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Article (refereed) - postprint

DR. MARTIN DIEKMANN (Orcid ID : 0000-0001-8482-0679)

Sándor Bartha

Patterns of long-term vegetation change vary between different types of semi-natural grasslands in Western and Central Europe

Running title: Grassland vegetation change

Martin Diekmann[1*], Christian Andres [2], Thomas Becker [3], Jonathan Bennie [4], Volker Blüml[5], James M. Bullock[6], Heike Culmsee[7], Miriam Fanigliulo[8], Annett Hahn[9], Thilo Heinken[10], Christoph Leuschner[11], Stefanie Luka [12], Justus Meißner[13], Josef Müller[1], Adrian Newton[14], Cord Peppler-Lisbach[15], Gert Rosenthal[16], Leon J.L. van den Berg[17], Philippine Vergeer[18] & Karsten Wesche[19]

[1] Vegetation Ecology and Conservation Biology, Institute of Ecology, FB 2, University of Bremen, Leobener Str. 5, 28359 Bremen, Germany

[2] Andrena GbR, Burgweg 11, 97956 Werbach-Gamburg, Germany

[3] Geobotany, Regional and Environmental Sciences, University of Trier, Behringstraße 21, 54296 Trier, Germany

[4] Centre for Geography, Environment and Society, University of Exeter, Penryn Campus, Treliever Road, Penryn, Cornwall, TR10 9FE, United Kingdom

[5] BMS-Umweltplanung, Freiheitsweg 38A, 49086 Osnabrück, Germany

[6] NERC Centre for Ecology & Hydrology, Benson Lane, Wallingford, OX10 8BB, United Kingdom

[7] DBU Natural Heritage, German Federal Foundation for the Environment, An der Bornau 2, 49090 Osnabrück, Germany

[8] Parkstraße 1a, 27721 Ritterhude, Germany

[9] Thüringer Landesanstalt für Umwelt und Geologie, Göschwitzer Straße 41, 07745 Jena, Germany

[10] Biodiversity and Systematic Botany, University of Potsdam, Maulbeerallee 1, 14469 Potsdam, Germany

[11] Albrecht-von-Haller-Institute for Plant Sciences, Georg August University Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

[12] EU LIFE-Natur-Projekte, Stiftung NaturSchutzFonds Brandenburg, Heinrich-Mann-Allee 18/19, 14473 Potsdam, Germany

[13] Florastraße 22, 15370 Petershagen, Germany

[14] Centre for Ecology, Environment and Sustainability, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow Poole, Dorset BH12 5BB, United Kingdom

[15] Landscape Ecology Group, Institute for Biology and Environmental Sciences, University of Oldenburg, 26111 Oldenburg, Germany

[16] Department of Landscape Ecology, University of Kassel, Gottschalkstraße 26a, 34127 Kassel, Germany

[17] Expertmedewerker Ecologie Coöperatie Bosgroep Zuid-Nederland, Huisvenseweg 14, 5591 VD Heeze, The Netherlands

[18] Plant Ecology & Nature Conservation, Department of Environmental Sciences, Wageningen Unversity, Droevendaalsesteeg 3, 6708 PB Wageningen, The Netherlands

[19] Senckenberg Museum of Natural History, Goerlitz, PO Box 300 154, D-02806 Goerlitz, Germany; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany; International Institute Zittau, Technische Universität Dresden, Markt 23, 02763 D-Zittau, Germany;

* Corresponding author: tel +49 421 21862920, fax +49 421 21862929; mdiekman@uni-bremen.de

Abstract

Questions: Has plant species richness in semi-natural grasslands changed over recent decades? Do the temporal trends of habitat specialists differ from those of habitat generalists? Has there been a homogenization of the grassland vegetation?

Location: Different regions in Germany and the United Kingdom.

Methods: We conducted a formal meta-analysis of re-survey vegetation studies of semi-natural grasslands. In total 23 data sets were compiled, spanning up to 75 years between the surveys, including 13 data sets from wet grasslands, six from dry grasslands and four from other grassland types. Edaphic conditions were assessed using mean Ellenberg indicator values for soil moisture, nitrogen and pH. Changes in species richness and environmental variables were evaluated using response ratios.

Results: In most wet grasslands, total species richness declined over time, while habitat specialists almost completely vanished. The number of species losses increased with increasing time between the surveys and were associated with a strong decrease in soil moisture and higher soil nutrient contents. Wet grasslands in nature reserves showed no such changes or even opposite trends. In dry grasslands and other grassland types, total species richness did not consistently change, but the number or proportions of habitat specialists declined. There were also considerable changes in species composition, especially in wet grasslands that often have been converted into intensively managed, highly productive meadows or pastures. We did not find a general homogenization of the vegetation in any of the grassland types.

Conclusions: The results document the widespread deterioration of semi-natural grasslands, especially of those types that can easily be transformed to high production grasslands. The main causes for the loss of grassland specialists are changed management in combination with increased fertilization and nitrogen deposition. Dry grasslands are most resistant to change, but also show a long-term trend towards an increase in more mesotrophic species.

Keywords: dry grasslands, fragmentation, homogenization, management, meta-analysis, nitrogen deposition, quasi-permanent plot, re-survey, species richness, wet grasslands

1   Introduction

Semi-natural grasslands, defined as unploughed mown or grazed areas with moderate fertilization, are among the most diverse vegetation types in Western and Central Europe, including habitats such as dry grasslands on both calcareous and acidic bedrocks, wet grasslands, nutrient-poor or moderately nutrient-rich meadows or pastures on mesic soils in lowland and mountainous regions, as well as alpine grasslands. Some of these types are extremely species-rich (Dengler, Janišová, Török, & Wellstein, 2014), on a local scale holding the world records in vascular plant species richness (Wilson, Peet, Dengler, & Pärtel, 2012; Chytrý et al., 2015). The high species richness of some semi-natural grassland types, their threat and high conservation value are reflected in the EU Habitats directive that recognizes several grassland types as NATURA 2000 habitats, including dry calcareous grasslands (code 6210), acidic *Nardus* grasslands (code 6230*), *Molinia* meadows (code 6410) and *Arrhenatherion* meadows (code 6510).

Over many centuries semi-natural grasslands occupied considerable areas in Western and Central Europe, as they were important for farmers in providing fodder for their animals (Dengler et al., 2014; Dengler & Török, 2018). While some grassland types were mainly managed by mowing (wet grasslands), others were predominantly used as pastures (e.g., dry grasslands) (Leuschner & Ellenberg, 2017). All semi-natural grasslands are sensitive to changes in management, and as early as in the 19th century the range of semi-natural grasslands started to decline as a result of altered land use practices, notably the decline of sheep grazing. The most drastic change started in the middle of the 20th century with the introduction of agro-industrial farming triggered by the use of artificial fertilizers (Leuschner & Ellenberg, 2017). Most grasslands were either transformed into cropland or forest (Eriksson, Cousins, & Bruun, 2002), or subjected to more intense land use practices, including increased addition of nutrients, earlier and more frequent mowing or higher stocking densities, drainage (in wet areas), and the use of pesticides and sowing mixtures (Dierschke & Briemle, 2002). Even where the traditional low-intensity farming was maintained or re-installed through conservation actions, grasslands suffered from eutrophication due to atmospheric nitrogen deposition (Payne et al., 2017) and from habitat fragmentation (Cousins, Ohlson, & Eriksson, 2007; Krause et al., 2011; Krause, Culmsee, Wesche, & Leuschner, 2015). A consequence of these changes has been that many species typical for semi-natural grasslands have become rare and threatened as evidenced by national and regional Red Lists (for Germany, see Ludwig & Schnittler, 1996).

