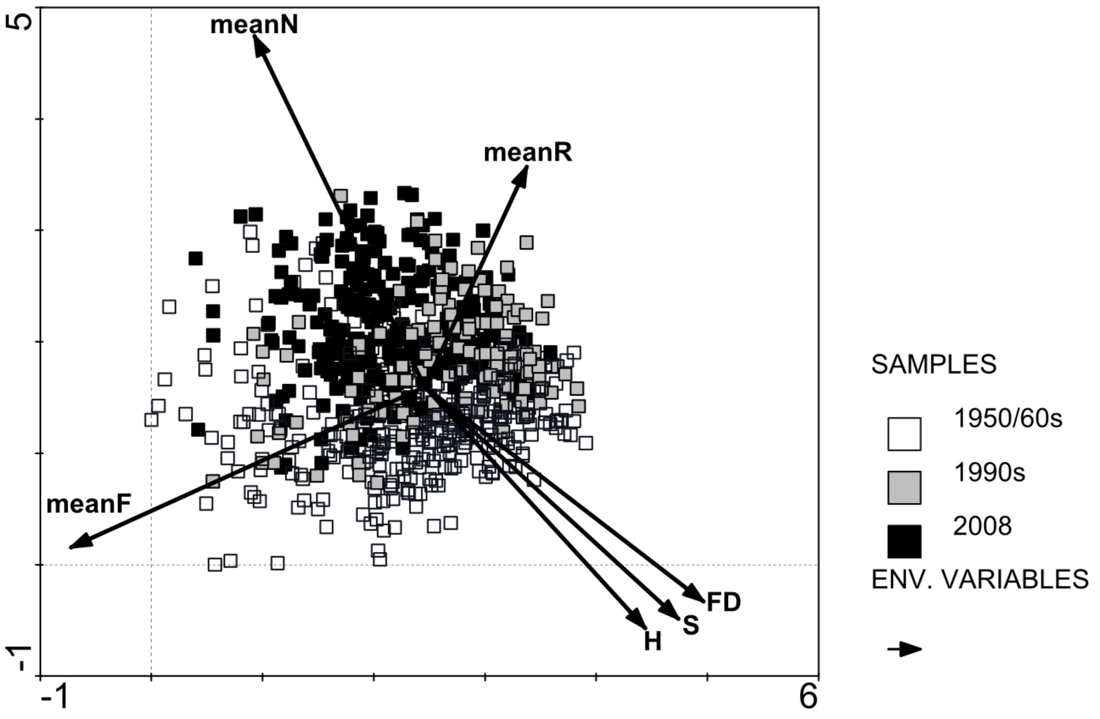

Fig. 2 DCA ordination of the dataset SET$_{mulva}$ (779 samples, 286 species, Havel and 9 outliers excluded). Species with frequency <3 were removed; species cover values were log-transformed. Supplementary variables were fitted *post hoc* on the ordination plot: mean Ellenberg IVs, S richness, H Shannon diversity, FD functional diversity (detrending by 26 segments; downweighting of rare species; eigenvalues / length of gradient axis 1 0.33 / 3.9, axis 2 0.27 / 3.3, axis 3 0.22 / 4.1).

Table 2 Indicator Species Analysis (sensu Bakker 2008) for vascular plant species that showed similar significant trends in at least 3 of the 5 regions analysed. a) Species frequency based on pooled samples for the two periods. b) Indicator value (ISA-IV) for the two periods based on weighted averaging of study-wide indicator values (1999 permutations, samples for two census periods only, $\mathrm{SET}_{\mathrm{funct}}$). The higher values for a given pair-wise comparison is written in italics, also indicated is the number of regions, where change was significant ($p < 0.05$).

	a) Frequency		b) ISA-IV		Regions
	1950/60s	2008	1950/60s	2008	signif.
Rumex acetosa	*70*	22	*56*	9	4
Ranunculus acris	*62*	18	*51*	9	4
Silene flos-cuculi	*58*	10	*47*	10	4
Anthoxanthum odoratum	*53*	6	*45*	5	4
Bellis perennis	*50*	0	*41*	10	4
Festuca rubra	*53*	14	*38*	17	4
Trifolium pratense	*44*	17	*31*	11	4
Achillea millefolium	*36*	21	*27*	9	5
Trifolium repens	*45*	35	*27*	25	4
Caltha palustris	*16*	1	*12*	4	4
Daucus carota	*25*	7	*19*	7	4
Leucanthemum vulgare	*20*	4	*17*	3	4
Cirsium palustre	*19*	2	*15*	5	4
Angelica sylvestris	*21*	1	*24*	1	3
Briza media	*7*	0	*7*	1	3
Cardamine pratensis	*56*	9	*39*	12	3
Centaurea jacea	*14*	1	*11*	3	3
Cirsium oleraceum	*25*	21	*22*	7	3
Galium uliginosum	*14*	2	*14*	2	3
Lathyrus pratensis	*33*	16	*23*	7	3
Myosotis scorpioides	*17*	4	*16*	1	3
Pastinaca sativa	*11*	3	*10*	4	3
Plantago lanceolota	*52*	15	41	*8*	3
Phleum pratensis	20	*26*	13	*15*	4
Lolium perenne	17	*35*	12	*22*	4
Rumex obtusifolia	2	*21*	3	*15*	4
Urtica dioica	5	*38*	3	*36*	4
Cirsium arvense	10	*43*	12	*27*	3
Elymus repens	19	*32*	13	*19*	3
Persicaria amphibia	6	*20*	4	*16*	3

Table 3 Plot-level species richness per region and site (median, interquartile ranges) for a) all samples ($\mathrm{SET}_{\mathrm{main}}$) and b) grassland samples only (sites dominated by perennial grasses, excluding forb communities and scrub from $\mathrm{SET}_{\mathrm{main}}$). The Havel region was included for comparison but left out of summary statistics.

Period	Weser	Aue	Helme	Elster	Nuthe	Havel
a) All						
1950/60	27 (22-32)	29 (27-33)	20 (14-28)	23 (17-33)	27 (26-29)	15 (12-18)
1990				28 (20-35)	15 (12-19)	26 (22-32)
2008	15 (11-17)	13 (10-15)	16 (13-18)	22 (17-26)	17 (13-22)	26 (21-33)
b) grassland only						
1950/60	27 (22-31)	29 (27-33)	22 (17-29)	24 (17-35)	27 (26-29)	16 (13-19)
1990				28 (19-34)	16 (12-25)	25 (22-32)
2008	16 (11-16)	13 (10-15)	16 (13-18)	23 (18-27)	17 (14-22)	27 (22-33)

Changes in biological traits

The analysis of changes in functional trait diversity covered only those species that occurred at least three times in the complete dataset (dataset $\mathrm{SET}_{\mathrm{funct}}$). When considering the presence/absence data, plot-based functional diversity decreased considerably over time (Fig. 3a); however, the reduction was similar in relative magnitude to that of species richness. In terms of species cover, RAO's index indicated a qualitatively similar temporal trend, which corresponded closely to changes in Shannon diversity (Fig. 3b). Both indices (RAO and FD) showed a significant negative correlation with the mean Ellenberg IV for N as an indicator for grassland management intensity (FD: Spearman rho = -0.69, $p < 0.001$; RAO's diversity: rho = -0.61, $p < 0.001$). The correlation with the EIV for soil reaction was less apparent (0 > rho > -0.3).

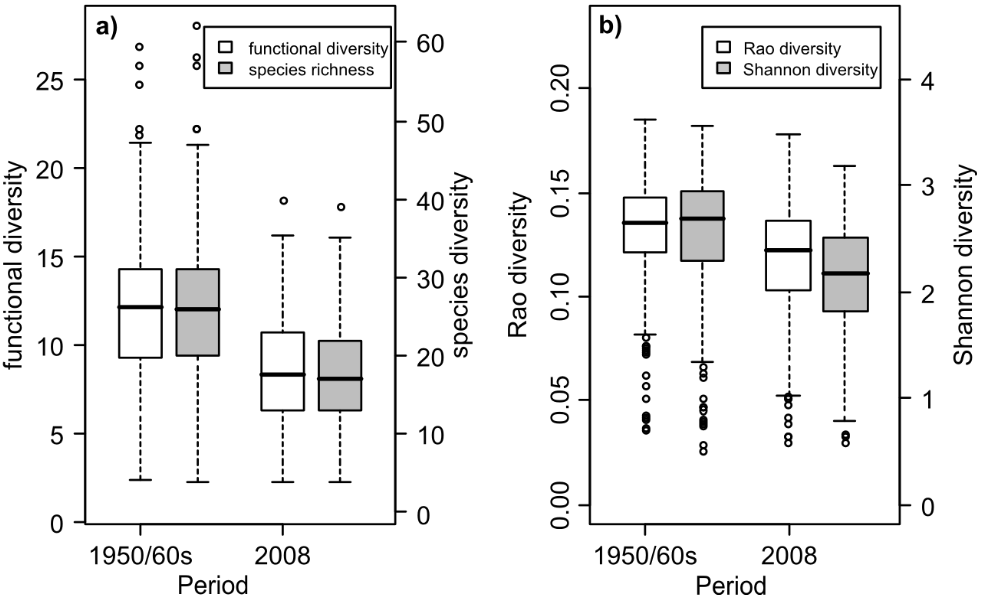

Fig. 3 Changes in functional diversity between the 1950/60s and 2008; the corresponding measure of species diversity is given for comparison (dataset $\mathrm{SET}_{\mathrm{funct}}$ - 654 relevés, 281 species). a) Functional diversity for presence /absence (FD) and species richness. b) Functional traits weighted by species abundance (RAO) and Shannon species diversity.

Fourth-corner statistics indicated changes of individual traits over the two main periods (Tab. 4). The abundances of therophytes and hemicryptophytes tended to be lower in 2008 than in the 1950/60s. Plants with ruderal strategy types decreased in abundance, as did a number of plants with predominantly clonal growth strategies. In contrast, species belonging to phenological groups with late-summer development increased. The abundance of wind-pollinated taxa on any given plot increased from a mean of 50% in the 1950/60s to 70% in

2008, while insect-pollinated species decreased from a mean of c. 50% to only 30%. Thus, the availability of nectar resources declined in extant meadows along with decreasing numbers of plant species propagated by fruitlets or seeds, and an increasing number of species with fruits such as caryopses (Poaceae). Seed weight did not change between the two censuses. Species with higher fodder value were more abundant in 2008. Many of these trends were qualitatively similar when analysed against the mean Ellenberg IV for nutrients instead of sampling period (Tab. 4), and the EIV for nutrients showed a strong positive correlation with the abundance of mowing tolerant and grazing-tolerant species.

Table 4 Summary of fourth-corner analysis for 1950/60s vs. 2008 showing significance and direction of trends for traits, or traits groups. In groups of nominal traits, only overall significance is indicated plus direction of change for significantly responding groups ($p_{adjusted}$; (*) $0.05<p<0.1$, *** $p<0.001$). Test statistics indicate type of test, which depend on the scale of the given variables under consideration (chi², F-test, correlation r). Trends were tested against time ($trend_{time}$) and with respect to Ellenberg IV for nutrients.

Decreasing	$trend_{time}$	p_{adj}	$trend_N$	p_{adj}	Increasing	$trend_{time}$	p_{adj}	$trend_N$	p_{adj}
Lifeform	χ^2	***	F	***	**Lifeform**				
– Hydrophyte	ns		ns		– Phanerophyte	↑		↑	
– Hemicryptophyte	↓		↓		– Chamaephyte	↑		↑	
– Hemiphanerophyte	ns		↓		– Geophyte	↑		↑	
– Therophyte	↓		↓						
Strategy	χ^2	***	F	***	**Strategy**				
– CR strategy	↓		↓		– C	ns		↑	
– R strategy	↓							↑	
– CSR strategy	↓		↓		**Mowing tolerance** (F)	ns		↑	***
– CS	↓		↓		**Grazing tolerance** (F)	ns		↑	***
– SR strategy	↓		↓		**Fodder value** (F)	↑	***	↑	***
Clonality	χ^2	***	F	***	**Clonality**				
– runner	↓		↓		– fragmentation	ns		↑	
– running rhizome	↓		↓		– turions	↑		↑	
– bulbillae	↓		ns		– tuber	↑		↑	
– buds root	↓		ns						
– rhizome	↓		↓						
– pleiocorm	↓		ns						
Pollination	χ^2	***	F	***	**Pollination**	χ^2	***	F	***
– insect	↓		↓		Wind – pollination	↑		↑	
– cleistogamous	↓		↓						
– geitonogamous	↓		↓		Phenological groups	F	***	r	***
– snails	↓		↓		Season	↑		↑	
Diaspore	χ^2	***	r	***	**Diaspore**				
– Seed	↓		↓		– aggregate fruit	↑		↑	
– Fruitlets	↓		ns		– Fruits	↑		↑	
– Fruits + Appendage	↓		ns						
– Fruit part	↓		ns		**Seed weight**	F	ns	r↑	

Discussion

Our re-sampling study covered roughly 50 years and 5(+1) study regions that were more or less representative in physiography, land-use pattern and management development for floodplain grassland of the glacial lowlands of northern Germany. We confirmed previous case studies and literature reviews from Central Europe that documented severe and consistent species losses in mesic and moist grasslands in the course of agricultural intensification (Fischer and Stöcklin 1997; Prach 2008; Ellenberg and Leuschner 2010; Krause et al. 2011), and we showed that these trends are also apparent over longer time spans and extended regions. The data also imply that losses in terms of plant functional diversity have been equally severe and that the provision of important ecosystem services such as nectar production for pollinators has declined over the past 50 years.

Species richness

Species numbers remained stable or, in some cases, even increased in the protected Havel region, which presumably reflects successful conservation management activities (Burkart 1998). In contrast, the other five unprotected study regions showed uniformly negative trends. Expressed in percent of the 1950/60s figures, the data in Table 3 indicate richness losses of 10-50% at the releve scale depending on the region. In a recent large-scale survey of randomly selected meadow plots in northern Germany, median plant diversity was found to be 10-15 species only (Oppermann et al. 2009), which is even less than our values of 15-20 species and indicates that our figures are not overly pessimistic. Our data seem to be robust against effects of variable plot size, as is evidenced by the mixed model and the pattern of residuals in Figure 1. Plot size effects are known to become a problem when the range of sizes covers several orders of magnitude (Dupré et al. 2010), which was not the case here.

Several studies in European managed grasslands have indicated that rare specialist plants may suffer disproportionally high losses in respect of abundance when management is intensified (Fischer and Stöcklin 1997; Walker et al. 2009). However, our dataset indicates that some of the species with decreasing frequency had been very abundant in the 1950/60s (e.g. *Bellis perennis*). Significant frequency losses were detected for taxa currently considered threatened, which is expected because a decline in abundance is a key condition for red-listing (IUCN 2001). Many of these threatened species were already rare in the 1950/60s, which would provide some support in favour of the above-mentioned hypothesis that rare species are acutely suffering from abundance losses.

The close negative correlation between species richness and the mean Ellenberg IV for nutrient availability indicates that as opposed to changes in soil moisture, increased input of N (or other nutrients) was a key driver of vegetation change and species loss in the meadows. Remarkably, the median indicator value for moisture did not change between censuses, even though land-use intensification resulted in improved drainage and alteration of the rivers' hydrodynamic regimes. This is partly related to the fact that we deliberately excluded arable fields and forests from the 2008 survey, thereby focussing on sites that were probably less affected by changes in the hydrological regime. The interquartile range for the EIV for soil reaction was 6.1 to 6.9, indicating that the meadows mainly grow on soils in the circumneutral range, which is characteristic for river sediments in lowland floodplains. The well-buffered alluvial soils are typically less responsive to acidification in the course of long-term deposition of NH_4^+ and strong acids, and they are also less affected by ammonium toxicity than grasslands on acidic soils (Stevens et al. 2011). Moreover, intensively managed grasslands are typically limed to increase productivity (Dierschke and Briemle 2002; Ellenberg and Leuschner 2010).

The negative effect of nitrogen input on the taxonomic diversity of grassland communities of the temperate zone has been documented in numerous case studies (Dupré et al. 2010; Stevens et al. 2010) and is also confirmed by over-regional reviews (for Central Europe in Bobbink et al. 1998; Dierschke and Briemle 2002; Bobbink et al. 2010; Ellenberg and Leuschner 2010). Atmospheric deposition of N compounds has been found to affect temperate grassland communities if thresholds of about 15-20 kg N ha^{-1} yr^{-1} are exceeded (Bobbink et al. 1998; Bobbink et al. 2010). Strong and lasting effects are also caused by fertilization, and even a single application of a moderate amount of N is sufficient to cause permanent shifts in species composition and lasting reductions in species richness (Hegg et al. 1992). The separation of the more local effects of on-site fertilisation from those of chronic atmospheric N deposition is difficult in re-sampling studies as these two drivers of grassland eutrophication are related and both increased during agricultural intensification from 1950 to 1980 in Central Europe by factors of roughly 3 to 6 (Ellenberg and Leuschner 2010). Protected reference sites such as the Havel region may serve as a valuable control because they are exposed to atmospheric N deposition (and climate changes) but are much less influenced by N fertilisation. The

Havel region was indeed only marginally affected by management intensification and increased fertiliser application and it showed only modest changes in grassland vegetation, which were qualitatively different from changes detected for the five other study regions. However, since we could only access one historical dataset from a now protected area, any inference on the driving factors must remain tentative.

Species composition

Our data revealed marked differences in the species composition between historical and recent grassland relevés that were consistent in the five unprotected study regions. In the 1950/60s, *Caltha palustris* and *Cirsium palustre* were common phytosociologically diagnostic species (Burkart et al. 2004). These species now occur at very low frequencies and many grassland associations and alliances have lost the bulk of their characteristic species.

Species with a decreasing frequency also include widespread generalists without specific habitat requirements in terms of soil moisture and nutrient availability (e.g. *Rumex acetosa*, *Anthoxanthum odoratum* and *Bellis perennis*). In contrast, species with significant increases in frequency are known to benefit from high to very high nitrogen availability (*Rumex obtusifolia*, *Urtica dioica*), and two of the increasing grass species (*Lolium perenne*, *Phleum pratensis*) provide high quality fodder and are thus actively sown by German farmers (Dierschke and Briemle 2002). These species were relatively rare in the floodplain grasslands 50 years ago, but they have since become dominant. The ordination diagram showed that the main floristic gradient in both census periods is related to soil moisture with no clear differences between the 1950/60s and 2008. Only the second, less important axis correlated with nutrient availability and with time factor, reflecting the large change in N availability.

Several studies on grassland change in Europe found only small shifts in species composition (e.g. Smart et al. 2003; Morecroft et al. 2009). However, these studies investigated time spans covering only two decades, and therefore detected changes should be smaller than those found in longer lasting studies. In our study, additional relevés from the 1990s show that by the same time many northern German grasslands had already been converted to intensively managed swards, which is in line with another long-term case study from the region (Wittig et al. 2007). Thus, vegetation change occurred more rapidly in the first decades after the 1950s, and studies starting in the 1980s or 1990s may well have missed the most important shifts in species composition. This highlights the need to select reference data taken before the start of agricultural industrialisation (Tamis et al. 2005; Dupré et al. 2010).

Small changes in vegetation have also been reported from grassland areas with partial or full protection status. Walker et al. (2009) studied the change of British grasslands that were under conservation management over five decades and found only moderate alterations in species composition. A similar result was obtained in the Havel region of our study, where the long-term protection status resulted in only modest changes in grassland community composition over the study period. These case studies suggest that local management is a dominant factor determining community composition, irrespective of the potential action of supra-regional factors.

Plant functional trait composition

In animal communities, reductions in functional diversity may be even larger than losses in taxonomic diversity when land-use intensity increases (Flynn et al. 2009; Laliberté et al. 2010; Vandewalle et al. 2010). This is in contrast to plant communities, where functional diversity has been found to be reduced less than species diversity (e.g. Sasaki et al. 2009; Mayfield et al. 2010), perhaps due to functional redundancy buffering losses in taxonomic diversity. Our analysis offers only limited support to this idea as the relative magnitude of losses in functional diversity and in taxonomic diversity was similar in our dataset. Functional diversity is, however, a relatively crude measure for characterizing the variability in growth and survival strategies (Podani and Schmera 2006, 2007). The most widely applied index FD has been shown to be largely redundant to species richness (Villéger et al. 2008; Poos et al. 2009), which is also confirmed by our data. Alternative approaches, such as the abundance-weighted RAO index, are less closely associated with richness, but apparently show a correlation with Shannon diversity.

Fourth-corner statistics revealed an abundance decrease in ruderal plants and, more generally, in short-lived species. Land-use intensification over time results in the dominance of a few productive grassland species that build a permanently closed sward (Dierschke and Briemle 2002). Patches of bare soil that may serve as safe sites for establishment are becoming rare, posing a problem to short-lived species but also to small perennial plants or other weak competitors (Walker et al. 2009). In fact, a large number of weakly competitive perennial herbs have declined in our study regions, explaining the detected general decrease in the abundance of hemicryptophytes. The decline of herbs is associated with losses of insect-pollinated species and cleistogamous taxa, which in our study areas were replaced by wind-pollinated species (mainly grasses), which can also persist and spread by clonal growth. This indicates that modern grasslands represent less suitable habitats for pollinating insects than their equivalents 50 years ago, corresponding to negative trends in pollinator populations documented in other Central European cultural landscapes (e.g. Biesmeijer et al. 2006).

Frequently resown swards are harvested four to seven times during the summer, and the now dominant Poaceae (*Lolium perenne*, *Phleum pratense*) are indeed known for their high mowing tolerance coupled with high fodder value. The apparent increase in the importance of plants of phenological groups that flower later in the growing season is probably also a land-use effect and not caused by climate changes. Many of the early-flowering herbs decreased (such as *Bellis perennis*; phenological group 1 in the classification system of Dierschke 1995), probably because frequent and early mowing is nowadays preventing the successful reproduction of these species. In contrast, *Lolium perenne* and *P. pratense* start flowering relatively late (phenological group 7) and are able to develop inflorescences late into summer as long as intervals between mowing are sufficient to allow for flower production.