The decline in area and species richness of semi-natural grasslands has since long attracted the attention of ecologists, especially with regard to dry calcareous grasslands where, applying experimental approaches, nitrogen deposition was early recognized as a potential driving factor for an altered species composition (Bobbink & Willems, 1987). For some grassland types, general time series analyses have provided evidence for the profound changes in species composition, for example in acidic grasslands (Dupré et al., 2010) and in wet grasslands (Wesche, Krause, Culmsee, & Leuschner, 2012). Apart from a loss in total species richness there was a noticeable decline of habitat specialists and a shift in life form composition, for example an increase in grasses at the expense of small-statured forbs. For acidic *Nardus* grasslands these trends were confirmed in spatial comparisons (space-for-time substitutions) within the United Kingdom (Stevens, Dise, Mountford, & Gowing, 2004) and across different countries in Europe (Stevens et al., 2011a, b). A time series analysis of dry grasslands across Germany revealed less clear and consistent changes of the vegetation (Diekmann et al., 2014).

The most reliable information on vegetation changes is usually provided by re-survey studies based on permanent or semi-permanent plots characterized by a high precision of site relocation, in contrast to the previously mentioned time series analyses (Verheyen et al., 2017). Unlike in forests where dozens of (semi-)permanent plot studies have been published and summarized in meta-analyses (e.g., Verheyen et al., 2012), available data for semi-natural grasslands is surprisingly rare. One reason for this certainly is the difficulty to install permanent markings or to provide drawings of the exact location of plots in grasslands. The few re-survey studies from dry grasslands that were published in international journals (Bennie, Hill, Baxter, & Huntley, 2006; van den Berg et al., 2011; Newton et al., 2012) give contrasting results as to the trends in species richness and compositional change, while such studies from other semi-natural grassland types are to our knowledge largely unknown to an international audience. This paper aims to compile the existing re-survey data sets from semi-natural grasslands in Western and Central Europe and to subject them to a rigorous meta-analysis. We focused on the following research questions: (1) Has the general species richness in semi-natural grasslands changed over recent decades? Considering the available evidence from existing spatial and temporal comparisons, we expected a general decline in species numbers especially in those grassland types where management interventions such as drainage or fertilization are likely to result in a considerable increase in productivity (often associated with species loss), such as in wet or mesic grasslands. In contrast, grasslands with low productivity owing to aridity (dry grasslands) or low temperatures (mountain grasslands)

were predicted to show less pronounced changes. (2) Are habitat specialists in the different grassland types more strongly affected than generalists, i.e. has the number of habitat specialists declined more than total species richness? We expected this to be true for all grassland types, but less so for the low-productivity grasslands. (3) Irrespective of the changes in species richness, has there been a general change in species composition of the grasslands, and has there been a trend towards a homogenization of the vegetation? Under the assumption of an increase in the share of generalist species, and based on the evidence from previous studies from forests (Kopecký, Hédl, & Szabó, 2013; Reinecke, Klemm & Heinken, 2014; Heinrichs & Schmidt, 2017) and other types of semi-natural vegetation (Timmermann, Damgaard, Strandberg, & Svenning, 2015), we predicted that the grasslands will have become more similar in species composition.

2 Methods

2.1 Literature Search

To find articles with data from re-survey studies in grasslands we searched the ISI Web of Knowledge without restriction on publication year, using the following combinations of search terms: (resurvey OR re-survey OR revisitation OR permanent plot* OR semi-permanent plot*) AND (vegetation) AND (grassland*). The papers retrieved and considered relevant were downloaded and their reference lists screened for other articles. In many cases the publications did not include or provide a link to the original data so that the authors of the papers were contacted and asked to contribute to the study. In addition, some data bases were extracted from papers not published in peer-reviewed international journals, and another set of (yet unpublished) vegetation data was obtained from colleagues working with re-surveys. Although several countries in Western and Central Europe (e.g. the Netherlands) have compiled vegetation data bases with a large number of plots, re-survey plot data from grasslands are still rare and could be obtained for this study only from the United Kingdom and Germany. To be included in the meta-analysis several criteria had to be met.

(i) The study area should largely be confined to the Atlantic biogeographic zone of Western and Central Europe. (ii) Data sets were only considered if the communities represented semi-natural grasslands during the original survey and were at least until recently managed as grasslands at the time of the re-survey. Data sets with plots or single plots transformed to agricultural fields or forests, or having been abandoned for many years before the re-survey,

were omitted. Our meta-analysis thus documents the minimum vegetation change on a local scale, while it does not reflect any change in the area of different grassland types across landscapes. The following types of semi-natural grasslands were examined: (a) grasslands on mesic or wet, relatively fertile soils belonging to the class *Molinio-Arrhenatheretea*, namely the alliances *Arrhenatherion elatioris* (lowland to submontane mesic meadows) and *Phyteumato-Trisetion* (montane mesic meadows, both *Arrhenatheretalia elatioris*), and alliances in the order *Molinietalia caeruleae* (henceforth called wet grasslands); (b) mat-grass swards on acidic, nutrient-poor soils assigned to the *Nardetalia strictae*; (c) dry grasslands on base-rich and nutrient-poor, mostly shallow soils belonging to the *Festuco-Brometea* (for the classification of grassland communities, see Mucina et al., 2016). (iii) For the meta-analysis the only re-survey studies that were retained were based on permanent or semi-permanent (quasi-permanent sensu Kapfer et al., 2017) plots. Time series analyses including non-traceable plots - being from the same region but without reliable relocation - were excluded. (iv) Data sets with plots without a complete list of vascular plant species were omitted. (v) The minimum number of plots in a data set and the minimum number of years between the original survey and re-survey were both set to 15. This somewhat arbitrary number was considered a good compromise between the wish to include as many studies as possible and the analytical limitations of data sets with only few plots and a time span too short to observe a pronounced shift in species richness and composition. Verheyen et al. (2017) showed that data sets from various regions across a large geographic gradient including a sufficient number of replicates (plots) are suitable for disentangling the effects of different environmental drivers on changes in the vegetation. For comparative purposes, we also re-analyzed six data sets of wet grasslands in Germany including non-traceable plots with old and new records mostly not sampled in the same sites, but in the same regions (Wesche et al., 2012).

2.2   Data preparation

The literature search and subsequent application of criteria finally yielded 23 data sets, most of which referred to wet grasslands (from Germany) and dry grasslands (from the United Kingdom and Germany, see Table 1). Only a few studies from Germany included other grassland types.

Prior to performing the meta-analysis, the vegetation tables of the original and re-survey were transformed and standardized in several ways. With one exception the data sets included original plots that were associated with just one corresponding re-surveyed plot. In the re-inventory of dry grasslands by Hagen (1996), however, several (2–5) re-survey plots of the same size as the original plots were sampled close to the approximate location of the original plots. Here, only one of the re-surveyed plots was selected at random for each original plot. The majority of data sets did not or only incompletely contained information on species occurrences of bryophyte and lichen species so that all data entries of non-vascular plants were omitted. The next step was to harmonize species lists between and within data sets by applying the taxonomy published in Netzwerk Phytodiversität Deutschland & Bundesamt für Naturschutz (2013). Whenever there were discrepancies in the taxonomic concepts applied by the original and re-survey, taxa were merged to aggregates, for example *Luzula campestris* agg. (including *L. campestris* s. str. and *L. multiflora*) and *Poa pratensis* agg. (including *P. pratensis* s. str. and *P. angustifolia*). Another necessary simplification of the vegetation tables concerned the information on species abundance: the methods for estimating species cover differed widely between the studies, in some cases only presence-absence data were available. Therefore – although this may have resulted in an underestimation of the extent of change in the vegetation – all abundance values of species in the plots other than 0 were transformed to 1. Presence/absence data are also relatively robust to sampling error (Hirst & Jackson, 2007).

When information on plot sizes was provided in the original survey, the re-surveys mostly used the same plot sizes. For some of the oldest surveys the plot sizes were not known: in these cases, standard plot sizes of 20 or 25 m^2 - often being recommended as minimum area for grassland plots - were used in the re-survey. An additional source of potential bias is the subjective placement of the plots in old surveys conducted according to the Braun-Blanquet approach, often selecting larger plot sizes in species-poor vegetation and smaller sizes in species-rich vegetation. For the two data sets from wet grasslands with the longest time interval between original and re-survey, however, it was shown that the differences in species richness over time are unlikely to be attributed to possible differences in plot size between the surveys (Wittig, Waldmann, & Diekmann, 2007; Immoor, Zacharias, Müller, & Diekmann, 2017).

2.3　Data analysis

Except in a few cases, no measurements of environmental variables were available for the original data sets, and only in one study soil factors were measured in both the original and the re-survey. Therefore, the environmental conditions in the plots at both sampling periods were assessed by means of Ellenberg indicator values for soil moisture (F), soil nitrogen (N; often interpreted as general nutrient availability) and soil pH (R) (Ellenberg et al., 2001). Although potential changes of the vegetation due to climate change were not in the focus of this study and assumed to be less pronounced compared to the effects of the edaphic variables, we also applied the indicator values for light (L), continentality (C) and temperature (T). For each plot, mean indicator values of all species in the plot were calculated for all variables (abbreviated with mF, mN, mR, mL, mC and mT). The differences in mean values between original and re-surveyed plots were assumed to indicate changes in environmental conditions at the sites.

Several species richness variables were used to examine shifts in the vegetation between original and re-survey. First, the total number of vascular plant species per plot was calculated. As total species richness may not change even when there is a considerable species turnover (when gains and losses compensate each other), we also calculated the number of habitat specialists for the different grassland communities, i.e. the typical species of wet and dry grasslands, *Nardus* swards etc. Information on habitat specificity was obtained from Dierschke (1997), Burkart, Dierschke, Hölzel, Nowak, & Fartmann (2004), Diekmann et al. (2014), and Peppler-Lisbach & Könitz (2017). These publications also provided information about species that serve as indicators for the abandonment (cessation of grazing and / or mowing) of grasslands, such as *Lysimachia vulgaris* and *Phalaris arundinacea* in wet grasslands, and *Agrimonia eupatoria* and *Trifolium medium* in dry grasslands. As abandonment, or in general a less intensive management, may lead to a decline in species richness similar to that caused by eutrophication, the difference between the sums of 'abandonment indicators' in the original and re-surveyed plots was used as a control for the continued management of the sites. Finally, we calculated the number and proportion of grass (*Poaceae*) species in each plot to examine altered (relative) frequencies of grasses *vs* herbs.

The statistical comparison of species richness variables and mean indicator values between original and re-surveyed plots was carried out with meta-analytical tools, calculating mean response ratios ($RR = \ln (x_{new} / x_{old})$) for each study as the natural logarithm of the ratio between the new (re-surveyed) and the old (original) plot, with x being either a measure of

species richness or a mean indicator value (Hedges, Gurevitch, & Curtis, 1999). A positive *RR* indicates an increase and a negative value a decrease in the response variable, while zero values correspond to no change. As some data sets were small and possibly unbalanced, we did not apply conventional statistics based on normally-distributed populations to calculate confidence intervals (CI). Instead, for each value of *RR* we calculated a 95% bootstrapping CI with 1000 iterations, using the *Resampling Stats* Version 4 provided at http://www.resample.com/. If the CI for a data set does not intersect with the zero line of no change, there is a significant increase or decrease in the response variable. For the non-traceable plots from wet grasslands published by Wesche et al. (2012) we calculated the mean species richness separately for old and new plots together with their CI; here, a significant difference between original and re-surveyed plots was assumed if the two CIs did not overlap. The relationships between response ratios and the time between surveys or between different types of response ratios were examined by Pearson correlation analysis. For the statistical tests and the preparation of figures we used the program R 3.3.2 (R Core Team, 2016).

The change over time in the species composition of the grasslands was examined by means of Jaccard and Sørensen dissimilarity coefficients, using the R package *Vegan* 2.4-1 (Oksanen et al., 2016) and *Betapart* (Baselga & Orme, 2012). The latter package also served to partition dissimilarity into two components, on the one hand *species replacement*, constituting the temporal substitution in a site of species by other species (i.e., turnover), and on the other hand *species loss* (or *gain*), being the elimination (or addition) of species in a site and leading to nestedness (without replacement). First, we calculated, separately for the original and re-surveyed plots of each data set, the mean dissimilarity coefficients across all plots to examine whether the general species composition had become more or less homogeneous. Second, to examine whether the temporal change in species composition depends on the time between surveys or on the change in environmental conditions, we averaged the dissimilarity coefficients between all pairs of old and corresponding new plots in a study (i.e., n = number of plots) and correlated the means to the time between surveys and the response ratios of mean Ellenberg indicator values. As the Jaccard and Sørensen coefficients were highly positively correlated (for both wet and dry grasslands: $r = 0.997$, $p < 0.0001$, $n = 13$ and 6, respectively), we report only on the first-mentioned index.

The Jaccard dissimilarities between the pairs of original and re-surveyed plots were correlated to the years between surveys, mean Ellenberg values (mF, mR and mN) and species richness values. As the above variables are all calculated from the same vegetation data sets, especially the mean indicator values may inherit some information about compositional similarity, thus resulting in a potential bias (Zeleny & Schaffers, 2012). Correlation coefficients and significance probabilities of these analyses thus need to be interpreted with some caution.