Conclusions

Our supra-regional analysis confirms inferences of earlier case studies and shows that agricultural intensification, and in particular nutrient inputs, result in pronounced changes in grassland communities with associated losses in taxonomical as well as functional diversity. Comparison with studies covering shorter time intervals highlights the need to capture five decades or more if intensification effects are to be fully detected. The much more subtle change in the protected study region points to local rather than supra-regional drivers (climate change, atmospheric N deposition) as a cause of change. This long-term comparison emphasises the need to adopt adequate grassland management schemes on the local scale in order to preserve grasslands of high nature value. Disentangling the effects of local and supra-regional factors will, however, require a more thorough analysis based on the comparison of replicated protected and unprotected sites, which is a promising avenue for further research.

Data on functional trait composition provided no evidence that ecosystem functions are buffered against changes in plant species composition. Species dominating the recent intensively managed grasslands are typically tall, long-lived, strongly competitive grasses with a high fodder value that are often tolerant to frequent mowing and flourish under high levels of nitrogen input. The conspicuous decrease in flowering insect-pollinated herbs in Central European grasslands implies that nectar feeders and animal groups at higher trophic levels have also faced severe losses. Unfortunately, few quantitative studies on arthropod diversity in managed grasslands are available. In particular, the number of suitable reference datasets on long-term changes in the grassland fauna covering 4-5 decades or even more is extremely low. Our data do however demonstrate that there are strong directional changes that will undoubtedly have pronounced effects on a wide range of organisms, especially species dependent on insect-pollinated plants or on annual, short-lived herbs.

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Appendix

S1: Selected characteristics of the study areas. Since the phytosociological units have not been stable over time (Meisel & v. Hübschmann 1976), we employed a standard key which is the legally binding system in the relevant states of northern Germany (v. Drachenfels 2004). All sites were assigned to the v. Drachenfels groups and aggregated at higher levels (moist, mesic, intensive) provided by the key. Mean Ellenberg indicator values broken down to the respective locality are given for comparison.

Study area	Locality	Grassland extent (ha)			Median Ellenberg IV (1950s /today)		Remarks
		Mesic	Moist	Intensive	Moisture	Nutrients	
Lower Saxony							
Weser	Stolzenau	45/7	100/4	0/33	6.3/6.5	5.5/6.3	Extensive hydro-engineering, river straightened and incised
Aue	Braunschweig	159/5	28/8	77/108	6.4/6.3	5.4/6.4	Former river replaced by artificial “Mittelland” canal
Thuringia							
Helme	Kelbra	34/12	576/100	361/315	6.2/6.7	5.6/6.2	River partly still intact, partly dammed into reservoir
Elster	Zweimen	93/8	22/3	21/35	6.3/6.0	5.3/6	Two rivers, one still similar to 1950s, the other still present but straightened and incised
Saxony-Anhalt							
Nuthe	Nedlitz	27/7	344/49	0/228	6.2/6.1	5.2/6.1	River still in original bed, but deeply incised
Reference site Brandenburg							
Havel	Gülpe	72/33	109/101	12/87*	6.4/6.8	5.6/6.1	In original condition, rivers partly re-naturated, FFH protection (*Cnidium dubium* meadows)

Meisel, K., v. Hübschmann, A., 1976. Veränderungen der Acker- und Grünlandvegetation im nordwestdeutschen Flachland in jüngerer Zeit. Schriftenreihe für Vegetationskunde 10, 109-124.

v. Drachenfels, O., 2004. Kartierschlüssel für Biotoptypen in Niedersachsen. Niedersächsisches Landesamt für Ökologie, Hildesheim.

S2a List of species with diagnostic value for the phytosociological order Molinietalia (according to German SL, Jansen and Dengler 2008) that were present in our dataset.
S2b List of species included in the German Red List (according to German SL,) that were present in our dataset.

a) Molinietalia species
Achillea ptarmica
Allium angulosum
Angelica sylvestris
Betonica officinalis
Bistorta officinalis
Bromus racemosus
Caltha palustris
Cirsium oleraceum
Cirsium palustre
Cirsium tuberosum
Cnidium dubium
Crepis paludosa
Dactylorhiza majalis
Equisetum palustre
Euphorbia palustris
Filipendula ulmaria
Galium boreale
Galium uliginosum
Gentiana pneumonanthe
Geranium palustre
Geum rivale
Gladiolus palustris
Gratiola officinalis
Hypericum tetrapterum
Inula salicina
Iris sibirica
Juncus acutiflorus
Juncus atratus
Juncus conglomeratus
Juncus effusus
Juncus filiformis
Laserpitium prutenicum
Lathyrus palustris
Linum catharticum
Lotus pedunculatus
Lythrum salicaria
Ophioglossum vulgatum
Pseudolysimachion longifolium
Scirpus sylvaticus
Scutellaria hastifolia
Selinum carvifolia
Serratula tinctoria
Silaum silaus
Silene flos-cuculi
Stachys palustris
Succisa pratensis
Tetragonolobus maritimus
Thalictrum flavum
Valeriana dioica
Viola persicifolia

b) Red List species
Allium angulosum
Bromus racemosus
Calla palustris
Cardamine pratensis
Carex distans
Carex ligerica
Carex vulpina
Cerastium dubium
Chenopodium bonus-henricus
Cirsium tuberosum
Cnidium dubium
Crepis mollis
Dactylorhiza majalis
Epipactis palustris
Euphorbia palustris
Gentiana pneumonanthe
Gladiolus palustris
Gratiola offinalis
Helichrysum arenarium
Hieracium lactucella
Hippuris vulgaris
Hordeum secalinum
Inula hirta
Iris sibirica
Juncus atratus
Laserpitium prutenicum
Lathyrus palustris
Melilotus dentatus
Menyanthes trifoliata
Mentha pulegium
Oenanthe fistulosa
Ophioglossum vulgare
Peucedanum officinalis
Rhinanthus angustifolius
Scutellaria hastata
Senecio paludosus
Silene otitis
Tetragonolobus maritimus
Triglochin maritimum
Triglochin palustre
Viola persicifolia

Supporting Information

S3 List of R-Packages used in statistical analysis (depending packages not listed):

ade4: Chessel, D. and Dray, S. 2009. *Package 'ade4'. Analysis of ecological data: Exploratory and euclidean methods in environmental sciences*. CRAN web host, online.

cluster: Maechler, M., Rousseeuw, P., Struyf, A. and Hubert, M. 2005. *Package 'cluster': Cluster Analysis Basics and Extensions*. CRAN web host, online.

FD: Laliberté, E. and Shipley, B. 2009. *Package 'FD': Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*. CRAN web host, online.

lme4: Bates, D. and Maechler, M. 2009. *lme4: Linear mixed-effects models using S4 classes*. CRAN web host, online.

vegan: Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. and Wagner, H. 2010. *vegan: Community Ecology Package*. CRAN web host, online.

vegdata: Jansen, F. 2010. *vegdata: Functions to use vegetation databases (Turboveg) for vegetation analyses in R*. CRAN web host, online.

CHAPTER

4

Historical and recent fragmentation of temperate floodplain grasslands: Do patch size and distance affect plant species richness of wet meadows?

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Abstract

Patch size and isolation are thought to have a large influence on the extinction risk in grassland fragments in the modern agricultural landscape. We combined a re-sampling study in semi-permanent grassland plots with a GIS-based analysis of historical (1950s/1960s) and recent landscape patterns to analyse the importance of fragmentation on the diversity of specialist species of floodplain meadows in northern Germany. Based on historical and recent vegetation maps and relevés from six study areas (plus a protected reference area) covering 50-60 years of vegetation change following agricultural intensification, we found 30-66% losses in plot-scale diversity over time and an associated increase in the fragmentation of grassland habitats. Distance to the nearest suitable habitat had a modest negative effect on plot-scale richness while the other tested landscape metrics (total meadow area, mean patch size and landscape proximity index distribution) had no significant influence. There was also no evidence for a legacy of historical landscape structure on current richness of specialist species. Instead, management intensity and its change over the past decades as indicated by altered Ellenberg Indicator Values for nutrients and moisture had a strong influence on plot-scale diversity. The results suggest that habitat deterioration, and not fragmentation, is the main proximate cause of impoverishment. We conclude that conservation measures in Central European floodplain meadows should not only focus on large grassland areas, but should also consider small meadow patches if they remained species-rich, because they may still function as important source areas.

Keywords

Extinction debt; Germany; landscape metrics; landscape history; land use change; managed grasslands

Nomenclature

plant species: Wisskirchen and Haeupler (1998); habitat types: von Drachenfels (2004); phytosociological syntaxa: Rennwald (2000)

Abbreviations

EIV	Ellenberg Indicator Value
PID	Proximity index
PS	Patch size
TMA	Total meadow area

Introduction

Species-rich wet and mesic meadows have drastically declined throughout the course of land use intensification, and they now count among the most threatened grassland types in Central Europe (Bergmeier and Nowak 1988; Dierschke and Briemle 2002; Riecken et al. 2006; Ellenberg and Leuschner 2010; Wesche et al. 2012). Over the past 60 years, the agricultural industrialisation has led to significant increases in the amount of fertilizer applied, mowing frequency and stocking densities. These factors, along with the substantial decline in overall grassland area, have been associated with the progressive fragmentation of the remaining meadows and pastures in a matrix of arable land and other land-use types (Treweek et al. 1997; Joyce and Wade 1998; Norderhaug et al. 2000; Hodgson et al. 2005; Krause et al. 2011). Large fractions of former managed grassland in Central Europe have been transformed to cropland, afforested or subjected to urbanisation (Riecken et al. 2006; Walz 2008). In addition, the habitat quality of the remaining grassland fragments has often fundamentally changed as a consequence of drainage and modified management (Rosenthal 2003; Dietrich et al. 2012; Schaich and Barthelmes 2012).

The theory of island biogeography (MacArthur and Wilson 1967) suggests that habitat fragmentation may affect biodiversity through decreased size of habitat patches and reduced colonisation and gene flow (Debinski and Holt 2000; Fahrig 2003; Ewers and Didham 2006). Thus, the population size of a species is usually positively correlated with the area of its habitat (Honnay et al. 2006; Lennartsson 2000; Hanski 1999) and smaller populations are particularly vulnerable to extinction (Lande 1988, Matthies et al. 2004). Habitat quality is also often lower in smaller patches as a result of stronger edge effects (Oostermeijer et al. 1994). Specialist species with narrow niches are expected to be particularly sensitive to the consequences of isolation.

The vast majority of typical meadow species in Central Europe are perennials, many of which can survive extended periods of unfavourable conditions following fragmentation and land-use change (Eriksson 1996; Eriksson and Ehrlen 2001). This points to the importance of historical factors with present-day species diversity and distribution patterns being explained to a considerable extent by land use history. Lag periods are often observed and populations may persist for generations after fragmentation or habitat alteration have occurred (extinction debt, Tilman et al. 1994; Kuussaari et al. 2009). In grasslands, such slow responses of plant species richness to fragmentation and habitat loss were observed by Eriksson et al. (2002), Helm et al. (2006) and Rusterholz and Baur (2010). Responses can, however, be very slow, with periods of 50-100 years being described (Lindborg and Eriksson 2004) or even more than a century (Gustavsson et al. 2007).

A number of recently published studies found no or only little influence of past landscape patterns on present-day plant species richness in grasslands (Adriaens et al. 2006; Bruun 2000; Cousins et al. 2007; Öster et al. 2007). Instead, fragmentation and isolation are often related to changes in land-use on the plot-scale. The latter affect local plant communities often more directly, and may thereby override any potential effects of landscape structure (Korneck et al. 1998; Klimek et al. 2007).

The main objective of our study was to disentangle the possible roles of landscape fragmentation and habitat deterioration as drivers of grassland community impoverishment in Central European floodplains

Most studies on fragmentation effects in Central European grasslands focussed on relatively dry, mostly calcareous sites (e.g. Adriaens et al. 2006; Krauss et al. 2004, 2010) though effects are more widespread (Cousins 2009). We investigated the effects of land use change on meadows and pastures of moist and fertile sites in Central Europe, which have been subject to melioration and management intensification since the 1950s (Joyce and Wade 1998; van Dijk 1991). We selected floodplains in which wet and species-rich mesic grasslands were the dominant habitat type in the 1950/60s. Since then, grassland area has markedly declined and the habitat conditions of the remaining grassland have greatly changed (Krause et al. 2011).

The investigated grassland habitats were divided into two major groups, (a) habitats still harbouring the formerly widespread species-rich wet or moist grassland communities (hereafter referred to as optimal habitats), and (b) habitats where the grassland communities have been largely modified due to melioration or fallowing (subsequently termed suboptimal habitats). We further distinguished between (1) the local scale (i.e. recent vegetation relevés with exactly known location in the landscape matrix), and (2) the landscape scale (i.e. the species pool of a study area) and related both to the landscape structure. Our study covers six study areas and one additional reference area (which has been under nature protection for decades) that are spread over the lowlands of northern Germany. For the majority of study areas, detailed historical (1950/60s) and actual vegetation maps and corresponding vegetation relevés were available. We focussed on typical floodplain meadow vascular plants (termed 'characteristic meadow species'), that predominantly or exclusively occur in wet or moderately moist grasslands in our region.

With respect to the regional species pool, we hypothesized that (i) suboptimal grassland habitats possess smaller numbers of characteristic taxa for wet and mesic grasslands than optimal habitats in both historical and present-day surveys, and (ii) that the diversity of characteristic species has declined over time in all grassland types.

Exploring the effects of fragmentation on species richness at two different spatial scales, we further hypothesized that (iii) effects of current landscape structure, notably patch size and isolation, reduce the number of characteristic meadow species at both the landscape (species pool) and the local (relevé) scale. With respect to legacy effects, we examined whether (iv) historical landscape patterns influence current species richness. Finally, we tested the alternative hypothesis that (v) the characteristic species richness is mainly dependent on local habitat conditions using Ellenberg Indicator Values (EIV) for nutrient availability and moisture as indicators. Because no direct information on changes in site conditions during the past 50-60 years was available for the study areas, we had to rely on indicator values as an indirect approach.

Material and Methods

Study areas

The study was carried out in seven floodplains in the Pleistocene lowlands of northern Germany spanning from the Ems River in the West (Lower Saxony) to the Havel River in the East (Brandenburg; Table 1). In the 1950/1960s, wet meadows and periodically flooded grasslands (plant communities of the orders *Molinietalia caeruleae* Koch 1926 and *Potentillo-Polygonetalia* Tx. 1947) and species-rich mesic meadows (moist variants of communities of the order *Arrhenatheretalia elatioris* Pawl. 1928) were the most common habitat types, but these have decreased dramatically in their extent since then. An exception is the seventh study area (Havel, Brandenburg), which experienced only moderate change in land use intensity over the last few decades due to its protected status since 1967. Given that the Havel area is the sole protected study site available, it was used in the analysis only as a reference area. Further information on study area selection and a more detailed description of site conditions are given in Krause et al. (2011).

Data collection and processing

Vegetation maps and phytosociological relevés were available for both the historical (data published in the 1950/1960s; before agricultural intensification) and recent time periods (own survey in 2008; after land use intensification; Table 1). Historical and recent maps were standardised using a widely applied key for habitat classification developed by governmental conservation agencies in Germany (von Drachenfels 2004), and maps were analysed using ArcGIS-ArcInfo v. 9.2 (ESRI 2006-2009, see Krause et al. 2011). All phytosociological relevés were located within the mapped grassland areas. The number of vegetation samples conducted corresponded to the historical and recent size of the grassland areas with approximately one relevé taken per 5 ha area, resulting in 559 historical and 306 recent relevés from the seven grassland areas (registered in the Global Indiex of Vegetation Data Base under GIVD-EU-DE-009, Glöckler 2012). Historical relevés were available for six of the seven study areas (exception: River Ems area). None of the historical surveys provided coordinates for the relevés, which could thus not be assigned to individual meadow patches and were used for landscape-scale analysis only. Resampling followed a spatially stratified random sampling scheme applying Hawth's Tools (Beyer 2004) and visited sampling localities in 2008 using a GPS (Garmin, Olathe, Kansas). Only habitats referring to grasslands in the wider sense were resampled, including related successional communities such as grassland fallows with abundant forbs. Since our target species were specialist grassland plants, we did not sample arable fields or forest communities that had replaced former grassland. For the sake of comparability with the historical sampling method, we also deliberately sampled well developed (particularly species-rich) stands wherever they were encountered. Plot size in 2008 was 16-20 m^2, a common size used in Central European grassland surveys (Chytrý and Otýpková 2003). Relevés in the historical data set were slightly larger (median 25 m^2), but effects were too small to introduce a major confounding effect (see Wesche et al. 2012 for detailed analysis). Vegetation sampling was conducted in May-July 2008 with all vascular plant species being listed and percentage cover estimated following the extended Braun-Blanquet scale (Wilmanns, 1998). Species' EIVs (Ellenberg et al. 2001) were calculated using the community mean EIV for moisture (EIV-M), and the mean EIV for nutrient availability (EIV-N) as an indicator for grassland fertilisation and thus management intensity.

Table 1. Basic data for the seven study areas in northern Germany. Climate data from German National Meteorological Service, DWD, based on the reference period 1961—1990.

Study area	**Total size of study area (ha)**	**Coordinates (GC-WGS 1984)**	**Mean annual precipitation (mm yr^{-1})**	**Mean annual temperature (°C)**	**Year of historical inventory**	**Total number of historical relevés**	**Total number of recent relevés**	**Historical source**
Ems	390	N 52°56'54'' E 07°17'32''	757	8.8	1954	n.d.	52	Ernsting et al. (unpubl.)
Weser	155	N 52°30'58'' E 09°05'52''	654	9.1	1956	132	25	Hübschmann et al. (unpubl.)
Aue	264	N 52°16'20'' E 10°22'48''	620	8.9	1946	51	38	Ellenberg (unpubl.)
Helme	1081	N 51°26'33'' E 10°57'02''	484	8.5	1969	60	58	Hundt 1958
Luppe	186	N 51°21'43'' E 12°07'57''	500	9.5	1967	107	20	Gräfe (unpubl.)
Nuthe	376	N 52°02'44'' E 12°14'40''	560	8.8	1958	35	74	Hundt 1969
Havel	293	N 52°43'44'' E 12°13'00''	526	8.7	1953 (1980)*	174	39	Fischer 1980

* Oldest relevés from 1980

Defining characteristic floodplain meadow species

Species were classified as being characteristic of floodplain meadows (wet meadows or moist variants of species-rich mesic meadows) if they were listed in the German standard plant species list as characteristic species of wet meadows (Korneck et al. 1998, formation number 15; BfN (2000 onwards): http://www.floraweb.de) or of Potentillo-Polygonetalia communities (Korneck et al. 1998; formation number 8; BfN (2000 onwards): http://www.floraweb.de). In addition, taxa were required to have EIV-M values of 6 to 9. Neophytes were not considered; they were in any case negligible in terms of species numbers and cover. Out of 482 vascular plant species recorded in total, 78 species were defined as characteristic floodplain meadow species (see Appendix Table A); the subsequent analyses focused on these species.

Grassland classification and habitat type richness analysis

Historical and current map and releve-data were classified resulting in ten grassland communities (p1-p10, Appendix Table B). The grassland communities p1-p4 (alliances and orders *Cnidion*, *Molinion*, *Calthion* and *Potentillo-Polygonetalia*, Drachenfels 2004) were pooled to yield a single group (wet meadows c1) and the other communities (p5-10) subsequently received the labels c2 to c7 (see Appendix Table B). Differences in character species richness were tested by ANOVA. We applied a Wilcoxon rank sum test for testing for significant differences in species richness over time for a given vegetation unit. Tests were performed using R software v. 2.13.2 (R Development Core Team 2010).

Estimating the pool of characteristic species on the landscape scale

The pooled size of characteristic meadow species at the landscape scale was estimated in the seven study areas with sample-based rarefaction curves (ESTIMATES v. 8.2.0 (Colwell 1997; 50 runs; randomized samples without replacement; see Appendix: Figure A) for (1) the smallest number of relevés taken in any of the study areas (n = 20), (2) the sample size for which all curves reached species saturation (n = 200) and (3) an intermediate sample size (n = 100) using the software. If fewer than 100 or 200 relevés were available for a study area, the species number was extrapolated using logarithmic regression ($r^2 = 0.96$–1.00). Because the species accumulation curves showed congruent patterns, we present only the estimated richness for $n = 20$ plots in order to avoid multiple testing.

Spatial pattern analysis

Spatial patterns were analysed on two scales. Landscape scale metrics were calculated for each meadow area for both the historical and the recent survey (12 maps from the six unprotected study areas plus two maps from the protected Havel reference area). The regional pool of characteristic meadow species was assessed against these metrics. The local scale analysis focused on the species composition and species richness of a given recent relevé and related these to meadow patch size and the distance to other meadow patches (wet or moist) in the direct neighbourhood.

At the landscape scale, landscape proximity index distribution (PID), area-weighted mean of patch size (PS) and total meadow area (TMA) were calculated based on grid maps (4 x 4 m resolution corresponding to the relevé size) using FRAGSTATS software (version 3.0, McGarigal et al. 2002). PID and PS indicate the degree of fragmentation with lower values standing for a higher level of fragmentation. PID considers the patch area and, additionally, the distance between the focal patch and other similar habitat patches (here with 100 m buffer range). Fragmentation was analysed for the grassland units c1 to c7, and separately for the grassland types particularly rich in characteristic floodplain meadow species (see Appendix: Table B, vegetation units c1and c2 pooled). Hedgerows, larger ditches or creeks, and agricultural access roads were recognized in the map analysis, while spatial resolution rendered detection of smaller structural elements impossible. Recent or historical species pool size and the landscape metrics PID, PS and TMA were analysed with Pearson correlation

A patch was defined as a delimited, homogenous grassland patch containing only one of the considered meadow types (see Appendix: Table B), which has been subject to a more or less uniform management regime and was not dissected by (larger) structures. These patches often corresponded to units of land tenure. We distinguished two different precision levels in the analysis. First, for the analysis of local patch size effects, we used the original very detailed phytosociological classification of vegetation types, i.e. four subunits of wet meadows (p1 – p4; *Cnidion*, *Molinion*, *Calthion* and *Potentillo-Polygonetalia* communities). For all patches that contained a recent relevé, the number of characteristic floodplain meadow plant species in each relevé was related to the size of the historical and recent patches. Secondly, for analysing spatial isolation, we aggregated these four subunits (p1 – p4) to one category of wet meadows (c1; Appendix: Table B) to account for their limited spatial extent in recent time. The degree of spatial isolation was quantified as the smallest distance of a recent relevé in a patch to the edge of the next nearest patch of wet or species-rich moist meadows in the recent survey (units c1 and c2; see Appendix: Table B and Fig. 1b) using the ArcGIS add-on Multiple Minimum Distance (Chasan 2005). Richness of characteristic species was analysed by fitting separate linear mixed models for each of the continuous predictor variables. In all cases, model simplification suggested that all predictor variables should be retained in the analysis (model comparison using ANOVA). Mixed models were fitted using the lme function in R; the residuals of the mixed models were inspected for deviations from a random pattern.