3 Results

3.1 Wet grasslands

Altogether 13 re-survey studies of wet grasslands fulfilled the criteria for inclusion in the meta-analysis. Most of these studies refer to locations in the lowlands of northern Germany: only four data sets were from the hilly regions in the central part of the country. Five sites were located in nature reserves. Mean total species richness in the data sets varied between 15 and 36 in the original plots and between 12 and 24 in the re-surveyed plots. In nine of the studies, mean total species richness had significantly declined, in three studies there had been an increase (Figure 1). For the wet grassland specialists, species losses were more pronounced than for total species richness: whereas the mean number of species in this group varied between 3 and 11 in the original surveys, the corresponding values ranged from 0 to 6 in the re-surveys. The response ratios revealed a strong decline in the number of typical wet grassland species in eight studies and unchanged or slightly increased numbers in those five studies that were located in protected sites. For both species richness variables there was a negative correlation between response ratios and time between surveys ($r = -0.787$, $p = 0.001$ and $r = -0.843$, $p < 0.001$, respectively). In six studies the proportion of grass species had significantly increased, a decrease was found only in two studies. In the data sets with plots located outside nature reserves (Appendix S1, columns 1-7 and 9), most wet grassland specialists had not only declined, but almost or completely disappeared, such as *Bromus racemosus*, *Comarum palustre*, *Senecio aquaticus* and *Valeriana dioica*. The results coincided well with the six data sets of wet grasslands based on non-traceable plots: here, both total species richness and the number of wet grassland specialists had significantly declined in four studies and increased in one study (again representing plots located in a nature reserve) (Appendix S2).

Mean Ellenberg moisture values (mF) in the original surveys ranged from 5.5 to 8.0 (Appendix S3). Until the time of the re-surveys, they had significantly decreased in five studies and increased in four studies (Figure 2a), showing a negative correlation with time between surveys ($r = -0.698$, $p = 0.008$). In contrast, mean Ellenberg nutrient values (mN) had increased in nine studies and decreased only in three cases, being positively correlated with time between surveys ($r = 0.623$, $p = 0.022$). Across studies, the response ratio for total species richness was negatively correlated with the response ratio for mN ($r = -0.815$, $p < 0.001$), indicating that species richness had decreased over time with increasing nutrient availability. There was no significant correlation for mF with time ($r = 0.453$, $p = 0.120$; Figure 2b). For the number of wet grassland specialists, the correlations between response ratios were significant for both soil indicator value variables (mF: $r = 0.691$, $p = 0.009$; mN: $r = -0.863$, $p < 0.001$; data not shown). The mean Ellenberg values for temperature and continentality showed minor changes (low response ratios) over time compared to the soil variables, mostly varying between 0.05 and -0.05 (Appendix S4). The mT decreased in two and increased in six studies, the mK in two and five studies, respectively. A relatively high increase in both values was found only in data sets 1 and 2 having the largest time intervals between the two survey periods.

Abandonment indicators, generally being represented only by few, low-frequent species, had decreased in five and increased in three studies, suggesting a somewhat more intensive management in the majority of sites. Not consistent with this observation, the mean Ellenberg values for light showed a weak, but significant decrease in five studies and an increase in only one data set (Appendix S4). Across studies, the response ratio for species richness was (marginally) positively correlated with the response ratio for the abandonment indicators (total species richness: $r = 0.540$, $p = 0.057$; number of wet grassland specialists: $r = 0.668$, $p = 0.013$), indicating a positive effect of a less intensive management on species richness (abandoned grasslands, however, were excluded from the analysis).

Within-data set mean Jaccard dissimilarity varied between 0.568 and 0.864 for the old plots and between 0.503 and 0.858 for the new plots (Appendix S5). Comparing the two time periods, values were higher in the re-surveyed plots in nine data sets and lower only in four data sets, suggesting that there was no general homogenization in species composition but rather an opposite trend. The mean Jaccard dissimilarity between the pairs of old and new plots varied between 0.552 and 0.886 (mean = 0.720); in two data sets the maximum values reached 1, meaning that there were some cases where old and corresponding new plots no longer had a single species in common. The dissimilarity in species composition increased

with an increasing number of years between the surveys (Table 2). It was also significantly related to the response ratios for the changes in mean Ellenberg values, marginally negatively for mF and positively for mR and mN. This means that species similarity between old and new plots stayed relatively high in those data sets where soil moisture had increased or at least not strongly decreased, whereas it was low where the values for soil pH and nutrients had increased. Finally, data sets with a strong loss of species in general and of habitat specialists in particular also showed the highest mean Jaccard dissimilarities, as suggested by the high negative correlation between the response ratios for species richness and dissimilarity coefficients (Table 2). Total dissimilarity was mainly attributable to true species replacement (72–89%, mean across studies 84%), not to the nestedness component (11–29%, mean 16%). The reported correlations of Jaccard dissimilarity with changes in species richness and environmental drivers were also driven by species replacement, while there was no significant relationship between the nestedness component and time or changes in species richness and mean Ellenberg values (Table 2).

3.2 Dry grasslands

Six data sets of dry grasslands were retrieved, three from Germany and three from the United Kingdom (Table 1). Mean species richness was high compared to other grassland types, across studies ranging from 25 to 40 in the old plots and from 22 to 44 in the new plots. In two out of the six data sets, total species richness significantly increased over time, whereas in two studies it decreased (Figure 3a). There was no relationship between the response ratio and the number of years between surveys. The same was true for the number of dry grassland specialists, but here a significant decrease over time was found in three data sets, while an increase was observed only once. Remarkably, the proportion of dry grassland specialists relative to the total number of species showed a clear decrease over time ($r = -0.980$, $p < 0.001$, $n = 6$). Most dry grassland specialists showed a tendency to decline, but the variation among the species was high, alongside species with a strong decrease in frequency (*Euphrasia stricta*, *Pulsatilla vulgaris*) there were also taxa that increased over time, most notably the grasses *Bromus erectus* and *Brachypodium pinnatum* (Appendix S6).

While the mean response ratios for mR were all close to 0 (results not shown), the three data sets with the longest time periods between original and re-surveys showed significantly positive mean response ratios for mF and mN (Figure 3b). For the three other data sets with about 20 years difference between the surveys, the changes were less

pronounced especially for soil moisture. There were no consistent changes in the mean Ellenberg values for temperature and continentality over time (Appendix S4).

In four data sets the number of woody species and abandonment indicators significantly increased, while a decrease in the number of species belonging to these groups was observed only in one case, suggesting an overall decline in grazing and / or mowing intensity. This was consistent with a significant decrease in the mean Ellenberg values for light in four data sets (Appendix S4). However, the changes in species richness were not related to the changes in the frequency of these species (correlations of response ratios: total species richness - woody species: $r = 0.714$, $p = 0.111$, - abandonment indicators: $r = 0.645$, $p = 0.167$; number of dry grassland specialists - woody species: $r = 0.014$, $p = 0.978$, - abandonment indicators: $r = -0.085$, $p = 0.873$, all $n = 6$).

Within-data set mean Jaccard dissimilarity was remarkably stable across studies, varying between 0.668 and 0.798 in the old plots and between 0.707 and 0.830 in the new plots, without any obvious general increase or decrease in homogeneity (Appendix S5). The mean Jaccard dissimilarity between the pairs of original and re-surveyed plots was generally lower than for the wet grasslands, varying between 0.462 and 0.773 (mean = 0.642). Unlike in wet grasslands, pair-wise species dissimilarity between old and new plots was unrelated to the time between surveys and the response ratios for mean Ellenberg values or species richness, both for total dissimilarity and for the replacement and nestedness components (results not shown). Of the total Jaccard dissimilarity on average about 85% (71–93%) were attributed to species replacement.

3.3   Other types of semi-natural grasslands

Few data sets were available for other types of semi-natural grasslands. In two studies of *Nardetalia* communities in Germany there was no significant decline in total species richness, but a loss of habitat specialists (Figure 4a). Significantly positive response ratios for mean Ellenberg values (mR, mN) indicated an increase in soil pH and nutrient availability (Figure 4b). One study of *Trisetion* meadows and one study of *Arrhenatherion* meadows both showed similar results: a significant decrease in total species richness and in the number of habitat specialists as well as an increase in nutrient availability and no change in soil acidity (Figures 4a, b). Within-data set mean Jaccard dissimilarity varied between 0.6 and 0.8 both in old and new plots (Appendix S5), and there was again no trend towards a systematic change in homogeneity. The pair-wise mean Jaccard dissimilarities of original and re-surveyed plots

also were in the range of those for wet and dry grasslands, with a much higher proportion of the replacement than nestedness components.

4   Discussion

In accordance with hypotheses 1 and 2, most wet grasslands showed a drastic decline in overall species richness and in the number of habitat specialists. For the dry grasslands, the temporal trends in total species richness were not uniform across studies, but there was an overall decline in the proportion of specialist species, which became more pronounced over time. For other types of semi-natural grasslands, data were too scarce to allow any generalization, but the results of the few existing studies were in line with the hypothesized decline in species numbers, especially of habitat specialists. Contrary to our expectations we found no general homogenization of the vegetation in any of the grassland types. Below, we discuss the potential causes for the changes in species richness and composition of the grasslands. It has to kept in mind that this study is concerned only with the vegetation changes in those sites that are still managed as grasslands: in most regions of Western and Central Europe, large parts of semi-natural grasslands were converted to croplands or forests (for the UK: Fuller, 1987; Stevens et al., 2010; Hooftman & Bullock, 2012; for Central Europe: Leuschner & Ellenberg, 2017). Grassland sites with clear evidence of abandonment (increase in shrubs and other abandonment indicators) were also omitted from this analysis. Moreover, the patterns of vegetation change found in this study are based on data only from one or two countries, meaning that the results may not be representative for the whole study area.

The maintenance of an appropriate (traditional) land use is of crucial importance for the conservation of semi-natural grasslands. Grassland types in which productivity can be considerably improved through fertilization, drainage and increased mowing or grazing intensities are at particular risk. This is the case in wet grasslands that, while not being widespread in Western Europe, once covered large areas of Central Europe, which since the middle of last century have largely been drained and either turned into cropland or transformed to highly productive meadows or pastures (Rosenthal et al. 1998). In the lowlands of northern Germany, wet grasslands lost about 88% of their area between the 1950's and 2008 (Wesche, Krause, Culmsee, & Leuschner, 2009; Krause et al., 2011). The altered frequencies of single species (Appendix S1) show that the wet grassland specialists

have almost completely vanished. In the two studies spanning the longest time intervals between original and re-surveys, vascular plant species richness dropped by more than 60% (Wittig, Waldmann, & Diekmann, 2007; Immoor, Zacharias, Müller, & Diekmann, 2017). As indicated by altered mean Ellenberg values, the underlying likely causes are a decrease in soil moisture due to drainage and an increase in soil nutrients, accompanied by higher mowing frequency, favouring species of drier soils with a high mowing and / or grazing tolerance, high competitive ability and high fodder value such as many grasses, namely *Alopecurus pratensis* and *Lolium perenne* (Wesche et al., 2012; Immoor et al., 2017). A rare case study from the Holtumer Moor area (NW Germany) with original plots from 1963 and re-surveys both in 1988 and 2006 showed that the strongest changes had already taken place until the mid 1980s, but also that land use intensification and subsequent vegetation changes have continued since then (Wittig et al., 2007). In western Central Europe, intact wet grasslands are currently largely confined to nature reserves where conservation management is conducted (Table 1, study numbers 8, 10–13; Appendix S2a, study number 6). In our study, the maintenance of a constantly high water level or even re-wetting in some cases even resulted in an increase in total species richness and in the number of specialists, as shown in a large-scale and long-term restoration project at Lake Dümmer in NW Germany (Blüml, 2011; Blüml, Belting, Diekmann, & Zacharias, 2012).

The decrease in species richness at the local scale (α-diversity) was not only caused by a loss of the many rare species in an otherwise unchanged matrix of common taxa, but was accompanied by a pronounced shift in species composition as evidenced by (a) ordinations (results not shown, but see, for example, Immoor et al., 2017) suggesting a complete or partial turnover of communities, (b) an increase in the frequency of some species groups, including tall grasses (e.g., *Alopecurus pratensis*) and ruderal species (*Rumex obtusifolius*, *Stellaria media*), and (c) very high pair-wise Jaccard dissimilarities between old and new plots (Appendix S5). A part of this dissimilarity is certainly due to methodological problems of re-surveys (plot re-location error, differences in plot size, differences in observer expertise). However, we compared the Jaccard values of our meta-analysis with corresponding values of wet grasslands from a monitoring program in the region of Bremen, NW Germany, using data of 50 grassland sites from two areas with very stable environmental conditions (water level) and management (mowing or grazing regime, fertilization). Here, the mean Jaccard indices over a period of 10–12 years were 0.405 and 0.349, in contrast to values ranging from 0.552 to 0.886 in the meta-analysis. More importantly, in the latter the

replacement component was mostly higher than 80%, while it reached only 66% and 69% in the monitoring programme. In general, more reference data is needed to distinguish systematic, environment-driven changes in species composition from random changes or spurious effects related to methodological problems.

Unexpectedly, there was no homogenization of the wet grasslands, rather the contrary. Unlike in forests for which most studies indicate a homogenization in species composition, within-data set similarities in grasslands appear to change in an idiosyncratic way: biotic homogenization was shown for example for Pampa grasslands (Puhl, Perelman, Batista, Burkart, & León, 2014), whereas no trends or even a "heterogenization" was observed in a wide range of grasslands in Scotland (Mitchell et al., 2017). Urban Grasslands (homogenization) responded differently from rural grasslands (no change in similarity) in southern Australia (Zeeman, McDonnell, Kendal, & Morgan, 2017). A possible explanation for the decrease in the overall homogeneity of species composition is that the wet grasslands in former times were managed in a relatively uniform way, with mowing twice a year and the constant application of moderate amounts of fertilizer, while there is currently a stronger divergence into on the one hand intensively managed grasslands (with high fertilizer doses and repeated mowing and / or grazing) and on the other hand extensively managed sites often being part of agri-environmental schemes, or abandoned grasslands.