Results

Richness in characteristic species and its change since the 1950/1960s

There was a large shift in grassland community composition from the 1950/60s to 2008. The proportion of relevés that were classified as wet or species-rich mesic meadows greatly decreased over time, whereas the fraction of relevés assigned to intensively managed and species-poor grasslands increased (Table 2). In addition, two new intensively managed grassland community types that were absent in the 1950/1960s had to be defined in 2008 (c3 and c6).

The landscape-level pool of characteristic meadow species tended to decline over time (Table 3), although trends were not significant due to large differences between study areas ($p = 0.095$, Wilcoxon test on richness estimates based on $n = 20$ samples). Diversity loss was largest in the Aue area (-67 % in the 20-sample data set, Table 3).

At the plot scale, species loss since the 1950/60s was most significant in the wet meadows (unit c1, Fig. 1), where historical communities contained on average 9.9 characteristic species per plot in the 1950/60s but only 7.0 species per plot in 2008. The overall mean number of characteristic meadow species declined from 7.9 (± 4.3 s.d.) in historical relevés to 4.2 (± 2.7 s.d.) in 2008. Differences in the richness between optimal (units c1, c2) and suboptimal habitats (in particular the units c4 and c5) tended to be large in both periods, but were significant in the historical survey only. This prompted us to treat these two community categories separately in further analysis.

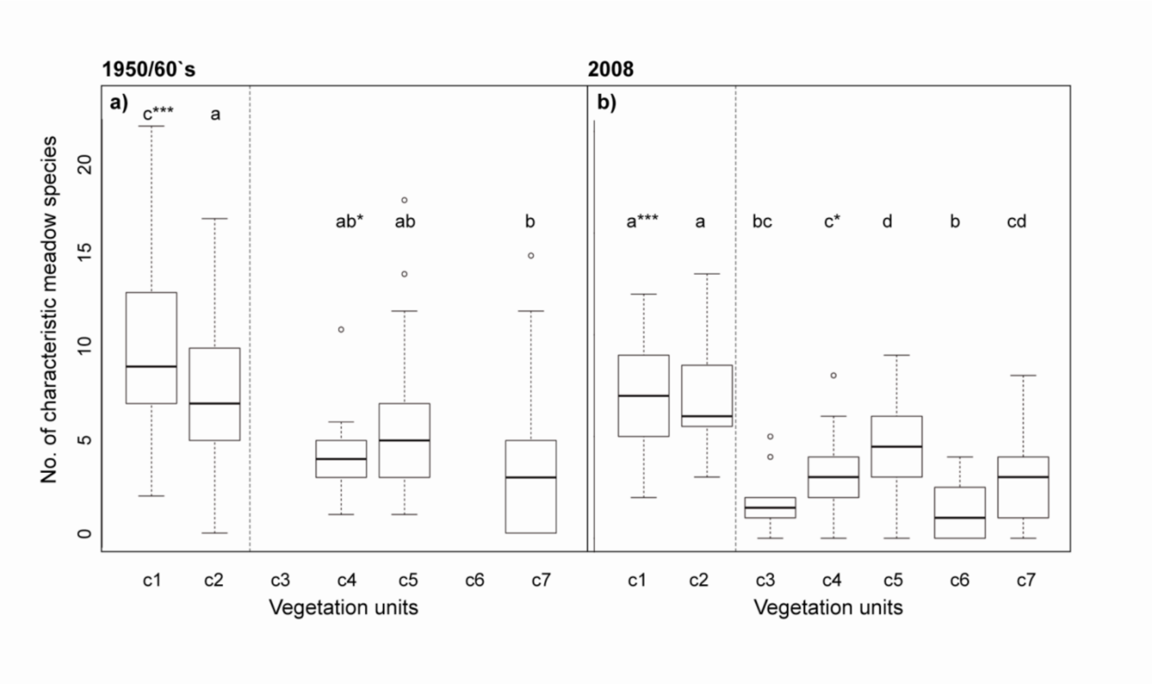

Figure 1. Box-and-whisker plots for relevé-scale richness of characteristic meadow species (a) 385 historical relevés and (b) 268 recent relevés in six study areas (excluding Havel study area). Significant differences between the vegetation units at the same point in time (letters) were tested with ANOVA, and differences in the same group but between time-points with a Wilcoxon test (. Letters indicate significant differences among groups within a given period at $p \leq 0.05$ and asterisks indicate significant differences within groups over time at $p \leq 0.05$ = *, $p \leq 0.01$ = **, $p \leq 0.001$ = ***. Optimal habitat group: c1 = wet meadows, c2 = species-rich mesic meadows. Suboptimal habitat group: c3 = intensively managed grasslands at relatively dry sites, c4 = intensively managed grasslands at moist to wet sites, c5 = species-poor managed but non intensive managed grasslands, c6 = sown synthetic grasslands, c7 = grassland fallows and extensively managed vegetation types (low intensity) dominated by sedges or reed at moist sites.

Table 2. Absolute numbers of relevés taken in historical time (HIST= 1950/60s, *n* = 559) and in recent time (REC = 2008, *n* = 306) in the seven study areas and in the main types of meadow vegetation (c1-c7, see Appendix: Table B); n.d. = no data available. Totals include the six unprotected study areas (n_{HIST} = 385, n_{REC} = 268); total (%) refers to the percentage of relevés in a vegetation unit relative to the total number of relevés taken in the respective survey. The protected Havel area is given for comparison only.

Study area	**Wet meadows (c1)**		**Species-rich mesic meadows (moist variants) (c2)**		**Intensively managed grasslands at relatively dry sites (c3)**		**Intensively managed grasslands at moist to wet sites (c4)**		**Species poor, extensively managed grasslands (c5)**		**Sown synthetic grasslands (c6)**		**Grassland fallows and similar vegetation units (c7)**	
	HIST	REC	HIST	REC	HIST	REC	HIST	REC	HIST	REC	HIST	REC	HIST	REC
Ems	n.d.	5	n.d.	1	n.d.	0	n.d.	31	n.d.	8	n.d.	6	n.d.	1
Weser	49	0	62	0	0	0	5	14	16	2	0	1	0	8
Aue	17	4	16	0	0	1	0	27	16	5	0	0	2	1
Helme	20	19	14	1	0	6	5	11	5	11	0	4	16	6
Luppe	62	3	32	6	0	0	4	2	6	9	0	0	3	0
Nuthe	20	26	15	3	0	3	0	13	0	15	0	8	0	6
Total (*n*)	**168**	**57**	**139**	**11**	**0**	**10**	**14**	**98**	**43**	**50**	**0**	**19**	**21**	**22**
Total (%)	**44**	**21**	**36**	**4**	**0**	**4**	**4**	**37**	**11**	**19**	**0**	**7**	**5**	**8**
Havel	29	27	21	2	0	2	49	5	35	1	0	0	40	2

Table 3. Landscape metrics (PID, PS, TMA) and estimated richness of characteristic meadow species in historical (1950/60s) and recent time (2008). N.d. = no data. Richness of characteristic species was estimated by rarefaction from species accumulation curves (using *n* = 20, 100 and 200 relevés). Differences between 1950/60s and 2008 were tested by a Wilcoxon signed rank test on site means (p ≤ 0.1= (*); p ≤ 0.05 = *; not tested = nt). PID = proximity index; PS = patch size; TMA = total meadow area.

Study area	**Period**	**PID**	**PS (ha)**	**TMA (ha)**	**Estimated richness of characteristic species**		
		c1-c7	c1-c7	c1-c7	*n* = 20	*n* = 100	*n* =200
Ems	1950/60	2243.1	83.8	390.1	n.d.	n.d.	n.d.
	2008	934.9	25.1	206.2	20	28	31
Weser	1950/60	460.0	28.2	155.4	34	46	51
	2008	363.2	6.6	75.2	19	28	32
Aue	1950/60	1730.7	9.3	264.2	39	50	55
	2008	243.5	6.8	129.1	13	19	21
Helme	1950/60	15374.0	143.2	1080.7	26	38	44
	2008	3880.9	48.5	491.6	29	41	47
Luppe	1950/60	3264.5	49.9	186.0	40	51	59
	2008	114.3	13.4	48.6	30	42	48
Nuthe	1950/60	8762.0	100.3	375.6	25	34	38
	2008	2927.7	28.5	287.5	24	34	39
Mean	1950/60	5305.7	69.1	408.7	32.8	43.8	49.4
	2008	1410.8 *	21.5 *	206.4 *	22.5(*)	32.0nt	36.3nt
Havel	1950/60	4099.0	76.3	292.6	23	36	40
	2008	3523.8	64.5	254.7	33	46	51

Changes in landscape structure and its effects on diversity of characteristic meadow species

The total area occupied by meadow communities (TMA) decreased on average by ~50 % between the 1950/60s and 2008 in the six unprotected study areas, while losses in the protected Havel area were only marginal (Table 3). Wet and mesic meadows were particularly affected (Appendix: Table C). The reduction in meadow area was accompanied by reductions in PID and PS indicating fragmentation of the remnant meadow area. The decrease in PID and PS was significant when all meadow types were pooled in the analysis (including fallow meadows and related communities) but also persisted if the optimal habitats were analysed separately (i.e. the combined group of wet and species-rich mesic meadows, Wilcoxon signed rank test, $p \leq 0.05$ in both cases).

Landscape-scale species richness were assessed for (1) the relation between recent landscape metrics and recent diversity patterns, (2) historical landscape metrics and historical diversity patterns and for testing on extinction debt, (3) for the relation between historical landscape metrics and recent diversity patterns (Table 4; Table D (Appendix)). At the landscape scale (regional species pool), none of these three relations between landscape metrics and the size of characteristic species pool were significant at $p \leq 0.05$.

In the plot-scale analysis, recent distance and patch size were positively related ($r = 0.17$, $p = 0.005$), as were historical and recent patch size ($r = 0.16$, $p = 0.010$). No significant correlation existed between recent distance and historical patch size ($r = -0.10$, $p = 0.099$). Simple correlation analysis with the plot-scale data pooled over the six study areas in the two habitat categories ‘optimal’ and ‘suboptimal’ indicated only a relatively weak relationship between species richness in the recent relevés and recent distance ($r = -0.37$), historical patch size ($r = 0.24$) and recent patch size ($r = -0.05$, Fig. 2). Mixed model analysis (landscape metrics and habitat type as fixed and study area as random factors) yielded a significant overall effect only for recent distance ($p_{\text{dist\_rec}} = 0.0004$) while historical patch size and recent patch size had no effect ($p_{\text{ptach\_akt}} > 0.7$ and $p_{\text{patch\_hist}} > 0.6$ respectively). There was no evidence that the two habitat categories differed in their response to the landscape metrics (interaction terms not significant in all cases).

The majority of relevés (57.3 %) in the recent survey was located at distances of <100 m to neighbouring patches of wet or species-rich mesic meadows; only 6.9 % of the recent relevés were more strongly isolated (distance to next comparable neighbour patch >500 m). The average distance to a comparable patch was 125.3 m (± 226.0).

Table 4. Pearson correlations (r) between richness of characteristic species and landscape metrics (PID, PS, TMA) in the six study areas (considering vegetation units c1 to c7; see Table C for correlation with vegetation units c1 and c2 only). Correlations were calculated separately for recent and historical data. Species richness was based on *n* = 20 relevés according to species accumulation curves. ns = not significant. (1) Recent species richness vs. recent parameters of landscape metrics (without Havel area); (2) historical species richness vs. historical parameters of landscape metrics (without Ems and Havel areas); (3) recent species richness vs. historical parameters of landscape metrics (without Havel area). PID = proximity index; PS = patch size; TMA = total meadow area.

	PID	**PS (ha)**	**TMA (ha)**
	r	r	r
(1)	0.47 ns	0.59 ns	0.37 ns
(2)	-0.79 ns	-0.84 ns	-0.66 ns
(3)	0.62 ns	0.66 ns	0.45 ns

Relationships between species richness and indicator values for nutrients and moisture

The mean plot-scale EIV for nutrients was significantly smaller in optimal than suboptimal habitats (5.9 ± 0.6 vs. 6.5 ± 0.6) while the EIV for moisture was higher (6.9 ± 0.7 vs. 6.2 ± 0.8; t test, $p < 0.0001$ in both cases). Pooled across the two habitat categories, correlation analysis indicated relatively strong relations between both EIVs and species richness ($r = -0.64$ for EIV-nutrients and $r = 0.44$ for EIV-moisture, Fig. 3). This was confirmed by the mixed model analyses with EIV and habitat as fixed factors and area as random which indicated significant effects of the EIVs for nutrients and for moisture on species richness ($p_{\mathrm{EIV\_N}} = 0.0007$, interaction $p_{\mathrm{EIV\_N*habitat}} = 0.3$; $p_{\mathrm{EIV\_M}}=0.016$, interaction $p_{\mathrm{EIV\_M*habitat}}>0.7$).

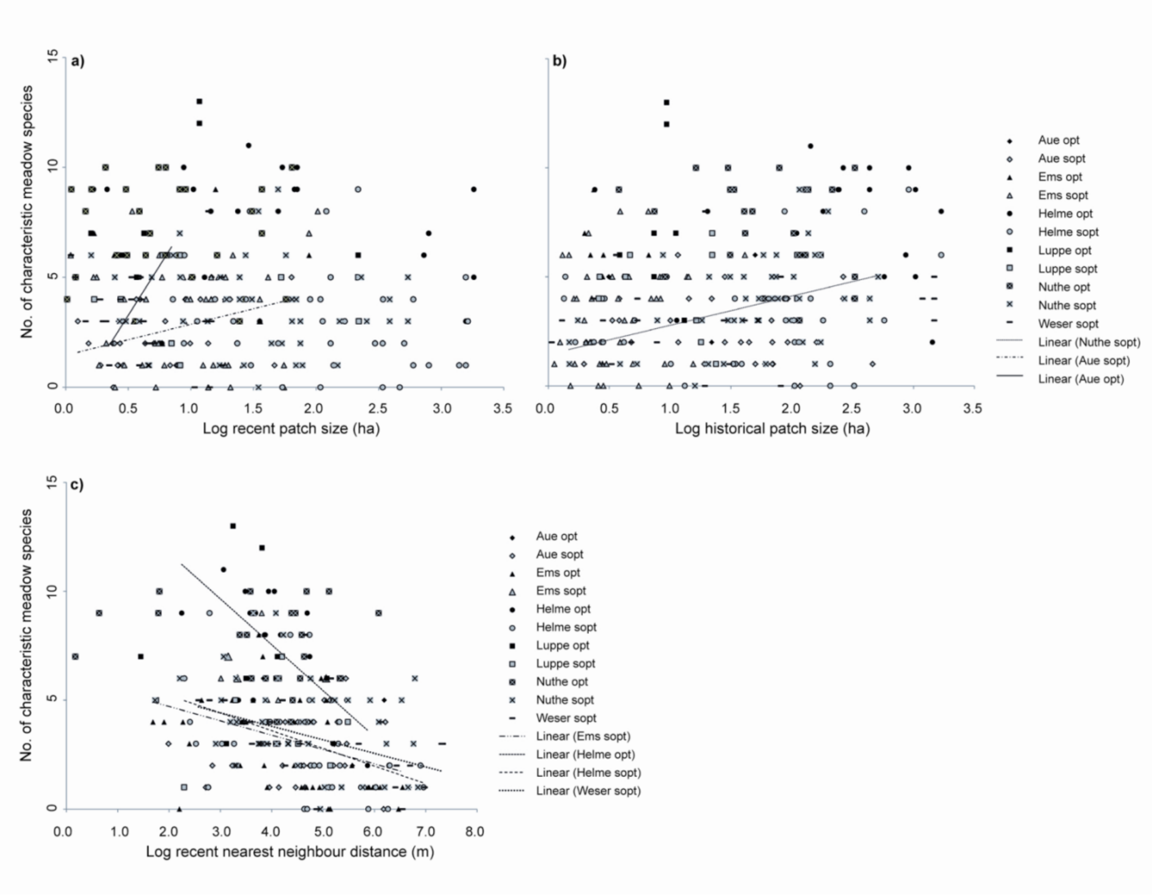

Figure 2. Number of characteristic meadow species in recent relevés (without Havel study area) as dependent on (a) log recent patch size (in ha), (b) log historical patch size (in ha), and (c) log recent distance of a meadow patch to the nearest neighbour patch of wet or species-rich mesic meadows of the optimal group (in m; see Fig. 1 and Table 2). Calculations were made separately for recent relevés located either in wet or species-rich mesic meadows (opt = optimal group, see Fig. 1), or in other grassland habitat types (sopt = suboptimal group). Regression lines are indicated only for study areas with significant relationships.

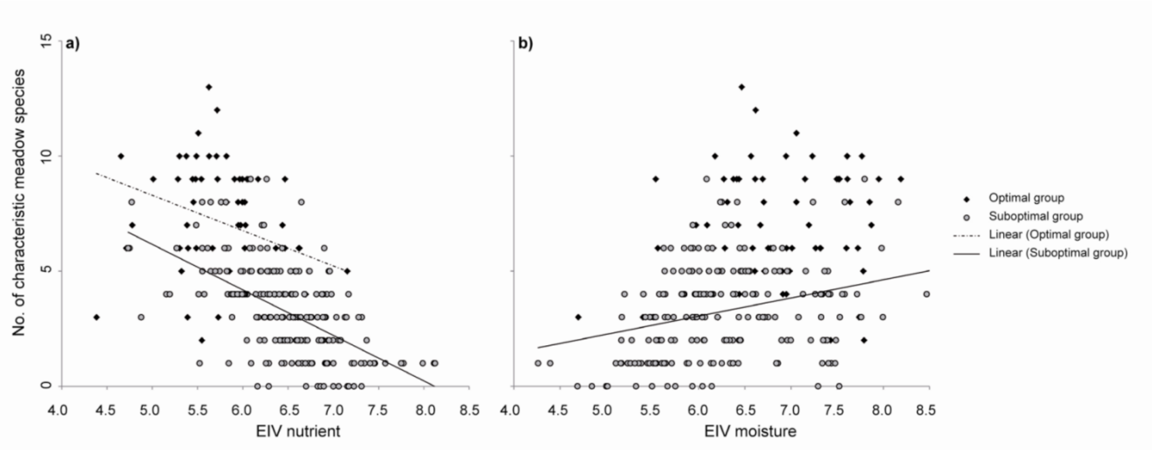

Figure 3. Number of characteristic floodplain meadow species per recent relevé in relation to the EIV for (a) nutrients (nitrogen) and (b) moisture. Correlations given separately for recent relevés located in wet or species-rich mesic meadows (units c1 and c2: = optimal group; 3a: r = -0.34 **; 3b: r = 0.12 n.s.), and recent relevés located in other grassland habitat types (suboptimal group; 3a: r = -0.58 ***; 3b: r =0.30 ***).

Discussion

Impoverishment in grassland specialist species since the 1950s

To our knowledge, this is the first analysis of long-term grassland vegetation change in Central European floodplains that examines fragmentation effects not only in one or two study areas but attempts to achieve a cross-regional perspective. Our six plus one study areas represent three of the four main alluvial plains of the north German Pleistocene lowlands (rivers Ems, Weser, Elbe) and cover a broad range of small (< 200 ha; Luppe and Weser) to large grassland areas (> 1000 ha; Helme). Our sample also cuts through the two main political spheres of post-war Central Europe.

An earlier analysis on the entire species plant species set documented large losses in richness at both the landscape (species pool) and local (plots) scales (Wesche et al. 2012; Krause et al. 2011), which is in line with our analysis with a focus on the specialist taxa. Optimal and suboptimal meadows differed in diversity in both historical and present-day surveys in diversity (hypothesis (i)), but the differences are more apparent in recent times. All grassland types experienced large species losses in the last 50-60 years (hypothesis (ii)), but they were most pronounced in the wet meadows (c1) and also in the intensively managed grasslands at moist to wet sites (c4). The latter had already represented impoverished stands in the 1950s. Similar trends of vegetation change in managed grasslands have been detected in other regions of Central Europe, for example in the Dümmerniederung of Lower Saxony (Blüml et al. 2012) and for the uplands of Saxony (Walz and Müller 2009).

Fragmentation effects on the richness in grassland specialist species

Fragmentation of grassland habitats in general, and of wet and mesic grasslands in particular, increased in the last decades, indicated by declining values of all three landscape metrics tested (landscape scale). TMA becomes relevant when its size falls well below the area needed for saturating the regional species pool.

However, none of the three landscape metrics PS, PID and TMA showed a strong influence on species pool size, as derived from regional species accumulation curves. Relatively high correlation coefficients point to trends; low statistical power (n=5) combined with high variance resulted in relationships being non-significant. This implies that fragmentation and isolation are not the proximate causes of shrinking regional species pools, and we cannot confirm the first part of hypothesis (iii) for the landscape scale. The observed pattern may be interpreted as mere coincidence between increasing species loss and fragmentation, which are caused by the same driver, i.e. management intensification.

At the plot-scale fragmentation and isolation effects may be of greater importance. Recent distance and thus isolation had an effect on species richness at the plot-scale, which is evidence in support of plot-scale part of hypothesis (iii) that postulated patch size and isolation effects on diversity. Increasing plant diversity with decreasing isolation was also found for Swedish semi-natural grasslands (Reitalu et al. 2009). The distance effect seems to be more pronounced in suboptimal meadow habitat types (Fig. 2c), which may point to the importance of source areas. Survival rates are presumably relatively high in optimum grasslands, rendering regular immigration less important. In contrast, suboptimal sites should represent sink habitats for specialised meadow taxa that should depend more strongly on the presence of source habitats in the neighbourhood.

No relationships were found for plot-scale species richness and either recent patch size or historical patch size, irrespectively of whether optimal meadow habitats or suboptimal meadow habitats were considered. This contrast with the general assumption that species richness increases with patch size (for grasslands: e.g. Cousins and Eriksson 2008). Several studies are in accordance with our results by reporting an only weak or unclear dependence of species diversity on the size and isolation of grassland patches in fragmented cultural landscapes (Eriksson et al. 1995; Kiviniemi and Eriksson 2002; Herrera and Laterra 2011; Öckinger et al. 2012). Several studies reported effects of patch size on the relation between plants with clonal and non-clonal growth (e.g. Robinson 1992; Lindborg et al. 2011; Saar et al. 2012), which suggests that patch size may well influence community composition even when no size effect is detectable on the level of species richness. Such an effect was, however, not observed in our data.

The small meadow patches in our study regions (mean size 0.27 ± 0.16ha) still contain an unexpectedly high richness of characteristic meadow species (7 ± 0.25 per plot). This indicates that the quality of site conditions must be more important than assumed patch sized and distance effects. Most of the characteristic meadow species seem capable of colonizing already relatively small grassland patches and can form viable populations there, provided that site conditions are suitable (favourable soil moisture, relatively low N and P).

No evidence for a legacy of historical landscape structure on current richness of specialist species

We assume that isolation and fragmentation were no relevant factors during the 1950/60s, since historical vegetation maps show a nearly complete and continuous cover of wet and mesic grassland. In contrast, impoverishment of potential source areas may now be an important factor (e.g. Poschlod and Biewer 2005; Hölzel and Otte 2003). Even though several typical grassland species have capacities for dispersal covering well over 100 m (Geertsema et al. 2002), others are only capable of dispersal over shorter distances (e.g. Jensen 1998; Cousins and Aggemyr 2008). Transport with flooding water was once an important dispersal agent in floodplain meadows (e.g. Hölzel and Otte 2001), but the construction of dikes has rendered this pathway unimportant in most of the studied grassland areas in recent time. Moving cattle and hay transport have most likely lost their importance as dispersal agents with the expansion of modern agriculture (Poschlod and Bonn 1998).

Published evidence for the ‘extinction debt’, i.e. the positive effect of historical patch size on recent diversity (e.g. Cousins 2009), mostly comes from relatively dry grasslands (Eriksson et al. 2002; Helm et al. 2006; Rusterholz and Baur 2010; Gustavsson et al. 2007). Our supra-regional analysis produced no coherent evidence for effects of historical landscape configuration on the richness of characteristic species in floodplain meadows, and thus leads to rejection of our hypothesis (iv). Among the historical and recent landscape metrics tested, only recent distance and no historical metric had an effect on species richness. Extinction debts most likely develop in grasslands with long continuity that are subject to gradual environmental or management change (Gustavsson et al. 2007). In support of this assumption, historically old grasslands have been found to harbour larger species pools than younger grasslands on the same soil (e.g. Waesch and Becker 2009). Instead, many managed grasslands in our study areas have since decades been ploughed and resown in order to increase fodder quality. Hence, we assume that the low number of characteristic meadow species in recent suboptimal vegetation units (that mostly were optimal habitats in the 1950/60s) indicates that the extinction debt is already paid. Cross-linking of areas by linear elements like ditches or way-sides may have buffered against those losses (Tikka et al. 2000; Blomqvist et al. 2003; Cousins 2006). However, the function of linear landscape elements as corridors for plant migration has often been found to be rather limited (van Dorp et al. 1997).

Richness of specialist species is mainly determined by local environmental conditions

In contrast to the ambiguous effects of landscape structure on species richness, we found a much clearer influence of the local site conditions. Our data show a strong negative correlation between the mean indicator value for nutrients and the richness of characteristic meadow species in both optimal and suboptimal habitats, which is evidence in support of hypothesis (v). This is in agreement with the findings of Stevens et al. (2010), Wellstein et al. (2007) and Klimek et al. (2007) among others. Impoverishment is mainly attributed to local nutrient (mostly N) input, which promotes competitive N-demanding species and excludes less responsive specialist species. Additional to increasing N-input by fertilization, the atmospheric N deposition has increased since the 1950s (Ellenberg and Leuschner 2010).

Exceptions from the widespread pattern of diversity loss are the Helme area and the protected Havel reference area, which both showed increases in richness since the 1950/60s. Again, landscape structure can only be of secondary importance as shown by the decreases in TMA, PS and PID that occurred in these two areas as well. The increase in species richness in the protected Havel area but also in the conventionally managed Helme area are probably related to the local increase in soil moisture levels. In the Helme area, a dam was constructed in 1969 that lifted the groundwater level of the upstream meadow areas, and in the Havel area nature conservation management also reduced the drainage of water after flooding. Wet meadow species profited from these measures, as is indicated by the slight (non-significant) increase in the mean EIV for moisture in the Helme region between 1968 (6.5) and 2008 (6.7). Similar trends and plant species responses to river regulation were described by Leyer (2005). The overall positive relationship between richness and the EIV for moisture was closer in the suboptimal habitats, while the moisture conditions remained more favourable in the optimal habitats and the across-site variation in the EIV-moisture value was smaller than in the suboptimal grassland habitats.

Conclusion and implications for the conservation of floodplain grasslands

Our results suggest that fragmentation does not play a key role for the species richness of floodplain grasslands in northern Germany, probably because this factor is masked by more influential site-level factors. Dominant drivers of grassland impoverishment were in most cases local alterations of site conditions, notably increased fertilisation, more frequent and earlier mowing, drainage. This finding implies that conservation measures in floodplain meadows should at least consist of two elements, the establishment and proper management of one or a few large-scale sanctuaries, but also of a net of smaller reserves of meadow patches with remaining populations of endangered species. The large sanctuaries have a high conservation value because they typically host a larger proportion of the regional species pool and may also be indispensable for conserving viable populations of characteristic animals such as breeding waders that require large open wet grasslands (Wilson et al. 2012). The preservation of small meadow patches with high nature value represents another useful short- to medium-term conservation strategy because it allows to specifically targeting few remaining and often small stands of high-value grassland vegetation. Our results on the role of patch distance at the local (relevé) scale underpin the importance of small remaining meadow patches with still high plant diversity that seem to function as viable source populations for the characteristic meadow species. Several examples from Central Europe demonstrated that intensively managed grasslands can be successfully restored to their former state of higher nature conservation value if management regimes is changed (e.g. Rosenthal 2006; Hölzel and Otte 2003; Blüml et al. 2012); our results show that restoration is much more promising when potential source areas are in close vicinity.

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Appendix

Table A: List of characteristic floodplain meadow plant species in historical and recent relevés of seven study areas in northern Germany. EIV-M indicates Ellenberg Indicator Value for moisture according to Ellenberg et al. (2001); underlined values indicate flooding indicator species. The assignments to phytosociological communities correspond to Korneck et al. (1998).

Characteristic species	EIV-M	Molinietalia species	Potentillo-Polygonetalia species	Present in historical relevés	Present in recent relevés
Achillea ptarmica	8	X	-	X	X
Agrostis canina	9	X	-	X	X
Ajuga reptans	6	X	-	X	X
Allium angulosum	8	X	-	X	0
Alopecurus geniculatus	8	-	X	X	X
Angelica sylvestris	8	X	-	X	X
Bistorta officinalis	7	X	-	X	X
Bromus racemosus	8	X	-	X	0
Calamagrostis canescens	9	X	-	X	X
Cardamine pratensis	6	X	-	X	X
Carex distans	6	X	X	X	0
Carex flacca	6	X	-	X	X
Carex hirta	6	-	X	X	X
Carex otrubae	8	-	X	X	X
Carex panacea	8	X	-	X	X
Cirsium oleraceum	7	X	-	X	X
Cirsium palustre	8	X	-	X	X
Cirsium tuberosum	6	X	-	X	0
Cnidium dubium	8	X	-	X	X
Colchicum autumnale	6	X	-	X	0
Crepis paludosa	8	X	-	X	0
Dactylorhiza majalis	8	X	-	X	0
Deschampsia cespitosa	7	X	-	X	X

Epilobium hirsutum	8	X	-	0	X
Epipactis palustris	9	X	-	0	X
Equisetum palustre	8	X	-	X	X
Festuca arundinacea	7	X	X	X	X
Filipendula ulmaria	8	X	-	X	X
Galium boreale	6	X	-	X	X
Galium uliginosum	8	X	-	X	X
Gentiana pneumonanthe	7	X	-	X	X
Geranium palustre	7	X	-	X	X
Geum rivale	8	X	-	X	0
Gladiolus palustris	6	X	-	X	0
Holcus lanatus	6	X	-	X	X
Hypericum tetrapterum	8	X	X	0	X
Inula Britannica	7	X	X	X	X
Inula salicina	6	X	-	X	X
Iris sibirica	8	X	-	X	0
Juncus acutiflorus	8	X	-	0	X
Juncus articulates	9	X	X	X	X
Juncus compressus	8	-	X	0	X
Juncus conglomeratus	7	X	-	X	X
Juncus effuses	7	X	X	X	X
Juncus inflexus	7	X	X	X	X
Lathyrus palustris	8	X	-	X	X
Lathyrus pratensis	6	X	-	X	X
Lotus pedunculatus	8	X	-	X	X
Lysimachia nummularia	6	-	X	X	X
Lysimachia vulgaris	8	X	-	X	X
Lythrum salicaria	8	X	-	X	X
Mentha arvensis	8	X	-	X	X
Mentha pulegium	7	-	X	0	X
Molinia caerulea	7	X	-	X	X
Myosotis scorpioides	8	X	-	X	X

Ophioglossum vulgatum	7	X	-	X	0
Poa palustris	9	X	-	X	X
Potentilla anserine	6	X	X	X	X
Potentilla reptans	6	X	X	X	X
Pseudolysimachion longifolium	8	X	-	X	X
Pulicaria dysenterica	7	X	X	X	0
Ranunculus repens	7	X	X	X	X
Rorippa sylvestris	8	-	X	X	X
Rumex crispus	7	-	X	X	X
Rumex obtusifolius	6	-	X	X	X
Sanguisorba officinalis	7	X	-	X	X
Scirpus sylvaticus	8	X	-	X	0
Scutellaria hastifolia	8	X	-	X	0
Selinum carvifolia	7	X	-	X	X
Senecio aquaticus	8	X	-	X	X
Silene flos-cuculi	7	X	-	X	X
Stachys palustris	7	X	-	X	X
Succisa pratensis	7	X	-	X	0
Symphytum officinale	8	X	X	X	X
Thalictrum flavum	8	X	-	X	X
Trifolium fragiferum	7	-	X	X	X
Trifolium hybridum	6	-	X	X	X
Valeriana dioica	8	X	-	X	0

Table B. Habitat classification according to phytosociological units, site characteristics and habitat codes used for analyses on both landscape scale and local scale. Nomenclature of plant communities (syntaxa and their synonyms) and of habitats follows Rennwald (2000) and von Drachenfels (2004).

Habitat categories according to phytosociological units	**Habitat code after von Drachenfels (2004)**	**Vegetation units as used for landscape scale and nearest neighbour analyses**[1]	**Vegetation units as used for local scale patch size analysis**[2]
Molinion and other wet grassland communities at nutrient-poor sites	9.3.1, 9.3.2, 9.3.3, 9.4.1	c1	p1
Cnidion and related wet grassland vegetation units	9.3.4, 9.4.2	c1	p2
Calthion and related wet grassland vegetation units	9.3.6, 9.4.3, 9.3.5	c1	p3
Potentillo-Polygonetalia (temporarily flooded grasslands)	9.3.7, 9.4.4	c1	p4
Species-rich mesic meadows (moist variants of Arrhenatheretalia)	9.1.1, 9.1.5	c2	p5
Intensively managed grasslands at relatively dry sites	9.5.1	c3	p6
Intensively managed grasslands at moist to wet sites	9.5.3, 9.5.5, 9.5.6	c4	p7
Species-poor managed (low intensity) grasslands (often former intensive use or arable fields)	9.5.7, 9.1.6	c5	p8
Sown synthetic grasslands	9.6	c6	p9
Grassland fallows and extensively managed vegetation types (low intensity) dominated by sedges or reed at moist sites [3]	11.2.1, 5.1, 5.2	c7	p10

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[1] Units c1 and c2 were merged for further analysis at the landscape scale, and for analyses detecting the effect of nearest neighbourhood at the local scale

[2] Units were used for analyses at the local scale

[3] Urtica dioica-Phragmites australis-community and communities dominated by sedges or reed

Table C. Changes in landscape metrics and total grassland area in the floodplain meadows of the seven study areas between the 1950/60s and 2008 (consideration of the vegetation units c1 and c2`, i.e. optimal habitats only). n.d. = no data. Differences between the two surveys were tested by a Wilcoxon signed rank test on site means ($p \leq 0.1$= (*); $p \leq 0.05$ = *). PID = proximity index; PS = patch size; TMA = total meadow area.

Study area	**Period**	**PID**	**PS (ha)**	**TMA (ha)**
		c1, c2	c1, c2	c1, c2
Ems	1950/60	2393.7	65.7	352.2
	2008	82.3	1.8	37.6
Weser	1950/60	773.3	17	145.4
	2008	68.8	1.8	11.2
Aue	1950/60	969.8	7.4	186.7
	2008	21.5	2.4	12.5
Helme	1950/60	1227.1	29	610.3
	2008	371.3	9.1	112.6
Luppe	1950/60	1365.7	22.2	114.8
	2008	23.3	1.2	11.2
Nuthe	1950/60	7684.2	99.8	371.0
	2008	208.0	3.1	56.0
Mean	*1950/60*	*2402.*	*40.1*	*296.7*
	2008	*129.2 **	*3.2 **	*40.2 **
Havel	1950/60	1250.2	41.7	180.5
	2008	1829.5	18.9	141.5

Table D. Pearson correlations (r) between between richness of characteristic species and landscape metrics (PID and PS) as well as total meadow area (TMA) in the six study areas presented in table C (only the ‘optimal’ vegetation units c1 and c2 are considered). Species richness (SR) was estimated based on *n* = 20 relevés according to the species accumulation curves presented in Table 3. (1) Recent species richness vs. landscape metrics for recent conditions (without Havel area); (2) Historical species richness vs. landscape metrics (without Ems and Havel areas; (3) Recent species richness vs. landscape metrics for historical conditions (without Havel region). PID = proximity index; PS = patch size; TMA = total meadow area (ns = not significant, (*) 0.05<p<0.1).

	PID	PS (ha)	TMA (ha)
	r	r	r
(1)	0.51 ns	0.41 ns	0.50 ns
(2)	-0.62 ns	-0.72 ns	-0.84 (*)
(3)	0.14 ns	0.18 ns	0.37 ns

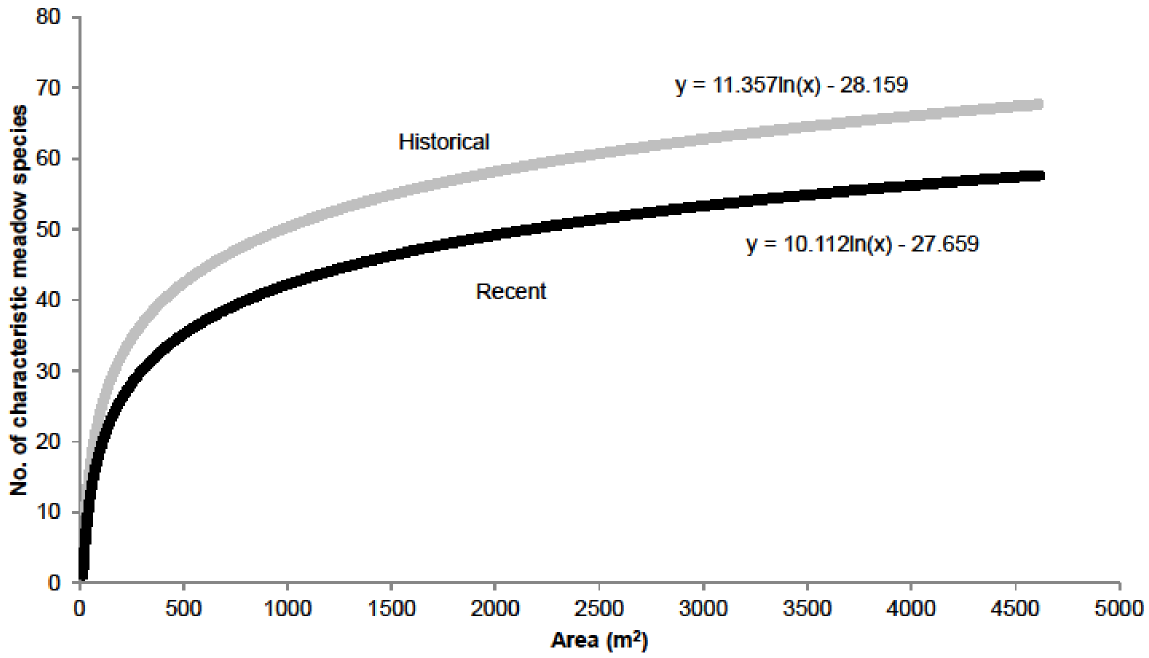

Figure A. Species accumulation curves for the historical (1950/60s) and recent surveys (2008), calculated for characteristic meadow species only (pooled over all regions) in relation to the cumulative sampled area (m^2) (based on the area given by relevés).

CHAPTER

5

The significance of habitat continuity and current management on the compositional and functional diversity of grasslands in the uplands of Lower Saxony, Germany

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Abstract

There is a growing concern that land use intensification is having negative effects on semi-natural grasslands and that it leads to a general loss of biodiversity among all types of formerly extensively managed grasslands of poor to medium nutrient richness. Since the 1950s, many Central European uplands have been subject to an increase in grassland coverage as a result of changes in land use practices. Using such a landscape in Lower Saxony, Germany as a model region, we assessed environmental factors that control grassland diversity, including plant community composition, species richness and pollination trait composition. In 2007, 189 vegetation sampling sites were randomly distributed among grasslands covering some 394 ha within a 2,500 ha study area. Plant communities were classified using TWINSPAN and the effects of environmental factors (soil, topography, current management and habitat continuity) were analysed by canonical correspondence analysis and regression analysis and reduced for the effects of spatial autocorrelation by using principal coordinates of neighbour matrices.

We found a wide range of six poor (<15 plant spp.) to extremely species-rich (>27 spp.) grassland types under mesic to dry site conditions, including sown, Cynosurion, Arrhenatherion and semi-natural grasslands. Grassland community composition was best explained by soil factors and species richness and pollination type composition by combined current management and habitat continuity. During the 1950/60s, the extent of grassland area within the studied landscape rapidly increased to more than double its previous extent, and in 2007, grasslands comprised 16%. NATURA 2000 grassland types comprised 1% of the surveyed site and medium-rich, high-nature-value grasslands a further 5%. While the number of wind-pollinated plant species was equal among all grassland types, there was a parallel decline in insect-pollinated plants and overall median species richness in the grassland communities along a gradient of increasing land use intensity (mowing, nutrient supply). Moreover, insect-pollinated plants occurring in intensively managed grasslands were found to additionally have the ability to do self-pollination. Species-rich grasslands - including semi-natural grasslands and a semi-improved, species-rich Arrhenatherion community - occurred exclusively on old sites (with >100 years of habitat continuity) that had been used for traditional sheep grazing (environmental contracting). Medium-rich Arrhenatherion grasslands were established primarily on less productive, formerly arable fields (<30 years). We conclude that conservation efforts should focus on extant species-rich grassland types and should aim to implement traditional land use practices such as sheep grazing. Additional restoration efforts should focus on establishing new grasslands on less productive sites in the proximate surroundings of species-rich grasslands to facilitate seed dispersal, but nitrogen deposition should be buffered where appropriate. These measures would enhance the interaction between nature reserves and agricultural grasslands and thus improve the ecological quality of grasslands at the landscape scale.

Keywords: community composition; historical and current management; land use intensification; mesotrophic meadows; plant functional traits; pollination; semi-natural grasslands; species richness;

Introduction

Agricultural intensification has driven large-scale changes in the composition and structure of European landscapes (Gustavsson et al. 2007; Krauss et al. 2010; Flohre et al. 2011). Since the beginning of the 20th century, formerly widespread semi-natural grasslands declined in favour of more productive hay meadows, pastures and arable land (Bakker and Berendse 1999; Poschlod et al. 2005). Land use intensification further accelerated with the advent of the Common Agricultural Policy (CAP) in Western Europe in the late 1950s. CAP was later identified as being responsible for increasing habitat degradation and biodiversity loss, and was reformed in several stages from the late 1980s until the European Union Agenda 2000 (Henle et al. 2008). Conservation and restoration efforts in agricultural landscapes previously focussed on semi-natural grasslands (Bakker and Berendse 1999). The tremendous decline of semi-natural grasslands has been documented for many Northern and Central European landscapes (e.g. Hodgson et al. 2005; Strijker 2005; Cousins and Lindborg 2008). However, it has now been recognized that grasslands generally show losses in plant species richness over time (Isselstein 2003; Wesche et al. 2012). In particular, mesotrophic grasslands have suffered alarming rates of species-decline, habitat loss and fragmentation over the last few decades (Rodwell et al. 2007; Krause et al. 2011). In order to understand the causes of such gradual grassland diversity loss, the ecological quality of grasslands must first be established with a view to identifying the underlying factors that control grassland diversity using a landscape scale approach that covers all types of grasslands, rather than solely focussing on conservation priority habitat types.