Compared to wet grasslands, dry grasslands offer very different environmental conditions: in Western and Central Europe usually being confined to south-exposed slopes with shallow soils under rather warm and dry climates, they are water-limited and partly also nutrient-limited. Many sites cannot or only to a small extent be improved by fertilization, because plants simply lack water to take advantage of the added nutrients (Leuschner & Ellenberg, 2017). Dry grasslands on very shallow and dry soils have therefore rarely been transformed to crop fields, but either been abandoned or, for conservation purposes, been protected and continuously managed in a traditional way, many since several decades. The vegetation changes are therefore expected to be clearly less pronounced than in wet grasslands, and time series data for Germany (Diekmann et al., 2014; see also Schuch et al. 2011) and a spatial analysis from the UK (Maskell, Smart, Bullock, Thompson, & Stevens, 2009) have indeed found few differences in total species richness across time or regions. Only in two of the six studies species richness had significantly declined, in both cases the authors suggested nitrogen deposition to be the main underlying force (Hagen, 1996; Bennie et al., 2006; see discussion below). However, decreased intensities of mowing and grazing – indicated in four

of the six studies – can also lead to an increase in woody species and abandonment indicators, and in the long run to a higher share of more mesotrophic species, similar to the effects of eutrophication. Although there was no significant correlation between the changes in species richness and changes in the numbers of species of the above-mentioned groups, the decline in the number of dry grassland specialists observed in three studies and the overall declining proportion of specialists with time suggest that dry grassland vegetation also changes, albeit more slowly. On the other hand, total species richness increased in two studies and the number of dry grassland species in one study, trends for which we see three possible explanations: (1) These may be caused by a better or re-installed proper management in intermittently less well managed grasslands, (2) The grasslands may have recovered from over-exploitation, especially high grazing intensity limiting species richness even with respect to some specialist species, (3) As there is a hump-shaped relationship in dry grasslands between species richness and nutrient availability (Diekmann et al., 2014), sites on highly infertile soils receiving nutrients from fertilization or nitrogen deposition may change in their environmental conditions to support a higher total number of species. This is likely the case in the study of Newton et al. (2012) where total species richness and the proportion of mesotrophic species increased at the expense of stress-tolerant specialist species. An increase in dry grassland specialists was only observed in the Kyffhäuser region in the most continental parts of Germany with rather hot and dry summers and with gypsum soils characterized by low water capacity (Hahn, Andres, & Becker, 2013). Even in this region, however, there was a decline in small annual, light-demanding species such as *Draba verna*, *Euphrasia stricta* and *Veronica praecox*, in line with the results of the spatial analysis by Diekmann et al. (2014). Generally, dry grasslands with different environmental conditions appear to respond differently to altered management and / or nutrient addition as shown by Bennie et al. (2006) for the United Kingdom, where sites on steeper and more south-exposed slopes were more resistant to vegetation change. Similar results were obtained for semi-natural grasslands on base-rich soils in SW Finland (Pykälä, Luoto, Heikkinen, & Kontula 2005). Dry grasslands on relatively mesic sites, however, were over the past decades often converted to croplands, as shown for semi-natural grasslands in Dorset in southern England (Hooftman & Bullock, 2012), and thus were excluded from this study focusing on the vegetation changes in extant grasslands.

A factor difficult to quantify is the widespread change in management type from grazing to mowing observed in many parts of Central Europe (Leuschner & Ellenberg, 2017), which may be associated with a change in general management intensity and result in altered

abundances of species being either favoured or hampered by grazing. The altered frequencies of several dry grassland species – decrease in most thorny and unpalatable species of genera such as *Carlina*, *Ononis* and *Gentianella*, increase in *Bromus erectus* (Appendix S4) – suggest that in many regions mowing in fact has increased at the expense of grazing. Even where grazing has been continued the grazing regime in terms of stocking density and grazing time may have changed and triggered subtle change in species composition. From our data, however, the causes for the dynamics of single species are difficult to disentangle. As in wet grasslands we found no general trend towards a homogenization in species composition in dry grasslands.

For the other types of semi-natural grasslands, data shortage does not allow us to draw far-going conclusions. *Arrhenatherion* meadows in lowland areas on mesic soils are likely to have declined equally much as wet grasslands, as their sites are suitable for intensive agriculture (Rosenthal et al. 1998). In northern Germany the loss of this grassland type has been even more pronounced than in wet grasslands (Wesche et al., 2009; Leuschner & Ellenberg, 2017). A different situation emerges for (sub-) mountainous *Trisetion* and *Nardetalia* communities in which productivity is partly temperature-limited making them less attractive for high-intensity agriculture. If not abandoned or transformed to forest, these grasslands are nowadays often protected and managed by conservation authorities or organizations. In the two studies of *Nardetalia* grasslands there was no change in total species richness (Figure 4), but a loss of specialist species. The study by Peppler-Lisbach & Könitz (2017) represents the only data set of our study for which also old measurements were available, and the authors conclude that the observed changes in the vegetation are likely to be caused by the combined effects of eutrophication (N deposition), recovery from acidification due to the decreasing deposition of sulphurous acid, and decreasing management intensity.

The importance of nitrogen (N) deposition for changes in grassland vegetation has been shown in several studies (for example, Stevens et al., 2004). However, in grassland types that can be improved to highly productive meadows or pastures, the effect of N deposition is masked by the addition of high amounts of fertilizers, namely in wet grasslands and possibly *Arrhenatherion* grasslands. In contrast, N deposition is the main source of additional N in naturally infertile, unimproved dry and acidic grasslands, and these two grassland types respond much differently to atmospheric pollution. As already discussed, many dry

grasslands are drought-limited, which is why the added N does not or only weakly translate into a higher productivity and altered competitive relationships. Maskell et al. (2009) did not find any correlation between plant species richness and N deposition in UK dry grasslands. Moreover, the grasslands are also co-limited by phosphorus, especially on steeper slopes (Bennie et al., 2006; Diekmann, Michaelis, & Pannek, 2015). The lime content of bedrock and soil also buffers the sites against acidification. In contrast, acidic grasslands have suffered strongly from N deposition and partly also acidification, as shown for different parts of western Europe in various papers based on both time series data (Dupré et al., 2010) and spatial comparisons (Maskell et al., 2009; Stevens et al., 2011a, b). Recent papers indicate that, while N deposition effects remain, there has been a recovery of low pH-sensitive species in some *Nardus* grasslands and other acidic grasslands, likely reflecting a decrease in acid deposition (Mitchell et al., 2017; Peppler-Lisbach & Könitz, 2017).

A factor that may contribute to the decline of habitat specialists in semi-natural grasslands is the increasing fragmentation of the sites (Rosenthal et al., 1998). For wet grasslands in the lowlands of northern Germany, Krause et al. (2015) showed that isolation only had a relatively weak effect on plot species richness and that habitat deterioration was the main driver of change. In contrast, in dry grasslands with their high number of rare species there is a negative relationship between frequency and extinction rate (Bennie et al., 2006; Sengl, Magnes, Wagner, Erdös, & Berg, 2016), suggesting frequent extinction events that are not compensated by immigration due to the often large distances to neighbouring sites with potential source populations of species. In UK grasslands, most colonizations were observed for mesotrophic species with relatively high Ellenberg N values (Bennie et al., 2006), in the long run resulting in decreasing proportions of dry grassland specialists as observed in this meta-analysis.

It remains unknown to what extent climate change may affect plant species composition and richness in grasslands, but the effects likely differ between grassland types. In dry grasslands of the Thüringen data set, for which increasing proportions of species with high Ellenberg values for temperature and continentality were found (Hahn et al., 2013), a warmer climate may counteract changes brought about by nutrient addition and altered management. However, the changes in mean Ellenberg values for T and K were relatively small and not consistent within and across grassland types, indicating that climate change either does not yet have a strong impact on semi-natural grasslands, or that its effects are masked by stronger effects of e.g. fertilization and N deposition.