Biodiversity patterns reflect the combination of past and present environmental conditions that have prevailed with respect to the species assemblage being observed (Lunt and Spooner 2005). Recent studies have indicated that, in addition to the type and intensity of current management practices, land use history and habitat continuity play a crucial role in the explanation of grassland diversity (Gustavsson et al. 2007; Aavik et al. 2008; Cousins and Lindborg 2008; Waesch and Becker 2009). In landscapes of south-eastern Sweden, total grassland area has declined over the last 100 years, with the current grassland proportion having a positive influence on grassland species richness across the landscape (Cousins and Vanhoenacker 2011). Considering the effect of the decline of overall grassland area on the most common or transformed landscapes, the influence of management history was absent or of minor importance as many grassland specialist plants had already become extinct (Adriaens et al. 2006; Cousins 2009). However, opposite trends were found in other

European temperate regions: Since the 1950s, along with agricultural intensification in more productive areas, grassland area increased in marginal rural landscapes, such as in the uplands of Germany and Great Britain (Peppler-Lisbach 2003; Hodgson et al. 2005; Wellstein et al. 2007; Waesch and Becker 2009). Young grasslands were mostly established on former arable fields (Peppler-Lisbach 2003; Hietel et al. 2005). Wellstein et al. (2007) found that younger grassland types indicated higher nutrient levels, and that grassland composition was most dependent on abiotic site factors such as geomorphology. In contrast, Waesch and Becker (2009) found that both species composition and richness of mesic grasslands were largely dependent on grassland continuity. From an ecological restoration point of view, grassland-enriched landscapes, which include grasslands of different ages, are therefore of particular interest, as they can serve as model regions to investigate the effects of habitat continuity in combination with present management practices.

In addition to changes in species richness and community composition, land use intensification causes changes in the functional diversity of grasslands (Flynn et al. 2009; Vandewalle et al. 2010; Wesche et al. 2012). For grassland specialists, the success of pollination is highly dependent on both species characteristics and landscape composition (Dauber et al. 2010). Flowering species which are mainly reliant on insect pollination are most negatively affected by habitat loss and fragmentation (Aguilar et al. 2006). In grasslands, intensification generally results in the promotion of wind pollinated grasses and the impoverishment of flowering herbs. This leads to a loss of associated pollinators and can result in losses at higher trophic levels (Biesmeijer et al. 2006; Weiner et al. 2011). Waesch and Becker (2009) found that the composition in plant species traits is largely determined by the age of the grassland. For the conservation of grasslands and associated diversity of plants and flower visitor networks, it is therefore important to disentangle the importance of pollination traits in different grassland communities with respect to historical and current management practices.

The overall objective of our study was to analyse plant diversity (community composition, species richness, and functional diversity) in relation to grassland habitat continuity and present management in a representative grassland-enriched region in the Central European uplands. The Solling Forelands in southern Lower Saxony, Germany are particularly well-suited for such a study because they possess the complete range of grassland types from semi-natural grassland remnants to young meadows, and because there is a large variability in abiotic site conditions as well as current grassland management practices.

Specifically, we addressed the following questions:

(1) How do grassland types differentiate in terms of floristic composition, species-richness and pollination traits?

(2) What are the primary factors that determine grassland diversity?

(3) How is local plant diversity affected by current management and grassland continuity?

Materials and Methods

Study area

The study was carried out in the Solling Forelands, an escarpment landscape east of the Solling highlands and west of the city of Göttingen in southern Lower Saxony, Germany (Fig. 1a). The landscape selected for the study had an area of 2,500 ha. A locality called Mühlenberg, situated in the centre of the study area (N 51.540486°, E 9.763554°, GC-WGS 84), is part of a Natura 2000 site (Special Area of Conservation (SAC) according to European Council Directive 92/43/EEC, site no. DE 4424-301). Two geological zonal subtypes are represented in the area, the Röt depressions and the limestone plateaus of the Dransfeld hills (Nagel et al. 1981). Of the 189 grassland samples, 23% were situated on Triassic sandstone (sand and silt stone), 39% were placed on Middle Triassic limestone (limestone and marl) and 38% on Tertiary and Quaternary basalt outcrops and loess deposits. Elevation ranges from 200 to 440 m a.s.l. and the regional climate is transitional between Atlantic and Continental Central European temperate with an average annual precipitation of 645 mm and average mean temperature of 8.7°C (Göttingen meteorological station, 167 m a.s.l., 1961-1990).

Sampling of grassland vegetation

Sampling was stratified by grassland area that was distinguishable from other land use types. Grassland patches were digitized based on colour infrared (CIR) aerial photographs (dated 17/05/1993, Aerowest Photogrammetrie) using ArcGIS-ArcInfo software, version 9 (ESRI 1999-2005) and validated in a field survey in the spring of 2007. Proportional to the grassland surface area, samples were randomly selected using an average number of 0.5

samples per hectare, with a 4 m minimum distance to polygon edges in order to avoid edge effects (GIS-Hawth's Analysis Tools; Beyer 2004). In 2007, the chosen coordinates were visited in the field using standard handheld GPS (Garmin, Olathe, Kansas). Vegetation was sampled on 189 plots of 16 m², which is a common sample size used in Central European grassland surveys (Chytrý and Otýpková 2003). Nomenclature follows Jäger and Werner (2005).

Environmental data

For each sample, some environmental data were surveyed in the field, others were extracted from historical, geological and soil maps (Table 1). Correlations between the environmental variables were assessed using Spearman's rank correlation test (R software, version 2.14.2, R Development Core Team 2010). Environmental variables with autocorrelations of $r \geq 0.9$ were excluded from further analysis, thereby removing 'environmental contracting', which highly correlated with the management type 'sheep'. Current grassland management was identified during field-surveys and to obtain additional information on mowing frequency, the mowing tolerance was analysed for each sample using species indicator values derived from the BIOLFLOR database (Klotz et al. 2002). Grassland habitat continuity was determined for each sampling site using historical and recent topographical maps (dating from 1786, 1894, 1956, 1962, and 1979), aerial photographs (dating from 1993) and during field surveys (in 2007). The historical age of grassland patches with continuous management was assumed to be equivalent to the latest grassland sequence without interruption from 2007 to the past. Topography and soil variables were derived from various sources (cp. Table 1); in order to obtain additional information on soil nutrient conditions, the respective Ellenberg indicator values (EIV-N) were calculated (Ellenberg et al. 2001).

Functional traits

Functional plant traits for pollination type (wind-, insect-, self-pollination, and combinations) were determined for the 220 grassland study species using the BIOLFLOR database (Klotz et al. 2002).

Classification of grassland communities

Classification of grassland communities was performed by TWINSPAN analysis (Hill and Šmilauer 2005) using six pseudo-species cut-levels (0, 2, 5, 15, 30 and 50 % cover of species) with equal weight being applied to each and excluding species with less then two occurrences in the data set. Clusters were named following the habitat type key of von Drachenfels (2011), a widely used key developed by nature conservation agencies, and the Natura 2000 code where applicable.

Table 1 Classes of environmental variables with their group memberships (M, current management type; A, grassland continuity; T, topography; S, soil), data type and obtained single values (nominal) or ranges of values (ordinal, metric).

Class	Group	Data type	Values
Management type [a]	M	nominal	mown; mown*pastured; pastured; sheep; fallow
Historical age (grassland continuity) [c]	A	nominal	1786; 1894; 1956; 1962; 1979; 1993; 2007
Elevation (m a.s.l.) [a]	T	metric	196–368
Slope (degree) [a]	T	metric	0–35
Topographical position[a]	T	nominal	valley; lower slope; mid slope; upper slope; plateau
Heat load [d]	T	metric	0.69–0.92
pH (H_2O) [e]	S	metric	4.1–7.7
$CaCO_3$ [e]	S	ordinal	0-7
Soil moisture content [f]	S	ordinal	2–6
Top soil texture [f]	S	nominal	loam; loamy silt; clay
Geological substrate [g]	S	nominal	siltstone; limestone; loess
Soil type [f]	S	nominal	eutric leptosol; rendzic leptosol; cambisol; gleyic cambisol; gleyic luvisol; vertisol; gleyic anthrosol

a = field observations
b = excluded for further analysis, because of high correlation of r ≥ 0.9 with the sheep management type
c = derived from topographical maps and aerial photographs
d = heat load specifies the potential annual direct incident radiation, which is calculated by using the variables latitude, slope and aspect (McCune and Keon 2002)
e = analysis of soil samples following Sponagel et al. (2005)
f = derived from digital soil maps (Boess et al. 2004)
g = derived from geological maps (Nagel et al. 1981)

Dissecting the spatial structure of vegetation data and direct ordination methods

The presence of a spatial structure shared by species with regard to environmental data sets might lead to an overestimation of the interactions between species and the measured environmental conditions (Borcard et al. 1992). To consider this spatial autocorrelation in the interpretation of results, the spatial relationship among the grassland sampling sites was decomposed using PCNM (Principal Coordinates of Neighbour Matrices) analysis (Borcard and Legendre 2002). PCNM variables were created using the following steps: (1) We created a matrix of Euclidean distances from the projected coordinates of the 189 samples; (2) we truncated the resulting matrix just above the smallest distance that keeps all sites connected into a single network (i.e. 591 m) and we filled the truncated portion of the distance matrix with the distance value of 2,400 (about four times the largest distance retained); (3) we computed principal coordinates, corrected for negative eigenvalues (Lingoes correction), using PrCoord, version 1.0 (Anderson et al. 1999, implemented in CANOCO 4.5 package, ter Braak and Šmilauer 2002); and (4) we reduced the number of explanatory spatial variables to those that were both significant after Holm correction (Legendre and Legendre 2006) and that contributed to the explanation of the response data. Response data to the spatial axes included ‘community composition’, which was analysed by Canonical Correspondence Analysis (CCA), and ‘species richness’ and ‘pollination trait composition’, both of which were analysed using multiple linear regressions. Significances were tested using a Monte Carlo permutation test (full model; with 9,999 permutations; step-wise forward selection, and p-value ≤ 0.05).

Variation partitioning of explained (a) environmental variation, (b) environmental and spatial variation, (c) spatial variation, and (d) unexplained variation followed Borcard et al. (1992) using CCA/partial CCA for community composition, and multiple linear regression/partial multiple linear regression for species richness and pollination trait composition. The effects of the four different groups of explanatory variables (cp. Table 1), i.e. management type (M), grassland continuity (A), topography (T), and soil (S), were tested separately for significant explanatory values by removing the effect of spatial structure and the remaining explanatory variables (net effect).

Ordination and regression were performed using CANOCO, version 4.5 (ter Braak and Šmilauer 2002).

Summary statistics

Samples were grouped by grassland community, habitat continuity and current management. Differences in the variation in species richness, EIV-N and mowing tolerance between the groups were tested by one-way-ANOVA and non-parametric Behrens-Fisher test for multiple comparisons and visualized by boxplot diagrams. All summary statistics were performed with the R software, version 2.14.2 (R Development Core Team 2010).

Landscape-scale analysis

In the grassland area of 2007, species richness was modelled using mass point triangulation of richness values given by the spatial distribution of the original 189 samples, with class thresholds being defined as significant differences in species richness between grassland community clusters 1-6 resulting from TWINSPAN analysis. The analysis of habitat continuity was based on the overlay of historical maps of given ages. Present management, derived from field-surveys for each sample, was extrapolated to the extent of the respective land parcel. Spatial analyses were performed using ArcGIS-ArcInfo software, version 9 (ESRI 1999-2005).

Results

Gradients in grassland diversity

In the Central European upland study area, we found a total grassland area of 394 ha, which represented 16% of the landscape surveyed in 2007 (Fig. 1a), and TWINSPAN analysis revealed six grassland communities occurring therein (Fig. 2, Table 2). These communities represented a wide range of mesic and dry grassland types along a land use intensity gradient. They included sown and species-poor, intensively managed Cynosurion grasslands mainly characterised by productive grass species of the genera *Lolium*, *Poa* and *Elytrigia* (communities 1 and 2). Mesic Arrhenatherion communities (communities 3 and 4) had the grasses *Arrhenatherum elatius* and *Festuca rubra* in common, while community 3 was differentiated by a number of characteristic herbs. Extensively managed grasslands of high nature conservation value at the European level included species-rich hay meadows (community 5) and semi-natural dry grasslands (community 6).

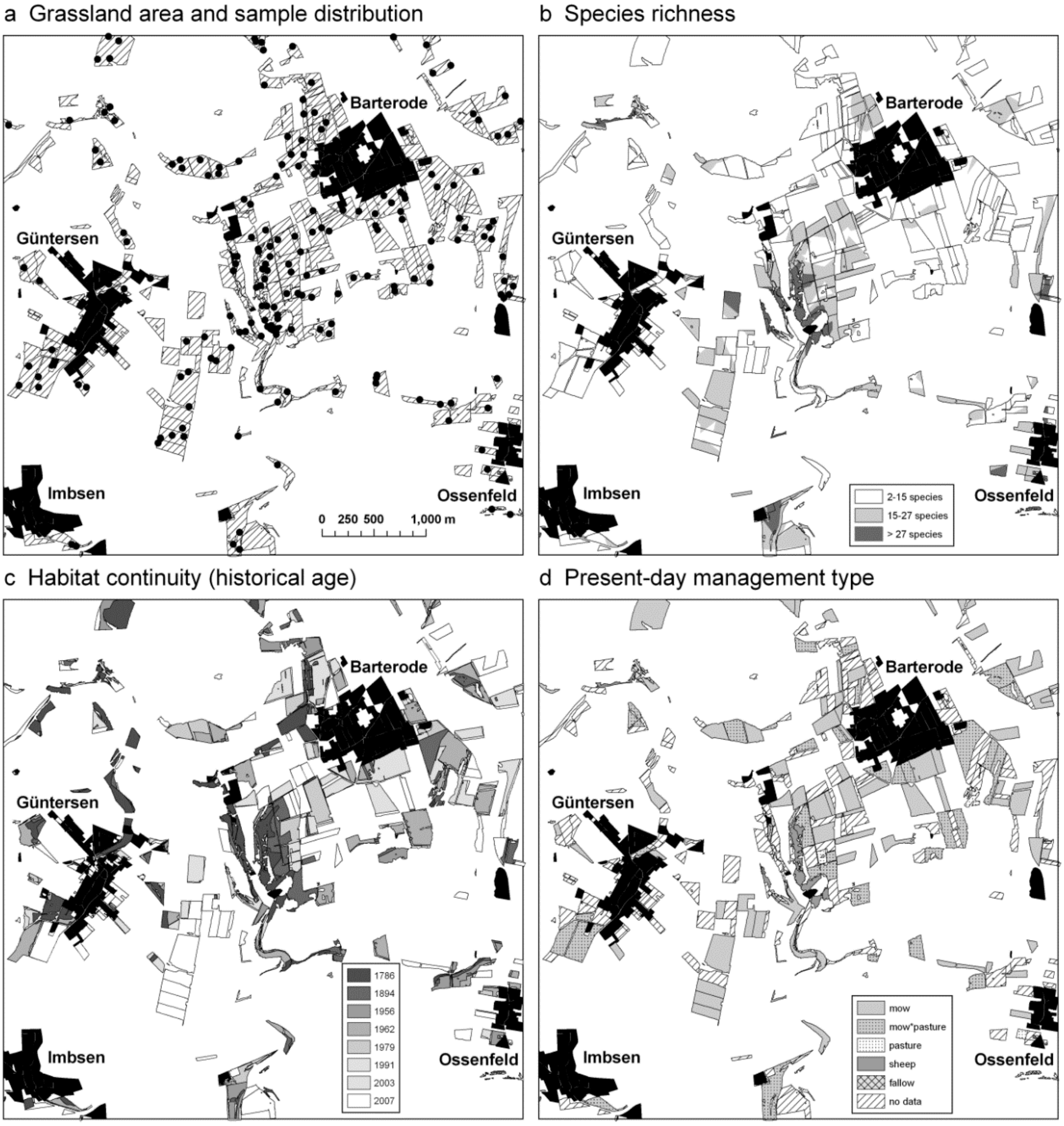


Fig. 1 Study area in southern Lower Saxony, Germany. a) Grassland area (hatched) and distribution of 189 random samples; b) species richness in three classes modelled on the landscape scale; c) habitat continuity (with oldest historical age of 1786); d) present-day management type. Black labelled areas represent settlements. Maps with Transverse Mercator projection, Germany Zone 3 (DHDN).

The grassland communities showed major differences in species-richness. Species-poor grasslands hosted up to 15 species (Fig. 3a, community 2, upper quartile), medium species-rich grasslands up to 27 species and species-rich grasslands hosted over 27 species (Fig. 3a, community 5, lower quartile). Increasing median species richness patterns correlated with decreasing median nutrient conditions and mowing tolerance of plant species (Fig. 3b and 3c). On the landscape scale, species-poor grasslands were most abundant, covering 63% of the total grassland area, followed by medium-rich grasslands, with 31% (Fig. 1b). Species-rich grasslands were limited to 6% of the total grassland area, which is equivalent to 1% of the studied landscape. The model-based spatial distribution of species-richness more or less paralleled with the number of samples assigned to the community clusters, based on random sampling.

A total of 220 vascular plant species were recorded in the grassland samples (see Appendix), which showed a large diversity in pollination traits (Fig. 4a). More than half of them were reliant on cross-pollination, with 68 species being dependent on insect pollination, 53 species on wind pollination, and two species alternatively on insect or wind pollination. Of the 97 species that were additionally able to self-pollinate, 88 species showed traits of insect-dependent cross-pollination. With respect to mean species richness of the grassland communities, wind pollinated species numbered 8.4 (± 2.3 SD) across each of the grassland communities (Fig. 4b). Large differences between communities were found in the proportion of insect pollinated plant species and insect/self-pollinated plant species. These were highly correlated to the overall species richness patterns (*r* = 0.97 ± 0.01, C.I. 95%, *n* = 189). Insect and insect/self-pollinated plants made up around two thirds of the species in the species-rich grassland communities (communities 5 and 6) and more than half of the species in the medium-rich Arrhenatherion community (community 3).

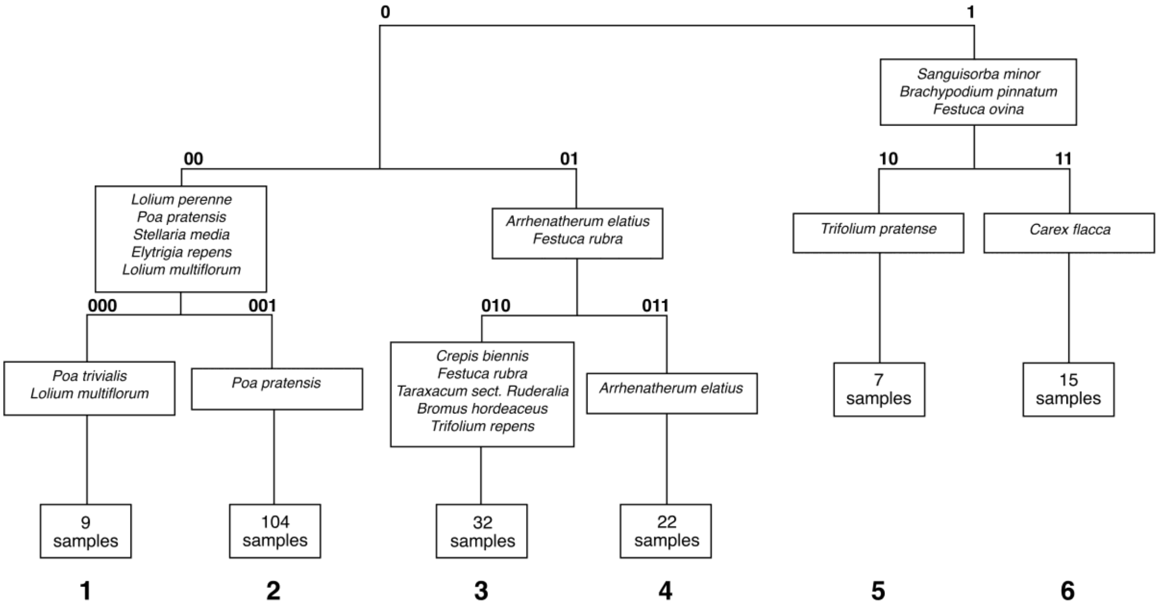


Fig. 2. TWINSPAN analysis resulting in six clusters (Communities 1-6, cp. Table 2).

Table 2 Description of grassland communities. TWINSPAN classification of 189 samples resulted in six clusters (communities 1-6). Assignment to community names follows von Drachenfels (2011); asterisks indicate Natura 2000 habitat types (habitats directive, 92/43/EEC, annexe I).

Community	**Grassland community description**	**No. of samples (*n*)**	**Relative no. of samples (%)**
1	**Sown grasslands**, recently drilled, often treated with herbicides and dominated by highly productive grass species (e.g. *Lolium multiflorum, Poa trivialis)*	9	4.8
2	**Species-poor intensively managed grasslands** (*Cynosurion* communities) dominated by grasses (e.g. *Lolium perenne,, Poa pratensis*) on well drained soils	104	55.0
3	**Mesic grasslands with medium species richness** (*Dauco-Arrhenatheretum typicum)*	32	16.9
4	**Species-poor extensively managed grasslands** (*Arrhenatherion* communities) with dominance of grasses and forbs	22	11.6
5*	**Species-rich, nutrient-poor, extensively managed grasslands** on calcareous substrates (including. *Dauco-Arrhenatheretum brizetosum* and *ranunculetosum bulbosi*); Natura 2000 habitat type 6510	7	3.7
6*	**Semi-natural dry grasslands** on calcareous substrates (*Gentiano-Koelerietum*); Natura 2000 habitat type 6210	15	7.9

Environmental determinants of grassland diversity

With its community composition, species richness and pollination trait components, grassland diversity was largely determined by the investigated environmental (management type, habitat continuity, topography and soil) and spatial variables (Table 3).

After adjusting for the effect of spatial autocorrelation (2% of the spatial component and 3% of the combined spatial and environmental components), environmental variables explained 25% of the total variance in community composition. When isolating for the effects of the single environmental variable groups, grassland community composition was mainly related to soil (7% explained variance), followed by topography (5% explained variance). Habitat continuity and current management were less pronounced, but they imparted a combined additive effect by explaining 9% of the variance in community composition.

Results of the regression analysis of species richness and pollination type composition were very similar. Together, environment and spatial structure explained an extraordinary 69% of the variance in species richness and 62% of the variance in pollination type composition. However, environmental factors were highly correlated to the spatial components (cp. Fig. 1b-d). Thus, only about 39% and 40% of the variance was explained by the environment alone. When examining isolated effects of the environment, soil and topography were not significant. In contrast, current management and habitat continuity were both primary determinants and together they explained 16% of the variance in species richness and 15% of the variance in pollination type composition.

The effects of grassland habitat continuity

The study area became subject to major land use changes from the 1950s (Fig. 5), but since the end of the 18th century, the grassland area had only occupied about 180 ha, i.e. 7% of the landscape. In the late 1950s/early 1960s, the grassland area rapidly increased and it more than doubled by 2007 to some 394 ha. Thus, the study area represented an enriched upland grassland landscape.

Species richness, classified by habitat continuity, indicated no consistent patterns, but extant grasslands dating from 1956/1962 and young grasslands were mostly species-poor (Fig. 3d).

Species-rich hay meadows and semi-natural grasslands were restricted to more than 100 year old grassland sites (Fig. 6a). The majority of medium-rich hay meadows were less than 20 years old. However, species-poor grassland communities were distributed over sites of all ages, including old intensified grassland sites, grasslands that had been intensively managed since the 1950s (even those partly ploughed and re-sown), and intensively or extensively managed young grasslands. The restriction of species-rich grassland types to old sites (>100 years) and the predominance of medium-rich grassland types on young sites (<30 years) is consistent with the observation that those grasslands with habitat continuity since the 1950s to 1970s were always the most intensively managed and composed of species with the highest mowing tolerance (Fig. 3f).

Table 3 Results of (partial) CCA for grassland community composition, and of (partial) multiple linear regression analyses for grassland species richness and grassland species pollination types, adjusted for the spatial component (SP) and isolating the effect of current management type (M), grassland age (A), topography (T), and soil (S) as environmental variables (cp. Table 1).

Expl. Variables	**Covariables**	**Eigenv. / mult. R^2**	**var (%)**	**F-statistics**	***p*-value**
Community composition					
M, A, T, S	SP	2.256	25.0	1.934	0.0001
SP	M, A, T, S	0.131	1.5	1.631	0.0001
M, A, T, S	-	2.562	28.4	2.179	0.0001
SP	-	0.438	4.9	4.748	0.0001
M, A, T, S, SP	-	2.693	29.9	2.160	0.0001
M	A, T, S, SP	0.356	4.0	2.215	0.0001
A	M, T, S, SP	0.375	4.2	1.555	0.0001
M, A	T, S, SP	0.778	8.6	1.934	0.0001
T	M, A, S, SP	0.480	5.3	1.490	0.0104
S	M, A, T, SP	0.625	6.9	1.412	0.0001
Species richness					
M, A, T, S	SP	0.404	40.4	7.078	0.0001
SP	M, A, T, S	0.007	-	1.791	0.1653
M, A, T, S	-	0.684	68.4	11.853	0.0001
SP	-	0.287	28.7	37.346	0.0001
M, A, T, S, SP	-	0.691	69.1	11.314	0.0001
M	A, T, S, SP	0.099	9.9	12.512	0.0001
A	M, T, S, SP	0.038	3.8	3.226	0.0072
M, A	T, S, SP	0.157	15.7	7.992	0.0001
T	M, A, S, SP	0.023	-	1.447	0.1909
S	M, A, T, SP	0.025	-	1.133	0.3428
Pollination					
M, A, T, S	SP	0.393	39.3	5.629	0.0001
SP	M, A, T, S	0.013	1.3	2.626	0.0332
M, A, T, S	-	0.610	61.0	8.566	0.0001
SP	-	0.230	23.0	27.744	0.0001
M, A, T, S, SP	-	0.622	62.2	8.347	0.0001
M	A, T, S, SP	0.079	7.9	8.247	0.0001
A	M, T, S, SP	0.050	5.0	3.433	0.0002
M, A	T, S, SP	0.146	14.6	6.068	0.0001
T	M, A, S, SP	0.022	-	1.168	0.2898
S	M, A, T, SP	0.040	-	1.518	0.0618

Expl. variables, explanatory variables ; Eigenv., sum of all canonical eigenvalues (CCA; total inertia in community composition = 9.008); mult. R^2, multiple R-squared (regression analysis; total variance = 1.000); var (%), percentage of explained variance; F-statistics, F-ratio for the test of significance of all canonical axes (test on the trace); *p*-value, corresponding probability value obtained by Monte-Carlo-permutation test (9999 permutations).

The effects of current grassland management

Grassland species richness was strongly related to the current management regime, which was reflected in the relationship between Ellenberg IV values and nutrients (Fig. 3g-h). Grasslands grazed by sheep were the most nutrient-poor and species-rich. Sheep grazing was strongly correlated with environmental contracting ($r = 0.93 \pm 0.04$, C.I. 95%, $n = 189$). Therefore, grassland communities managed under this scheme were exclusively semi-natural or species-rich hay meadows (Fig. 6b). Both sheep-grazed grasslands and fallows were composed of species of low mowing tolerance (Fig. 3i). Although the majority of fallows still counted towards the semi-natural grassland community, they were slightly less species-rich, which indicated an incipient diversity loss (Fig. 3g).

In contrast, hay meadows, pastures (grazed by cattle and/or horses) and grasslands with combined management were all nutrient-rich, species-poor and composed of species with high mowing tolerance (Fig. 3g-i). The vast majority of pastures and combined hay meadows/pastures were intensively managed Cynosurion communities (Fig. 6b). Hay meadows showed a larger variety of different community types. Of the investigated mown grasslands, 56% belonged to the species-poor Cynosurion communities and sown grasslands, 44% of which belonged mainly to the medium species-rich Arrhenatherion community type (community 3), but also of the species-poor and species-rich variants with lower mowing frequencies (communities 4 and 5, cp. Fig. 3c).

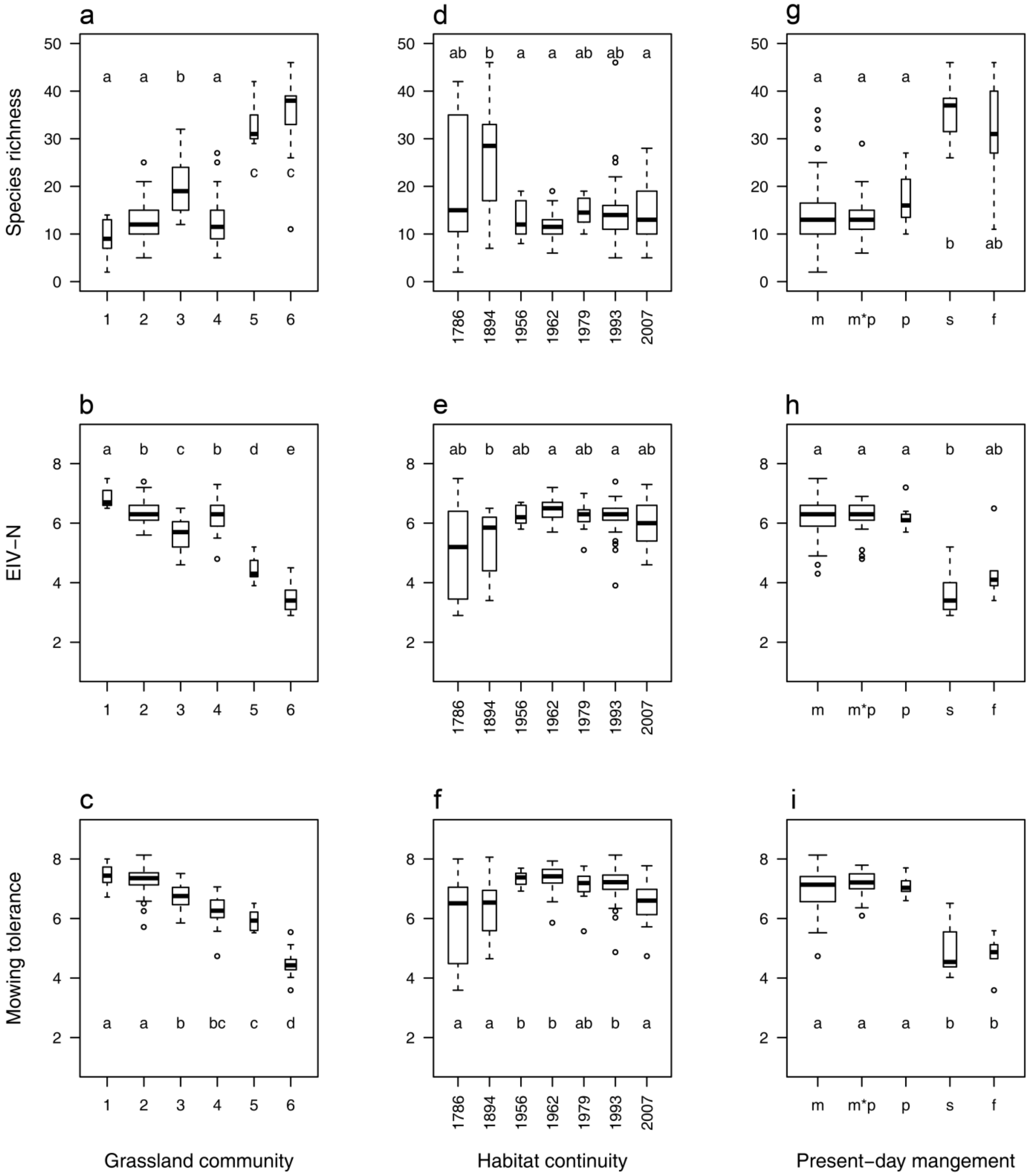


Fig. 3 Differences in species richness, soil fertility (EIV-N) and mowing tolerance between different grassland communities (cp. Table 2), time periods of habitat continuity and categories of present-day management (m, mown; m*p = mown and pastured; p, pastured; s, sheep; f, fallow). Boxes are drawn with widths proportional to the square-roots of the number of observations in the groups; different letters indicate significant differences between groups ($p \leq 0.05$ by non-parametric Behrens-Fisher test).

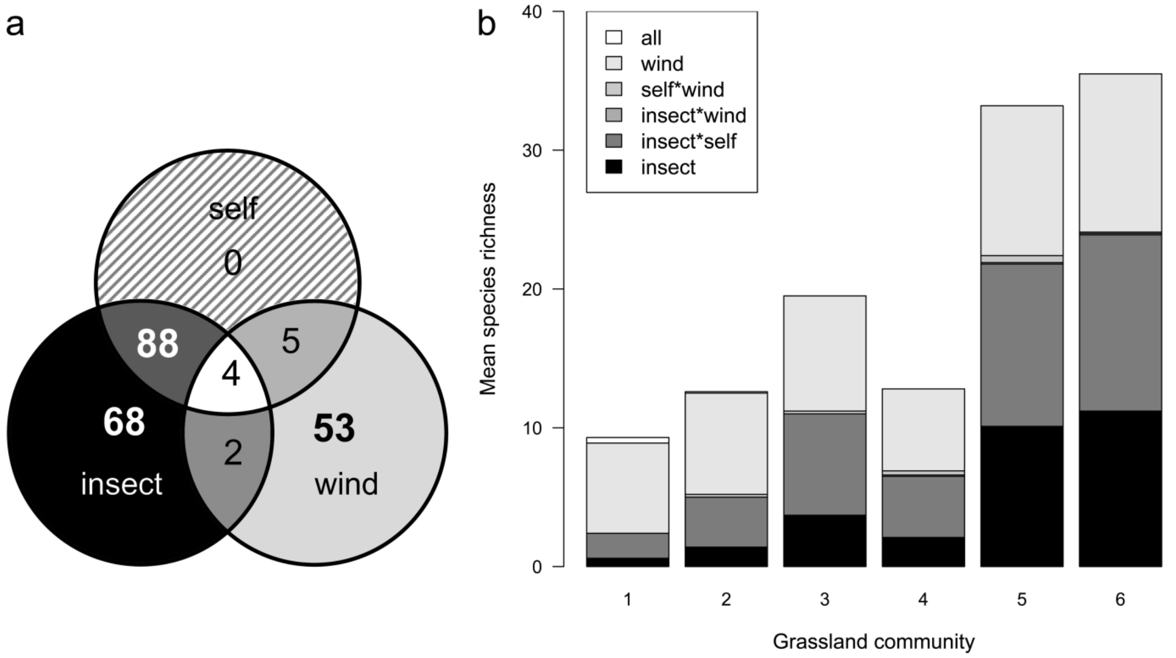


Fig. 4 Pollination types in grassland plant species of the study area. (a) Absolute number of insect, wind and/or self-pollinated plant species in the total of 220 species. (b) Proportion of pollination types related to mean species richness of six grassland communities.

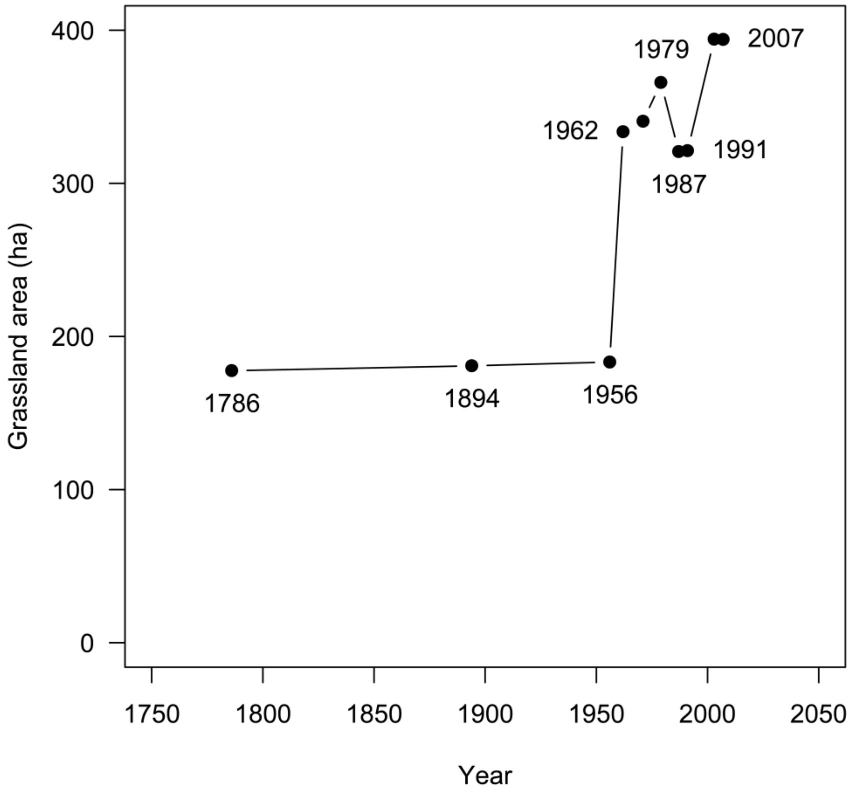
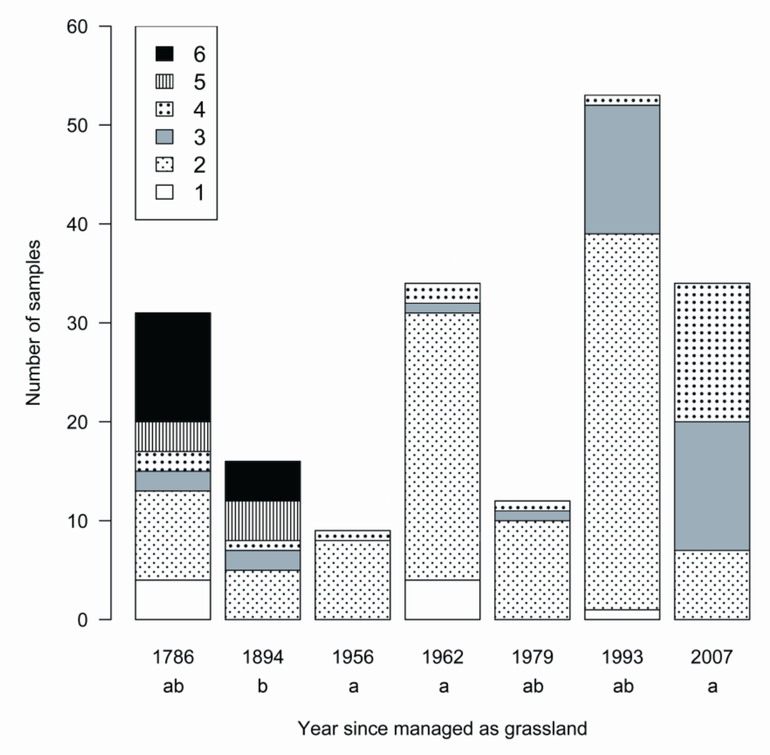


Fig. 5 Changes in total grassland area in the study area from 1786 to 2007

a)



b)

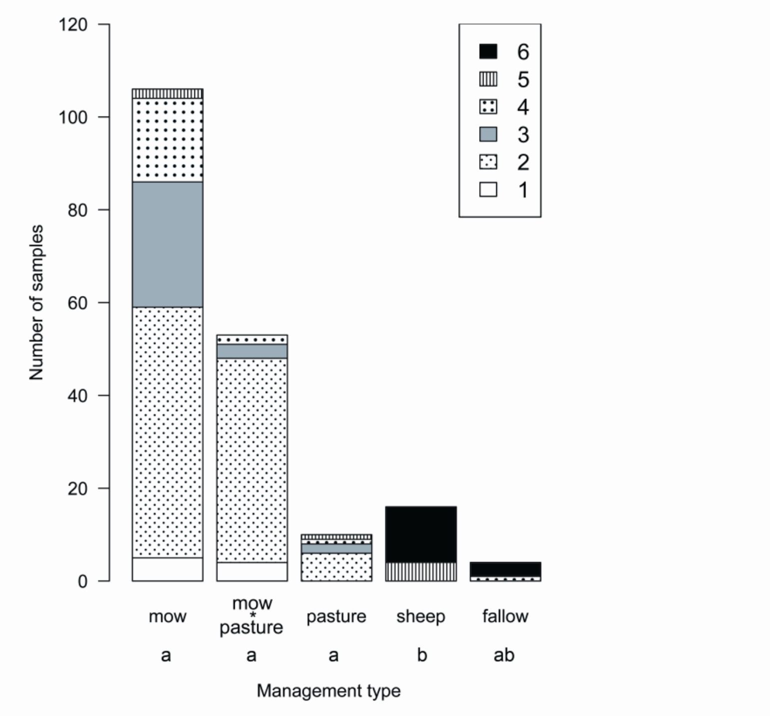


Fig. 6 Distribution of grassland communities (a) by grassland continuity (reference ages), and (b) by current management types. Different letters indicate significant differences between groups ($p \leq 0.05$ by non-parametric Behrens-Fisher test; cp. Fig. 3)

Discussion

Evaluating grassland diversity on the landscape scale

In order to understand the effects of agricultural land use practices with respect to biodiversity conservation, assessment should be undertaken at the landscape level (Tscharntke et al. 2005). Our comprehensive approach linked plot-scale studies to the landscape scale, which allowed us to undertake a regional qualitative and quantitative evaluation of grassland diversity.

We found a wide range of poor to extremely species-rich grassland types under mesic to dry site conditions. About two thirds of the grassland area was composed of species-poor, intensively managed Cynosurion and sown grassland communities. However, grasslands with high species richness (>27 species) that are of high nature conservation value at the European level were limited to 6% of the total grassland area, which amounts to only 1% of the landscape area. The two identified species-rich communities listed in Annex I of the European Habitat Directive (codes 6120 and 6510) are completely dependent on specific agricultural management (Halada et al. 2011). In the context of assessing High Nature Value (HNV) farmland for environmental impact evaluation of rural areas in the European Union (Paracchini et al. 2008), Sullivan et al. (2010) found that besides the rare semi-natural grassland relicts, semi-improved grasslands are important in the lowlands of Ireland. Based on their species composition and richness values, most of the medium-rich Arrhenatherion grasslands, which covered 5% of our studied landscape, may be classified as HNV farmland in Germany (PAN et al. 2011).

Land use intensification and losses in insect-pollinated plant species

We found major differences in pollination type composition of the six grassland communities (Fig. 4b), and we conclude that variations result from differences in grassland management (mowing, nutrient supply, Fig. 3b-c; Table 3). The intensively managed grasslands were mostly composed of wind-pollinated species (mainly grasses), which can additionally persist and spread by clonal growth. In comparison, semi-natural grasslands are usually dominated by flowering insect-pollinated herbs. Grasses like *Brachypodium pinnatum* that have a shallow root system producing several cohorts of shoots in a year may become dominant if semi-natural grasslands change to more mesic conditions (Bobbink et al. 1998; Bornkamm 2006). Abandonment of mesic *Arrhenatherion* grasslands also causes large losses in species richness and changes to forbs with large phytomass production and vegetative spreading of some highly competitive grass species, later followed by shrub encroachment (Dierschke and Briemle 2002).

Trends of an increase of wind-pollinated species in modern intensified grasslands in comparison to their extensively used (wet) meadow equivalents from 50 years ago were also described by Wesche et al. (2012). We observed a parallel decline in insect-pollinated plants (mainly herbs) and overall median species richness in the communities along the gradient of increasing land use intensity. Corresponding negative trends in insect-pollinated plants and pollinator populations were documented in other Central European landscapes (Biesmeijer et al. 2006). An impoverishment of flowering herb diversity may have strong effects on the diversity and species composition of specialised flower visitor groups (*Apidae, Lepidoptera*), but little effect on unspecialised flower visitors (Weiner et al. 2011). In our studied landscape, the large proportion of plant species exclusively dependent on pollinators for reproduction was limited to communities with high nature conservation value, but which are limited to only 1% of the landscape, and to HNV farmland. In such fragmented habitats, and in accordingly small plant populations, insufficient pollination is the most prominent cause of reproductive impairment (Aguilar et al. 2006). Because semi-natural and extensively used grasslands were formerly common Central European habitat types (Poschlod et al. 2005; Ellenberg and Leuschner 2010), we expect that the majority of the pollinator-dependent plant species are ‘new rare’ species (Becker et al. 2011). Most of the insect-pollinated plant species occurring in intensively managed grasslands of our study area additionally have the ability to do self-pollination. Following the results of Weiner et al. (2011), we expect that, where applicable, such species are pollinated by only a few or unspecialised flower visitors. We conclude for our studied landscape that the abundance and population viability of strictly pollinator-dependent plant species may be affected by pollen limitation, which may result in inbreeding depression (Becker et al. 2011). Retrospectively, this may have already altered both plant community composition with further within-community species losses (e.g. Isselstein 2003), and plant-flower visitor interactions, with losses of highly specialised insect species within pollinator networks (e.g. Fründ et al. 2010).