5   Conclusions

The results of this meta-analysis and of other time series analyses and spatial comparisons allow us to draw the following conclusions:

(1) Except in dry grasslands for which there is no unequivocal evidence, semi-natural grasslands in Western and Central Europe show a general decline in species richness, driven by a combination of changes in management and the intentional or unintentional addition of nitrogen and other nutrients. Species losses are especially severe in habitat specialists, even in dry grasslands these tend to decrease at a slow pace. Despite a widespread increase in more mesotrophic species, there is no sign yet of a temporal homogenization.

(2) Although many, in some regions even the majority of species-rich semi-natural grasslands (especially dry ones, but not wet grasslands not being recognized as NATURA 2000 habitat) are protected and managed for conservation purposes, it appears that these measures are not sufficient to halt species loss, in particular of specialist species. A possible explanation is that mowing or grazing intensities are too low compared to the traditional management or that an altered timing of management events is unfavourable for many species. Even with an appropriate management, however, N deposition and direct fertilization may lead to species decline. It is noteworthy that conservation actions in nature reserves have succeeded particularly well in wet grasslands that otherwise have suffered most from habitat deterioration among the different grassland types. However, drained peat soils in former wet grasslands may suffer from irreversible structural changes that remain after re-wetting.

(3) To counteract a continued loss of semi-natural grasslands and their typical species, it will be pivotal to understand the underlying causes of vegetation change, which likely differ between different vegetation types. Most importantly we need to disentangle the effects of nitrogen addition and altered management, a task that depends on the access to better, both old and new, soil data, a better quantification of management and a larger and more balanced set of re-survey studies.

Data accessibility

The data sets of plots from the original and re-surveyed grasslands are stored as separate data files at the working group of the corresponding author, Institute of Ecology, University of Bremen, Germany.

References

Andres, C. (1994). *Flora und Vegetation im Naturschutzgebiet „Badraer Lehde–Großer Eller" am Kyffhäuser*. Diplomarbeit, Universität Göttingen, unpubl.

Baselga, A., & Orme, C. D. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*, 808−812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Bennie, J., Hill, M. O., Baxter, R. & Huntley, B. (2006). Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, *94*, 355−368. https://doi.org/10.1111/j.1365-2745.2006.01104.x

Blüml, V. (2011). *Langfristige Veränderungen von Flora und Vegetation des Grünlandes in der Dümmerniederung (Niedersachsen) unter dem Einfluss von Naturschutzmaßnahmen*. Dissertation, University of Bremen.

Blüml, V., Belting, H., Diekmann, M. & Zacharias, D. (2012). Erfolgreiche Grünlandentwicklung durch Naturschutzmaßnahmen – Langfristige Veränderung von Flora, Vegetation und Avifauna am Beispiel des Ochsenmoores in der Dümmerniederung. *Informationsdienst Naturschutz Niedersachsen*, *4*, 171−235.

Bobbink, R., & Willems, J. H. (1987). Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to a species-rich ecosystem. *Biological Conservation*, *40*, 301−314. https://doi.org/10.1016/0006-3207(87)90122-4

Burkart, M., Dierschke, H., Hölzel, N., Nowak, B. & Fartmann, T. (2004). *Molinio-Arrhenatheretea* (E 1). Kulturgrasland und verwandte Vegetationstypen Teil 2: Molinietalia. *Synopsis der Pflanzengesellschaften Deutschlands*, *9*, 1−103.

Chytrý, M., Dražil, T., Hájek, M., Kalniková, V., Preislerová, Z., Šibik, J, ... Vymazalová, M. (2015). The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). *Preslia*, *87*, 217−278.

Cousins, S. A. O., Ohlson, H., & Eriksson, O. (2007). Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landscape Ecology*, *22*, 723–730. https://doi.org/10.1007/s10980-006-9067-1

Dengler, J., Janišová, M., Török, P., Wellstein, C. (2014). Biodiversity of Palaearctic grasslands: a synthesis. *Agriculture, Ecosystems and Environment*, *182*, 1–14. http://dx.doi.org/10.1016/j.agee.2013.12.015

Diekmann, M., Jandt, U., Alard, D., Bleeker, A., Corcket, E., Gowing, D. J. G., ..., & Duprè, C. (2014). Long-term changes in calcareous grassland vegetation in North-western Germany – No decline in species richness, but a shift in species composition. *Biological Conservation*, *172*, 170–179.

Diekmann, M., Michaelis, J., & Pannek, A. (2015). Know your limits – The need for better data on species responses to soil variables. *Basic and Applied Ecology*, *16*, 563–572. https://doi.org/10.1016/j.biocon.2014.02.038

Dierschke, H. (1969). *Die naturräumliche Gliederung der Verdener Geest. Landschaftsökologische Untersuchungen im nordwestdeutschen Altmoränengebiet.* Forschungen Deutsche Landeskunde, 177. Bonn-Bad Godesberg, Germany.

Dierschke, H. (1979). Die Pflanzengesellschaften des Holtumer Moores und seiner Randgebiete (Nordwest-Deutschland). *Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft N.F.*, *21*, 111–143.

Dierschke, H. (1997). *Molinio-Arrhenatheretea* (E 1). Kulturgrasland und verwandte Vegetationstypen Teil 1: *Arrhenatheretalia*. *Synopsis der Pflanzengesellschaften Deutschlands*, *3*, 1–74.

Dierschke, H., & Briemle, G. (2002). *Kulturgrasland*. Eugen Ulmer, Stuttgart, Germany.

Dierschke, H. & Wittig, B. (1991). Die Vegetation des Holtumer Moores (Nordwest-Deutschland) – Veränderungen in 25 Jahren (1963-1988). *Tuexenia*, *11*, 171–190.

Duprè, C., Stevens, C. J., Ranke, T., Bleeker, A., Peppler-Lisbach, C., Gowing, D. J. G., ..., Diekmann, M. (2010). Changes in species richness and composition in European acidic grasslands over the past 70 years – the contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology 16*, 344–357. https://doi.org/10.1111/j.1365-2486.2009.01982.x

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulißen, W. (2001). Zeigerwerte von Pflanzen in Mitteleuropa. 3rd ed. *Scripta Geobotanica*, *18*, 1–258.

Eriksson, O., Cousins, S. A. O., & Bruun, H. H. (2002). Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science*, *13*, 743–748. https://doi.org/10.1111/j.1654-1103.2002.tb02102.x

Fanigliulo, M. (2013). *Veränderungen der Grünlandvegetation im Streeseebecken bei Biesenthal in Brandenburg seit 1992*. Masterarbeit, Universität Potsdam, unpubl.

Fanigliulo, M., Seitz, B. & Heinken, T. (2014). Veränderungen der Grünlandvegetation im Streeseebecken bei Biesenthal seit 1992. *Verhandlungen des Botanischen Vereins von Berlin und Brandenburg*, *147*, 13−49.

Frese, E. (1994). *Wandel des Feuchtgrünlandes im mittleren Ostetal – ein vegetationsökologischer Vergleich 1964 – 1993*. Diplomarbeit, Universität Bremen, unpubl.

Fuller, R. M. (1987). The changing extent and conservation interest of lowland grasslands in England and Wales – a review of grassland surveys 1930–84. *Biological Conservation*, *40*, 281–300.

Ganzert, C. & Pfadenhauer, J. (1987). *Vegetation und Nutzung des Grünlandes am Dümmer*. Gutachten im Auftrag des NLVA, München. Unpubl. manuscript.