The effect of nutrient input on grassland community composition and related within-community richness patterns

Grassland community composition was mainly related to soil factors that characterise the different siliceous and calcareous substrates in the study area (Table 3). Moreover, Ellenberg IV-N (Fig. 3b) is a general indicator for soil fertility, which often correlates with phytomass production (Hill and Carey 1997; Schaffers and Sykora 2000), and we found that median grassland community richness strongly correlated with EIV-N values. Of particular note was the high within-alliance variation recorded in species richness in the Arrhenatherion grasslands, which resulted in three different communities (cp. Fig. 3a, communities 3-5). This decline in species richness from species-rich to species-poor Arrhenatherion grasslands correlated with an increase in nutrient supply, as indicated by the EIV for nutrient conditions (cp. Fig. 3b). The negative effect of nitrogen input on the diversity of European temperate grasslands has been discussed in several case studies and cross-regional reviews (Ellenberg and Leuschner 2010). It has also been demonstrated that species diversity in calcareous grasslands decreases rapidly with increasing nitrogen supply (Jacquemyn et al. 2003), and Hegg et al. (1992) found that even a single application of fertilizer can cause a reduction in species richness and change in the composition of species. The most negative effects on the taxonomic diversity of grasslands can therefore be attributed to the direct application of fertilisers, as well as the atmospheric deposition of nitrogen (Bobbink et al. 1998, 2010; Stevens et al. 2011). One of the most important abiotic constraints to grassland restoration is high residual soil fertility associated with repeated fertiliser application (Walker et al. 2004). Considering these facts in addition to our findings on the distribution of grassland communities over the habitats continuity classes (Fig. 6a), we conclude that: First, grasslands of the species-rich Arrhenatherion community 5, which occurred exclusively on old sites (>100 years), emerged from semi-natural grasslands that were improved by nitrogen deposition, either from direct minor application or by atmospheric deposition from nearby fertilised areas. Second, grasslands of the medium species-rich Arrhenatherion community 3, which occurred mostly on young sites (<30 years), were preferentially installed on less productive ex-arable fields on calcareous substrates. Third, the grand proportion of the species-poor Arrhenatherion community 4 occurred on the youngest sites (<15 years old), and the species composition indicated slightly higher median soil nitrogen content, but also a lower mowing tolerance than community 3. Both could be related to a more extensive management regime, and previous studies showed that the most efficient to counter the negative effects of nitrogen supply was using grazing or mowing management (Köhler et al. 2001; Jacquemyn et al. 2003; Walker et al. 2004). In addition, the creation of diverse grassland communities on ex-arable land can be limited by the lack of seeds of desirable species in close proximity to one another (Pywell et al. 2002).

Past and current management analysis and conclusions on grassland restoration potential

Species-rich grassland communities were only found on grassland sites with >100 years of habitat continuity that can be considered remnants of formerly widely distributed grassland types. Semi-natural grassland remnants have to be conserved by traditional extensive sheep grazing (Poschlod et al. 2005), and these management practices were re-established in the study area by nature conservation contracting. The high correlation of the occurrence of conservation valuable grasslands, sheep grazing and nature conservation contracting contrasts to the largely species-poor, intensively managed agricultural grasslands in the surroundings. A general trend has been observed in Europe that the floristic gap between agricultural grasslands and grasslands in nature reserves is widening every year (de Snoo et al. 2012).

However, conserving what is left is more effective than getting back what was lost (Kleijn et al. 2011). We therefore assume that, besides high residual soil fertility and pollinator impairment (see above discussions), seed limitation is the most prominent factor restricting restoration efforts (Donath et al. 2007). The natural enrichment of grasslands in formerly intensively managed landscapes through traditional, extensive farming practices – as promoted by agri-environmental schemes – has been limited by a lack of seed availability (Pywell et al. 2002; Blomqvist et al. 2009), while sowing a diverse mix of wildflowers results in a stable, perennial plant community that, through functional enrichment, further supports pollinator and herbivore species (Pywell et al. 2011). However, Öster et al. (2009) found that species richness and similarity to semi-natural grasslands of re-established grasslands on formerly arable fields were still lower than in semi-natural grasslands, even after more than 50 years of grazing. These observations are supported by our results. Medium-rich Arrhenatherion grasslands have primarily been established on ex-arable fields on less productive sites in the course of the European Union's 'set-aside policy' since the 1980s (Henle et al. 2008). In our study, these young grasslands shared more in common with the intensively managed Cynosurion grasslands than the semi-improved, species-rich Arrhenatherion grasslands (see Fig. 2); however, they contributed to an overall ecological improvement of the HNV farmland portion at the landscape scale.

We conclude that conserving species-rich and semi-natural grasslands by traditional, extensive management is of primary importance. In a landscape such as the study area, which still supports high levels of biodiversity in remnants of high nature conservation value grasslands, conservation initiatives would most (cost-)effectively be implemented in extensively farmed areas (Kleijn et al. 2009). In addition, in order to improve the ecological quality of grasslands at the landscape scale, the most effective option would be to establish new grasslands on less productive sites in the proximate surroundings of species-rich grasslands using diverse autochthonous mixtures, followed by appropriate extensive management techniques. Such measures enhance the probability of seed arrival (Wessels et al. 2008; Wessels-de Wit and Schwabe 2010; Schmiede et al. 2013) and provide a buffer to protect the most valuable sites from deposition of nitrogen of neighbouring intensively managed agricultural grasslands. Such a challenging approach, as promoted by de Snoo et al. (2012), would enhance the interaction between nature reserves and agricultural grasslands.

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Appendix

List of the 220 grassland study species and their attributes, including the main occurrence in community 1-6 (see Fig. 2, Table 2), pollination type (i, insect-pollinated; w, wind-pollinated; s, self-pollinated) and Ellenberg indicator value N (EIV-N).

Species	**Main occurrence in grassland community**	**Pollination type**	**EIV-N**
Acer campestre	5	i, w	6
Acer sp.	6	i, w	?
Achillea millefolium	5	i	5
Acinos arvensis	6	i	1
Aegopodium podagraria	4	i	8
Agrimonia eupatoria	6	i	4
Agrostis canina	3	w	2
Agrostis capillaris	1	w	4
Agrostis gigantea	4	w	6
Ajuga genevensis	6	i	2
Ajuga reptans	4	i	6
Allium oleraceum	5	i	4
Allium sp.	4	i	?
Alopecurus geniculatus	2	w	7
Alopecurus myosuroides	2	w	6
Alopecurus pratensis	1	w	7
Anthemis tinctoria	6	i	4
Anthoxanthum odoratum	3	w	x
Anthriscus sylvestris	5	i	8
Arenaria serpyllifolia	5	i, s	x
Arrhenatherum elatius	4, 5	w	7
Astragalus glycyphyllos	5	i	3
Barbarea vulgaris	2	i, s	6
Bellis perennis	3	i, w, s	6
Brachypodium pinnatum	6	w	4
Briza media	6	w	2
Bromus erectus	6	w	3
Bromus hordeaceus	3	w	3
Bromus sterilis	5	w	5
Calamagrostis epigejos	5	w	6
Campanula rapunculoides	6	i	4
Campanula rapunculus	3	i	4
Campanula rotundifolia	5	i	2
Campanula sp.	2	i	?
Capsella bursa-pastoris	2	i, s	6
Cardamine pratensis	3	i, s	x

Carex caryophyllea	6	w	2
Carex flacca	6	w	x
Carex hirta	3	w	5
Carlina vulgaris	6	i, s	3
Centaurea jacea	6	i, s	x
Centaurea scabiosa	5	i, s	4
Cerastium arvense	5	i, s	4
Cerastium glomeratum	5	i, s	5
Cerastium holosteoides	5	i, s	5
Cerastium sp.	2	i, s	?
Chaerophyllum temulum	4	i	8
Chrysosplenium alternifolium	3	i, s	5
Cichorium intybus	3	i, s	5
Cirsium acaule	6	i, s	2
Cirsium arvense	3	i, s	7
Cirsium vulgare	4	i, s	8
Convolvulus arvensis	5	i	x
Cornus sanguinea	6	i, s	x
Corylus avellana	6	w	5
Crataegus laevigata	6	i	5
Crataegus sp.	3	i	?
Crepis biennis	3	i, s	5
Crepis tectorum	3	i, s	6
Cruciata laevipes	5	i, s	7
Cynosurus cristatus	3	w	4
Dactylis glomerata	5	w	6
Daucus carota	6	i, s	4
Deschampsia cespitosa	4	w	3
Echium vulgare	6	i	4
Elytrigia repens	1	w	7
Epilobium lanceolatum	2	i, s	3
Epilobium parviflorum	4	i, s	6
Epilobium sp.	4	i, s	?
Equisetum arvense	4	w	3
Erophila verna	5	i, s	2
Fagus sylvatica	4	w	x
Fallopia convolvulus	2	i, w, s	6
Festuca ovina	5	w	1
Festuca pratensis	3	w	6
Festuca rubra	5	w	x
Fragaria vesca	3	i, s	6
Fragaria viridis	6	i, s	3
Fraxinus excelsior	6	w	7
Galium aparine	4	i, s	8

Galium mollugo	5	i, s	?
Galium pumilum	6	i, s	2
Galium spurium	4	i, s	5
Galium verum	6	i, s	3
Geranium columbinum	3	i, s	7
Geranium dissectum	3	i, s	5
Geranium molle	5	i, s	4
Geranium pusillum	2	i, s	7
Geranium robertianum	2	i, s	7
Geum urbanum	4	i	7
Glechoma hederacea	4	i	7
Gymnadenia conopsea	6	i	3
Helictotrichon pratense	6	w	2
Helictotrichon pubescens	4	w	4
Heracleum sphondylium	3	i, s	8
Hieracium aurantiacum	3	i, s	2
Hieracium caespitosum	3	i, s	3
Hieracium murorum	6	i, s	4
Hieracium pilosella	3	i, s	2
Hieracium piloselloides	6	i, s	2
Hippocrepis comosa	6	i	2
Holcus lanatus	4	w	4
Hypericum perforatum	5	i, s	3
Hypochaeris radicata	4	i, s	3
Impatiens parviflora	4	i	6
Inula conyzae	6	i, s	3
Juncus inflexus	3	w	4
Juniperus communis	6	w	x
Knautia arvensis	6	i	4
Koeleria pyramidata	6	w	2
Lamium album	3	i	9
Lamium maculatum	4	i	8
Lathyrus pratensis	5	i	6
Lathyrus sylvestris	4	i	2
Leontodon hispidus	6	i, s	6
Lepidium campestre	5	i, s	6
Leucanthemum ircutianum	6	i, s	3
Linum catharticum	5	i, s	2
Listera ovata	6	i	7
Lolium multiflorum	1	w	6
Lolium perenne	2	w	7
Lotus corniculatus	6	i	3
Lotus corniculatus agg.	6	i	?
Luzula campestris	5	w	2

Malus domestica	6	i	?
Matricaria recutita	2	i, s	5
Medicago falcata	5	i	3
Medicago lupulina	5	i	x
Medicago x varia	4	i	?
Melilotus altissimus	5	i	7
Myosotis arvensis	4	i	6
Myosotis sylvatica	4	i	7
Ononis spinosa	6	i	3
Origanum vulgare	6	i	3
Papaver rhoeas	2	i	6
Persicaria maculosa	1	i, w, s	7
Phleum pratense	2	w	6
Picris hieracioides	6	i, s	4
Pimpinella major	6	i, s	7
Pimpinella saxifraga	5	i, s	2
Pinus nigra	6	w	2
Plantago lanceolata	5	w	x
Plantago major	2	w	6
Plantago media	6	w	3
Poa angustifolia	5	w	3
Poa annua	2	w	8
Poa pratensis	2	w	6
Poa trivialis	1	w	7
Polygala comosa	6	i	2
Polygonum aviculare	1	i, w, s	6
Potentilla anserina	2	i	7
Potentilla tabernaemontani	6	i	2
Primula elatior	3	i	7
Primula veris	6	i	3
Prunella vulgaris	6	i	x
Prunus domestica	5	i	?
Prunus sp.	5	i	?
Prunus spinosa	6	i, s	x
Quercus robur	6	w	x
Ranunculus acris	3	i, s	x
Ranunculus auricomus agg.	2	i	x
Ranunculus bulbosus	5	i, s	3
Ranunculus lanuginosus	3	i, s	7
Ranunculus repens	1	i, s	x
Rhinanthus alectorolophus	4	i, s	3
Rhinanthus minor	3	i, s	3
Roegneria canina	5	w	8
Rosa sp.	6	i, s	?

Rubus sp.	6	i	?
Rumex acetosa	5	w, s	6
Rumex conglomeratus	2	w, s	8
Rumex crispus	3	w, s	5
Rumex obtusifolius	3	w, s	9
Rumex sanguineus	2	w, s	7
Rumex sp.	5	w	?
Sanguisorba minor	5, 6	w	2
Scabiosa columbaria	6	i	3
Sedum acre	6	i, s	1
Sedum sexangulare	6	i, s	1
Sedum telephium	3	i, s	x
Senecio erucifolius	4	i, s	4
Senecio jacobaea	3	i, s	5
Sisymbrium officinale	2	i, s	7
Sonchus asper	2	i, s	7
Sonchus oleraceus	6	i, s	8
Sorbus aucuparia	3	i, s	x
Stellaria media	1	i, s	8
Symphytum officinale	5	i	8
Taraxacum sect. *Celtica*	6	i, s	3
Taraxacum sect. *Erythrosperma*	5	i, s	2
Taraxacum sect. *Ruderalia*	3	i, s	7
Thlaspi perfoliatum	6	i, s	2
Thymus pulegioides	6	i	1
Tragopogon pratensis	5	i, s	6
Trifolium campestre	5	i	3
Trifolium dubium	5	i	5
Trifolium hybridum	3	i	5
Trifolium pratense	5	i	x
Trifolium repens	5	i	6
Tripleurospermum perforatum	2	i	6
Trisetum flavescens	3	w	5
Triticum aestivum	2	w	?
Tussilago farfara	3	i, s	x
Urtica dioica	4	w	8
Verbascum sp.	6	i, s	?
Veronica arvensis	5	i, s	x
Veronica chamaedrys	5	i, s	x
Veronica officinalis	3	i, s	4
Veronica persica	2	i, s	7
Veronica serpyllifolia	1	i, s	x
Veronica verna	3	i, s	1
Viburnum opulus	4	i, s	6

Vicia angustifolia	3	i	x
Vicia cracca	6	i	x
Vicia hirsuta	3	i	4
Vicia sepium	2	i	5
Vicia sp.	3	i	?
Vicia tetrasperma	4	i	5
Viola arvensis	2	i, s	x
Viola hirta	6	i, s	2

CHAPTER

6

Synopsis

Changes in the agricultural landscape and impacts on Central European grasslands

In most Central European regions, the landscape is characterized by agricultural activities with highest rates of transformation since World War II. The application of fertilizers and pesticides, as well as the frequency of cutting and/or mowing on grasslands increased dramatically. Additionally, a large number of wet or moist sites have been drained or became abandoned. This abandonment of land is a particular problem on marginal sites, e.g. steep hillside situations were cultivation is difficult and not rentable. The present study quantified landscape and vegetation changes from the 1950/60s, before agricultural intensification started, until 2008 in an over-regional approach in order to obtain representative and significant results.

In chapter two it was found that strong changes occurred in the extent of formerly wide-spread floodplain meadows during the last five to six decades. More than 80% of the unprotected wet and species-rich mesic meadows were lost and substituted either by more intensive land use types, such as cropland or species-poor, intensively managed grasslands, or by land use types indicating lower management intensity like marshes, fallows and shrublands. Both grassland types showed some similar trends, e.g. the substitution by intensively managed grasslands, but differences could also be detected. The formerly widespread species-rich mesic meadows were twice as often substituted by arable fields than wet meadows whereas the latter were twice as often substituted by fallows or shrublands indicating a significantly higher cost of land improvement of such wet locations. Overall, the grassland area (all types) decreased by 50%.

In chapter five a contrasting development was found in a typical upland area where the area of grassland doubled since the 1950s. However, looking at today’s quality of the grassland revealed that just a small part of it is ecologically valuable in terms of species diversity and species composition.

In addition to these direct changes in landscape composition due to grassland losses or management intensifications there are often further indirect influences on the remaining grassland sites, such as fragmentation, isolation and changes in the length of habitat continuity. This could be a potential threat, especially for grassland specialists (e.g. Winter et al. 2008; Saar et al. 2012; Münzbergovà et al 2013).

Fragmentation – a question of the observation scale

To analyse habitat fragmentation and its effect on plant species richness, it is necessary to determine the scale of observation. To detect land use changes, the fragmentation was investigated at different grassland habitat levels (scales). In study one, I analysed fragmentation at two different levels: At first wet respectively species-rich mesic meadows separately and secondly a combination of both (floodplain meadows). In study three, I additionally calculated the fragmentation on a third scale, the joint consideration of all grasslands in the broader sense. Many species (grassland generalists) with broad ecological amplitude are able to occur in different grassland types and are therefore only affected by fragmentation in the sum of all grassland types. Other grassland plants are adapted to specific conditions, e.g. moist conditions (see chapter four), and are therefore influenced by the fragmentation level of this specific grassland type. Hence, the scale of observation depends on the amplitude of site conditions which are tolerated by the investigated plant species.

The increase in area of individual grasslands patches caused by consolidation and removal of hedgerows and other structures did not lead to a lower fragmentation level for those specific grassland species. The newly established grasslands are more intensivly used and secondly managed more uniformly (mowing times and frequency), so that they are mostly not suitable as a habitat for the majority of grassland specialists on the long term. The grassland areas that today harbour a lot of characteristic grassland species and grassland specialists were mostly found to be fragmented. Only small remnants remained in isolated locations. This holds for calcareous grasslands on steep slopes as well as for floodplain meadows on sites which could only be cultivated in a complicated and unprofitable way (Dolek and Geyer 2002).

Similar trends and problems were discussed for the arable flora, where the increase in area of cropland led to widespread intensifications and decreasing areas of field margins. Consequently, the species number and abundance of most plants of the arable flora decreased rapidly and some species could only be found in field margins where management pressure is rather low (Fried et al. 2009; Kohlbrecher et al. 2012; Meyer et al. 2013). The reduction of suitable niches (due to herbicids, poor light conditions due to high coverage of crops) in the field center and declining edge structures which can act as a habitat refugium are the main threat for arable flora (Meyer et al. submitted a) . Even land set aside on marginal soils are a threath for arable plants in some regions (Henle et al. 2008; Storkey et al. 2012). The combination of these effects has led to small and isolated populations of arable plants.

Brütting et al. (2012) found a weak trend towards low genetic structure in threatened species of the arable flora. Recently Meyer et al. (submitted b) found a very low genetic diversity for the arable flora in general. These examples show that fragmentation and isolation affect plant species negatively even if they still persist in the cultural landscape.

Fragmentation - Overall study results and consequences for extinction debt

A special characteristic of the study sites used in this survey (except study site Weser) was the contiguous and more or less non-fragmented grassland area in the 1950/60s whereas other study sites investigated in the search for fragmentation effect were more or less fragmented in the past (e.g. Lindborg and Eriksson 2004; Helm et al. 2006; Adriaens et al. 2006). Hence, the initial situation in the analysis presented here was more or less identical and mostly non-fragmented over all study sites. In chapter two and four we found a strong increase of grassland fragmentation on different spatial levels. This holds for the consideration of wet and species-rich mesic meadows, for floodplain meadows (combination of wet and species-rich mesic meadows) as well as for the grasslands in a broader sense. As mentioned above, fragmentation has often been identified as a driver of species decline. A lot of grassland species are perennials and so they can persist periods with non-optimal conditions (Eriksson 1996; Eriksson and Ehrlen 2001). Hence, time lags between changes and extinction can occur (extinction debt, see Tilmann et al. 1994).

In order to detect such an extinction debt, past landscape structures and recent plant species diversity were linked and tested for relationships (chapter four). No significant correlation and therefore no evidence for an extinction debt in contrast to other studies (Lindborg and Eriksson 2004; Helm et al. 2006) were found. However, there is evidence that recent diversity is better explained by recent landscape patterns (Adriaens et al. 2006; Cousins et al 2007). Weak evidence for an effect of recent fragmentation (isolation of meadow patches) on species diversity is given by the results of our analysis of fragmentation at the local scale (chapter four). The recent distance between meadow patches was significantly negatively correlated with the number of characteristic meadow species per plot (overall effect; mixed model analysis). Separated analyses performed for optimal and suboptimal habitats based on correlation analysis revealed interesting results: the significant effect of distance to the nearest neighbour seems to have a greater impact in the suboptimal habitats, which could be interpretated as evidence for a sink habitat with surrounding source habitats (optimal) of characteristic meadow plant species. Only a minor effect of distance between the optimal habitas was found on the number of characteristic species. An analysis based on mixed models detected no evidence for a pronounced difference between the two habitat categories in their response to the metrics (interaction terms not significant in all cases) and hence differences between optimal and suboptimal habitat are only trends.

The missing influence of fragmentation and patch size and the weak influence of isolation on the species richness of characteristic meadow plants found here is in accordance with several other studies. We can also confirm the low or unclear dependency of plant species diversity on the size and isolation of grassland fragments in fragmented cultural landscapes reported in the same studies (Eriksson et al. 1995; Kiviniemi and Eriksson 2002; Herrera and Laterra 2011; Öckinger et al. 2012).

The strong decline of short-lived vascular plant species found in chapter three is in agreement with the findings for isolated grasslands described by Lindborg (2007) and Saar et al. (2012). Such high extinction rates of short-lived plants could be evidence for an extinction debt also affecting perennial grassland species (Cousins 2009; Lindborg 2007; Kuussaari et al. 2009; Johannsson et al. 2011). Land-use intensification over time resulted in the dominance of a few productive grassland species that built a permanently closed sward (Dierschke and Briemle 2002). Patches of bare soil that may serve as safe sites for establishment are becoming rare, which is a problem for short-lived species but also for small perennial plants or other weak competitors (Walker et al. 2009).

Due to time lags in species' responses the detection of fragmentation effects is often difficult (Kuussaari et al. 2009). Hence, it was distinguished between optimal and suboptimal habitats (see chapter four). The low number of characteristic meadow species in today's suboptimal vegetation units (mostly optimal habitats in the 1950/60s) indicate, that the extinction debt is already paid in these areas, mainly by changed site conditions and management regimes (mowing frequency, ploughing and resowing, fertilisation). The situation for the remaining optimal habitats appears somewhat different. Today, we can still find a lot of characteristic meadow species in remnants, although the number declined during the last decades. Cousins (2009) pointed out that studies where less than 10% of former grasslands remained could not find any evidence for an extinction debt. The results presented in chapter two showed decreases in area since the 1950/60s of 84% for wet meadows and 85% (mean over all six unprotected study sites, range of 64-97%). So, different study sites fluctuate around this limit of 10% resulting in missing evidence for an extinction debt, but looking at changes in grassland areas in the broader sense, the limit of 10% remaining has not been exceeded.

An additional and at first sight invisible threat is a lower genetic diversity, e.g. due to fragmentation or low population sizes, which involves risks for population survival in the future and increases the risk for an extinction debt (Spielmann et al. 2004; Brütting et al. 2012; Meyer et al. submitted b). This is especially true if additional negative effects, e.g. intensification or changes in site conditions occur and lead to an additional pressure on remaining populations. The effects of climate change in the future are predicted to result in changing precipitation pattern and hydrological conditions in the floodplains of Germany (e.g. Huang et al. 2013; Wagner et al. 2013) also affecting moisture conditions of floodplain meadows. This results likely in an additional pressure on the remaining characteristic meadow species.

Even though, no evidence for an extinction debt for characteristic floodplain species was found, negative effects of fragmentation in addition to negative edge effects from the surrounding landscape (e.g. indirect nutrient input) on the remaining optimal and non-fertilized habitat areas are to be feared in the future.

In chapter four, it was shown that the vegetation unit wet meadows today harbours significantly less characteristic meadows species than in the 1950/60s. Due to the fact that no clear trend and over-regional fragmentation effect could be detected it is likely that other factors, e.g. changing site conditions (local fertilisation, management) are mainly responsible for the species decline. Management affects plant communities often more directly, and may thereby override any potential effects of landscape structure (Korneck et al. 1998; Klimek et al. 2007). The analysis of EIVs in chapter three indicated no clear trend in terms of moisture conditions but increasing nutrient conditions pooled over all study sites (without Ems and Havel) were found. These higher nutrient levels are negatively correlated with the overall species richness (chapter three) and the species richness of characteristic meadow species (chapter four). A similar trend could be detected for the grasslands in the uplands (chapter five). Hence, it is likely that the loss of species richness in wet meadows is mainly a result of increased nutrient supply. Species changes (Table A in the appendix of chapter four) since the 1950/60s show that the most characteristic meadow species which occured in the 1950/60s but being absent in 2008 were adapted to low nutrient conditions (16 species; EIV-N 3.3 ± 1.5).

Consequently, high species diversity and corresponding functional traits are important to ensure ecosystem stability under changing conditions (Cantarel et al. 2013). Human impacts on species diversity therefore also affect ecosystem stability which is to be considered a risk for the future.

The importance of habitat and management continuity for species-rich grasslands

Based on the landscape change and the resulting fragmentation, habitat and management continuity play a crucial role for functional traits and species diversity.

In chapter five, it was shown that grasslands with highest species diversity occurred exclusively on old grassland sites (habitat continuity >100 years) and these sites are still rare. This is in accordance with the results of other studies, e.g. Gustavsson et al. (2007), Aavik et al. (2008) or Waesch and Becker (2009). The fact, that not all old grasslands were species-rich, but all species-rich grasslands were old, suggests additional influences on the number of species. Here the influence of the current management regime (EIVs as indicators for mowing frequency and nutrient supply) on the number of species was tested and strong negative correlations were found (see previous chapter). This combination of site conditions (management, habitat continuity) shows the difficultyies in preserving species-rich grassland. Blüml et al. (2012) found differences between grasslands in the Dümmerniederung which were converted to cropland in the meantime (30 years ago) and grassland which were managed as grassland continuously, but long-lasting and intensive management in grasslands leading to similar negative results as detected by converting measures.

Due to the sound dataset used in chapter two, it was possible to study the extent of grasslands with habitat continuity not only at the level of grassland in the broader sense (study four) but on the specific grassland class (wet meadows, species-rich mesic meadows and more intensive grassland vegetation units). Considering the consequences of continued influence on species richness as revealed for the upland grasslands in chapter five, the very small extent of wet meadows or species-rich mesic meadows with long habitat continuity in our floodplain study areas indicate also a major and additional threat for their species richness.

If a species is extinct at the local scale due to intensification or transformation into cropland and a missing seedbank, the potential dispersal range and the distance to species sources are crucial for re-colonisation (Cousins and Lindborg 2008). These (theoretical) maximum dispersal ranges vary strongly between species (Jensen 1998; Geertsema et al. 2002; Cousins and Aggemyr 2008) and long-range dispersal events can be infrequent or rare for many species. The average dispersal ranges of most grassland species are low or species are partly dependent on specific ways of dispersal (e.g. by sheep or water) (Bonn and Poschlod 1998; Hölzel and Otte 2001; Wessels et al. 2008). These specific ways of dispersal are hampered today by e.g. decreasing numbers of sheep and decreasing flood plain areas due to dike constructions. The probabilities for successful colonization are determined by the fact of undirected and random dispersal and availability of suitable areas and niches for establishment (Piqueray et al. 2011). Therefore, management and habitat continuity is crucial as it takes sometimes long time periods for species to re-established on grassland areas. Additionally, the site conditions in terms of moisture and nutrients must be suitable for restoration success. A best practice example for the restoration of wet meadows is shown by Blüml et al. (2012) for the Dümmeniederung in Lower Saxony. Here a lot of characteristic species re-appeared even 20 years after first restoration efforts, but recolonization is still going on and a lot of areas were previously managed only with a relatively low intensity in contrast to the floodplain meadows and upland grasslands of the study areas used in the present investigation. Similar results were found by Poptcheva et al. (2009) where study species recolononized continuously but slowly during a period of 20 years. These experiences are in line with Bakker and Berendse (1999) who mentioned that the restoration of typical grassland habitats is difficult. In accordance to that, Öster et al. (2009) found that species richness and similarity to semi-natural grasslands of re-established grasslands on formerly arable fields were still lower than in semi-natural grasslands, even after more than 50 years of grazing.

Information about vegetation and land-use history are necessary and high-valued for nature conservation. Using this information the restoration success can be optimized and the very limited budget for conservation activities can be used targeted and to the best effect.

Conclusions for nature conservation

The present study shows that even isolated and small areas are able to harbour a high number of characteristic meadow species. Effects of fragmentation on species richness in the floodplain meadows of Northern Germany were not always evident. Landscape structure effects play a minor role in our study when compared to the results of Rösch et al. (2013) for mobile species like insects. Current grassland management and associated impacts on nutrient and moisture regimes at the local scale are the determinants for grassland diversity. However, predictions of fragmentation impacts on species diversity are difficult. In order to avoid local extinctions through random events, genetic impoverishment and changing site conditions (human impact, climate change, natural change) nature conservation activities should lead to several small and spatially aggregated meadow patches. This will increase population sizes and a higher nature conservation value can be achieved when compared to a single large patch. The risk of local extinctions is splited to few meadows and can be regulated by the re-colonization of species from surrounding habitats. This is necessary as the dispersal range of many grassland species is rather low (Soons et al. 2005; Bischoff et al. 2009). Restoring grasslands to their former ecological value is promoted if the selected sites are located in landscapes where meadow grassland patches of high diversity are still present. These can than act as seed sources (Rosenthal 2003). In addition, the history and habitat continuity is of a great importance for conservation and restoration efforts. The conspicuous decrease in flowering insect-pollinated herbs in Central European grasslands implies that nectar feeders and animal groups at higher trophic levels have also facing severe losses. Our data demonstrates that there are strong directional changes that will undoubtedly have pronounced effects on a wide range of organisms, especially species dependent on insect-pollinated plants or on short-lived herbs.

The present study also showed that the extinction debt in the studied floodplain grasslands is mostly paid within short time periods if melioration measures were strong. Restoration success on such strongly altered sites is complicated and uncertain. Conserving what is left is more effective than getting back what was lost (Kleijn et al. 2011).

The more subtle changes in species number in the protected study region points to local rather than supra-regional drivers (climate change, atmospheric N deposition) as a cause of change. This long-term comparison emphasises the need to adopt adequate grassland management schemes on the local scale in order to preserve grasslands of high nature value. This means that especially local activities for nature conservation are useful to improve site condidions. Decision makers are now asked to create incentives for preserving high-valuable grasslands and the related species diversity.

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Summary

Landscape and agricultural management has changed in Central Europe dramatically since the large-scale intensification processes (e.g. meliorations, synthetic fertilizer and herbicide use) started in the 1950/60s. Today, most croplands and remaining grasslands are used very intensively and many former grassland areas were converted to cropland resulting in an overall decline of grassland area in Germany. The reverse case of converting cropland to grassland is a regional phenomen on, e.g. in the uplands or initiated by compensation measures, but the species composition of the recent grasslands differs from continuously managed grasslands. To detect melioration effects on phytodiversity, landscape structure and the fragmentation of the remaining grasslands and species composition it is necessary to analyse long-term data dating back to the onset of major agricultural industrialisation in the middle of the 20th century.

Floodplain grasslands (wet and mesic species-rich grassland) were common and formerly widespread in the 1950/60s, but nowadays are threatened in Central Europe. There are no replicated studies at multiple locations that refer to the time before agricultural intensification started, and historical and spatially explicit vegetation data is rare. Although the extent of grasslands has increased in some upland regions, the ecological quality of these grasslands is arguable. Additionally, species-rich calcareous grasslands on steep slopes are threatened by abandonment (succession) and increasing nutrient supply.

The aim of this thesis was to detect landscape changes in six (+ one nature protected) floodplain study sites and one upland study site in Northern Germany by quantifying changes in grassland area, grassland replacement by other habitat types, habitat continuity, fragmentation and their effects on plant species and functional trait diversity as well as species composition. The studies on floodplain sites were based on fine-scale vegetation maps and corresponding vegetation relevés from the 1950/60s. In 2008, vegetation mapping of the almost 2.500 ha (+ 293 ha) historical area was repeated and vegetation relevés were sampled in the former grassland at stratified randomly selected sampling points. The case study in the uplands of Lower Saxony is based on recent vegetation relevés randomly distributed among grasslands covering 394 ha within the 2.500 ha of the study area. Additional environmental data for each relevé were surveyed in the field or were extracted from historical, geological and soil maps. The continuity of each grassland habitat was determined using historical and recent topographical maps and aerial photographs.

The first study in the floodplain grasslands pointed out that the wet and species-rich mesic meadows in the unprotected grassland sites decreased dramatically by over 80%. They were mainly replaced by species-poor and intensively managed grasslands, arable land or set-asides. Caused by this strong area decline, the fragmentation of remaining wet meadows as well as of species-rich mesic meadows also increased dramatically. The nature protected study site at the Havel River showed relatively small changes in the extent of wet and species-rich mesic grasslands indicating local effects such as fertilisation and drainage, but no overregional factors such as climate warming or atmospheric N deposition being responsible for the detected changes.

Our second study in the floodplain grasslands showed that the species richness at the plot-level declined by 30-50%, similar to losses in functional diversity. The species composition of floodplain grasslands changed tremendously in all study regions in the last five to six decades. The Ellenberg indicator values (EIV) for nutrient availability increased over time and the observed differences between the unprotected and the one protected study site support the assumption that the changes were mainly caused by local factors and not by overregional influences. The trend is on-going to species-poor communities which are dominated by mowing-tolerant and competitive grasses in all unprotected study sites. Early flowering and insect-pollinated plants decreased strongly with related effects on the fauna.

The third study in the floodplain grasslands connects the dramatic loss of floodplain grassland area and increasing fragmentation with the impoverishment in plant species richness since the 1950/60s. Therefore, a list of 78 characteristic floodplain grassland species was defined from 482 vascular plant species recorded in total and the analysis focussed on these specialist plants. We found a 30-66% diversity loss at the plot-level over time. The tested landscape metrics (total meadow area, mean patch size and landscape proximity index) had no significant influence on the richness of characteristic species at the landscape level. The distance to the nearest suitable habitat of characteristic meadow species had a slightly negative effect on the richness at the plot-level. Ellenberg indicator values for nutrient and moisture showed even for the characteristic meadow species that local management intensity and corresponding habitat deterioration, but not fragmentation, were the driving forces for species shift and species decline.

In contrast to the floodplain study site, the grassland area of our representative upland case study doubled since the 1950/60s. Species diversity and species composition differed strongly between six detected grassland types (<15 plant spp. to >27 spp. per relevé), while species-rich grasslands are rare (6% of the grassland area). The number of insect-pollinated plants as well as species richness declined with increasing land use intensity (as indicated by the EIVs for nutrient and mowing tolerance) in accordance with the results of the floodplain grassland studies. Species-rich grasslands only occured on areas grazed traditionally by sheep with a habitat continuity of more than 100 years, whereas medium-rich grassland occured mainly on former arable fields with a habitat continuity of less than 30 years.

The presented study showed dramatic losses in the extent of floodplain grasslands. Remaining areas were fragmented and suffered major losses in species and functional trait diversity. The case study in the upland meadows of lower Saxony shows, that the ecological quality of most grassland is low even if the percentage of grassland area is relatively high.

Zusammenfassung

Die Kulturlandschaft und ihre Bewirtschaftung haben sich seit dem Beginn der großräumigen Intensivierungsprozesse (z.B. Meliorationen, synthetischer Düngung und Herbizidgebrauch) in den 1950/60er Jahren in Mitteleuropa dramatisch geändert. Viele der ehemaligen artenreichen Grünlandflächen wurden in den letzten Jahrzehnten beseitigt (z.B. durch Umbruch zu Acker). Dies führte zu einem allgemeinen Grünlandrückgang in Deutschland. Heute werden die meisten Ackerflächen und die restlichen Grünlandflächen sehr intensiv bewirtschaftet. Die gegenläufige Entwicklung, die Umwandlung von Äckern zu Grünland, ist eher eine regionale Erscheinung, z.B. im Hügeland oder im Zuge von Kompensationsmaßnahmen. Die Artenzusammensetzung dieser Grünländer unterscheidet sich jedoch häufig von solchen mit längerer Habitatkontinuität. Um die Effekte von solch weiträumigen Meliorationsmaßnahmen auf die Phytodiversität, die Landschaftsstruktur und die hiermit einhergehende Grünlandfragmentierung sowie deren Auswirkungen auf die Pflanzenarten des Grünlandes zu erfassen, ist es nötig, historische Daten aus den 1950er Jahren, bevor die gravierenden, ackerbaulichen Intensivierungen begannen, auszuwerten.

Feucht- sowie artenreiche Frischgrünländer waren in den 1950/60er Jahren ein typischer und weit verbreiteter Habitattyp, gelten jedoch aktuell als sehr bedroht in Mitteleuropa. Wiederholungsstudien mit mehreren Untersuchungsflächen und einem Untersuchungszeitraum von 50-60 Jahren, der vor den weiträumigen Intensivierungen beginnt, fehlen bislang und klar verortete historische Vegetationsdaten sind selten. Obwohl der Graslandanteil in einigen Hügelregionen in Deutschland zugenommen hat ist die ökologische Qualität vieler dieser Flächen gering. Zusätzlich sind artenreiche Kalkmagerrasen als ein Relikt früherer Bewirtschaftsformen und typischer Bestandteil des Hügellandes durch Nutzungsaufgabe (Sukzession) und Nährstoffeintrag gefährdet.

Das Ziel dieser Doktorarbeit war es, den Landschaftswandel und die Veränderungen im Grünland in sechs Flussauengebieten (sowie einem durch Naturschutzstatus geschützten Gebiet) und einem typischen Gebiet des Hügellandes in Norddeutschland zu untersuchen. Hierzu wurden sowohl der Grünlandanteil, die Habitatkontinuität, der aktuelle Habitattyp, der Fragmentierungsgrad als auch die Auswirkungen auf die Artenzahlen, Artenzusammensetzung und die funktionelle Diversität untersucht. Die Studien in den Flussauen basieren auf fein aufgelösten historischen Vegetationskarten und dazugehörigen Vegetationsaufnahmen aus demselben Zeitraum. In 2008 wurden diese sechs Gebiete (+1 geschütztes Gebiet) mittels einer Biotoptypenkartierung erneut erfasst. Innerhalb dieser

kanpp 2800 ha (2500 + 293 ha) früherer Grünländer wurden randomisierte Punkte gelegt und zusätzlich Vegetationaufnahmen in allen aktuellen Grünländern (inklusive Sukzessionsstadien) angefertigt.

Die Fallstudie (2500 ha) aus dem niedersächsischen Hügelland basiert auf aktuellen Vegetationsaufnahmen, die ebenfalls mittels randomisierter Punkte in den bestehenden Grünländern (394 ha) angefertig wurden. Zusatzdaten über z.B. die aktuelle Bewirtschaftung oder die Habitatkontinuität (Auswertung historischer Karten) wurden ebenfalls erfasst.

Die erste Studie zeigte, dass die ehemaligen artenreichen Feucht- und Frischgrünländer in den ungeschützten Gebieten drastisch, um über 80% der ursprünglichen Fläche, zurückgegangen sind. Sie wurden größtenteils durch Äcker, Intensivgrünländer aber auch Brachestadien ersetzt. Bedingt durch diesen starken Flächenrückgang hat die Fragmentierung der Restflächen stark zugenommen. Die durch ein Naturschutzgebiet geschützte Untersuchungsfläche an der Havel zeigte im Vergleich relative geringe Veränderungen. Daraus lässt sich deuten, dass lokale Effekte wie Düngung oder Drainage und nicht überregionale Effekte wie Klimaerwärmung oder der Eintrag von Stickstoff durch Luft die Hauptursache für den dokumentierten Wandel sind.

Die zweite Studie in den Grünländern der Auen zeigte, dass sich die Artenzusammensetzung in den letzten fünf bis sechs Jahrzehnten in allen Gebieten stark verändert hat, die Artenzahlen der Vegetationsaufnahmen um 30-50% und auch die funktionelle Diversität in ähnlichem Maße zurückgegangen sind. Die Ellenberg-Zeigerwerte (EIV) für Nährstoffverfügbarkeit sind im Vergleich zu den 1950/60er Jahren stark gestiegen und die Unterschiede zwischen den ungeschützen und dem geschützten Gebiet unterstützen ebenfalls die Annahme, dass Veränderungen größtenteils durch lokale Faktoren und nicht durch überregionale Effekte verursacht wurden. Der Trend in den ungeschützten Gebieten geht zu artenamen Grünlandgesellschaften, die von wenigen konkurrenzstarken und mahdtoleranten Arten dominiert werden. Frühblühende und auf Insektenbestäubung angewiesene Pflanzen sind stark zurückgegangen, mit entsprechenden Auswirkungen auf die Tierwelt.

Die dritte Studie verknüpft den dramatischen Grünlandrückgang und die zunehmende Fragmentierung mit der Artenverarmung seit den 1950/60er Jahren. Hierfür wurden mittels definierter Kriterien eine Liste von 78 für das Feucht- und Frischgrünland charakteristischen Grünlandarten definiert, die die Grundlage für die weiteren Analysen bildeten. Die

Artenzahlen auf Ebene der Vegetationsaufnahmen nahmen um 30-66% ab. Die getesteten Landschaftsstrukturmaße hatten keinen nachweisbaren Einfluss auf die Artenzahlen auf Landschaftsebene. Die Distanz zum nächstgelegenen und geeigneten Habitat für die charakteristischen Arten hatte einen geringen negativen Effekt auf die Artenzahl der Vegetationsaufnahmen. Die Ellenberg-Zeigerwerte (N, F) und die Diversitätsmaßzahlen an charakteristischen Arten weisen ebenfalls auf den Effekt der lokalen Bewirtschaftung und nicht auf Fragmentierung als treibende Kraft beim Rückgang und dem Wandel der Artengarnitur hin.

Im Gegensatz zu den Untersuchungsgebieten in den Flussauen hat sich der Grünlandanteil in der Fallstudie im niedersächsischen Hügelland seit den 1950er Jahren verdoppelt. Es wurden sechs verschiedene Grünlandtypen mit einer Spanne von unter 15 bis zu deutlich mehr als 27 Arten pro Aufnahme erfasst. Die besonders artenreichen Bestände sind aber mit ca. 6% der Fläche sehr selten. Die Anzahl an insektenbestäubten Pflanzen als auch die absoluten Artenzahlen gehen mit steigender Nutzungsintensität (indiziert durch die Ellenberg-Zeigerwerte Nährstoffe (N) und Mahdtoleranz (M)) wie in den Untersuchungsgebieten in den Flussauen zurück. Artenreiche Grünländer kommen nur auf mit Schafen beweideten Flächen mit einer Habitatkontinuität von mindestens 100 Jahren vor. Grünländer mit mittleren Artenzahlen sind größtenteils auf früheren Äckern mit einer Habitatkontinuität von weniger als 30 Jahren zu finden.

Die dargestellte Untersuchung hat dramatische Verluste in den Grünlandflächen der Flussauen aufgezeigt. Die Restflächen sind fragmentiert und die Artenzahlen sowie die funtionelle Diversität stark zurückgegangen. Die Fallstudie im niedersächsischen Hügelland zeigt, dass selbst in Landschaften mit hohem Grasslandanteil die ökologische Qualität von den meisten Grünländern nur noch gering ist.

List of Publications

Peer reviewed journal publications

Krause, B., Culmsee, H., Wesche, K., Bergmeier, E. and Leuschner, C. 2011. Habitat loss of floodplain meadows in North Germany since the 1950s. Biodiversity and Conservation 20: 2347-2364.

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Krause, B. and Culmsee, H. 2013. The significance of habitat continuity and current management on the compositional and functional diversity of grasslands in the uplands of Lower Saxony, Germany. FLORA (http://dx.doi.org/10.1016/j.flora.2013.04.003).

Submitted:

Meyer, S., Bergmeier, E., Becker, T., Wesche ,K., **Krause, B.** and Leuschner, C. (submitted) Massive changes in Central Europe’s arable plant communities since the 1950s/60s. Journal of Vegetation Science.

Krause, B., Culmsee, H., Wesche, K. and Leuschner, C. (submitted). Historical and recent fragmentation of temperate floodplain grasslands: Do patch size and distance affect plant species richness of wet meadows? Folia Geobotanica.

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