Gauckler, K. (1938). Steppenheide und Steppenheidewald der Fränkischen Alb in pflanzensoziologischer, ökologischer und geographischer Betrachtung. *Berichte der Bayerischen Botanischen Gesellschaft*, *23*, 5−134.

Good, R. (1937). An account of a botanical survey of Dorset. *Proceedings of the Linnean Society of London*, *149*, 114−116.

Hagen, T. (1996). *Vegetationsveränderungen in Kalk-Magerrasen des Fränkischen Jura: Untersuchung langfristiger Bestandesveränderungen als Reaktion auf Nutzungsumstellung und Stickstoff-Deposition*. Laufener Forschungsbericht 4. Bayerische Akademie für Naturschutz und Landschaftspflege, Laufen, Germany.

Hahn, A., Andres, C. & Becker, T. (2013). Veränderungen der Steppenrasen des NSG „Badraer Lehde-Großer Eller" im Kyffhäusergebirge (Thüringen) zwischen 1993 und 2012. In: H. Baumbach & S. Pfützenreuter, S. (Eds.), Steppenlebensräume Europas – Gefährdung, Erhaltungsmaßnahmen und Schutz (pp. 101−115). Thüringer Ministerium für Landwirtschaft, Forsten, Umwelt und Naturschutz (TMLFUN), Erfurt, Germany.

Hedges, L. V., Gurevitch, J. & Curtis, P. S. (1999). The metaanalysis of response ratios in experimental ecology. *Ecology*, *80*, 1150–1156. DOI: 10.2307/177062

Heinrichs, S. & Schmidt, W. (2017). Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. *Applied Vegetation Science*, *20*, 271–281. https://doi.org/10.1111/avsc.12255

Hirst, C. N., & Jackson, D. A. (2007). Reconstructing community relationships: the impact of sampling error, ordination approach, and gradient length. *Diversity and Distributions*, *13*, 361–371. https://doi.org/10.1111/j.1472-4642.2007.00307.x

Hooftman, D. A. P., Bullock, J. M. (2012). Mapping to inform conservation: A case study of changes in semi-natural habitats and their connectivity over 70 years. *Biological Conservation, 145*, 30–38. https://doi.org/10.1016/j.biocon.2011.09.015

Immoor, A., Zacharias, D., Müller, J. & Diekmann, M. (2017). A re-visitation study (1948 – 2015) of wet grassland vegetation in the Stedinger Land near Bremen, North-western Germany. *Tuexenia*, *37*, 271–288. https://doi.org/10.14471/2015.35.004

Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F. H., & Grytnes, J.-A. (2017). Resurveying historical vegetation data – opportunities and challenges. *Applied Vegetation Science*, *20*, 164–171. https://doi.org/10.1111/avsc.12269

Kopecký, M., Hédl, R., & Szabó, P. (2013). Non-random extinctions dominate plant community changes in abandoned coppices. *Journal of Applied Ecology*, *50*, 79–87. https://doi.org/10.1111/1365-2664.12010

Krause, B., Culmsee, H., Wesche, K., Bergmeier, E. & Leuschner, C. (2011). Habitat loss of floodplain meadows in north Germany since the 1950s. *Biodiversity and Conservation*, *20*, 2347–2364. https://doi.org/10.1007/s10531-011-9988-0

Krause, B., Culmsee, H., Wesche, K., & Leuschner, C. (2015). Historical and recent fragmentation of temperate floodplain grasslands: Do patch size and distance affect the richness of characteristic wet meadow plant species? *Folia Geobotanica*, *50*, 253–266. https://doi.org/10.1007/s12224-015-9220-1

Lenski, H. (1953). Grünlanduntersuchungen im mittleren Oste-Tal. *Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft N.F.*, *4*, 26–58.

Leuschner, C, & Ellenberg, H. (2017). *Ecology of Central European Non-Forest Vegetation: Coastal to Alpine, Natural to Man-Made Habitats*. Springer Nature, Cham.

Ludwig, G., & Schnittler, M. (Eds.) (1996). Rote Liste gefährdeter Pflanzen Deutschlands. *Schriftenreihe für Vegetationskunde*, *28*, 1–744.

Luka, S. (2014). *Auswirkungen von Revitalisierungsmaßnahmen auf die Vegetationsentwicklung in drei Braunmoosmooren Brandenburgs*. Masterarbeit, Universität Potsdam, unpubl.

Maskell, L. C., Smart, S. M., Bullock, J. M., Thompson, K., & Stevens, C. J. (2010). Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, *16*, 671–679. https://doi.org/10.1111/j.1365-2486.2009.02022.x

Meisel, K. (1967). *Erläuterungen zu den Vegetationsaufnahmen und Wasserstufenkarten des Ostetales zwischen Bremervörde und Eitze sowie des unteren Bevertals*. Gutachten der Bundesanstalt für Vegetationskunde, Naturschutz und Landschaftspflege, Bonn, unpubl.

Meißner, J. (1992). Zur Entwicklung der Wiesengesellschaften im NSG "Lange-Damm-Wiesen" bei Strausberg (1952–1992). *Verhandlungen des Botanischen Vereins von Berlin und Brandenburg*, *125*, 101–130.

Mitchell, R. J., Hewison, R. L., Britton, A. J., Brooker, R. W., Cummins, R. P., Fielding, D. A., ... Riach, D. (2017). Forty years of change in Scottish grassland vegetation: Increased richness, decreased diversity and increased dominance. *Biological Conservation*, *212*, 327–336. https://doi.org/10.1016/j.biocon.2017.06.027

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., ..., Tichý, L. (2016). Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, *19*, *Suppl. 1*, 3–264. https://doi.org/10.1111/avsc.12257

Netzwerk Phytodiversität Deutschland & Bundesamt für Naturschutz (Ed.) (2013). *Verbreitungsatlas der Farn- und Blütenpflanzen Deutschlands*. Landwirtschaftsverlag, Münster, Germany.

Newton, A. C., Walls, R. M., Golicher, D., Keith, S. S., Diaz, A., & Bullock, J. M. (2012). Structure, composition and dynamics of a calcareous grassland metacommunity over a 70-year interval. *Journal of Ecology*, *100*, 196–209. https://doi.org/10.1111/j.1365-2745.2011.01923.x

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ..., Wagner, H., (2016). Vegan: Community Ecology Package. R Package Version 2.4-1. http://CRAN.Rproject.org/package=vegan

Partzsch, M. (2007). Flora, Vegetation und historische Entwicklung der Porphyrkuppenlandschaft zwischen Halle und Wettin (Sachsen-Anhalt). *Schlechtendalia*, *15*, 1–91.

Payne, R. J., Dise, N. B., Field, C. D., Dore, A. J., Caporn, S. J. M., & Stevens, C. J. (2017). Nitrogen deposition and plant biodiversity: past, present, and future. *Frontiers in Ecology and the Environment*, *15*, 431–436. https://doi.org/10.1002/fee.1528

Peppler, C. (1987). *Nardetalia*-Gesellschaften im Werra-Meißner-Gebiet. *Tuexenia*, *7*, 245−265.

Peppler-Lisbach, C. & Könitz, N. (2017). Vegetationsveränderungen in Borstgrasrasen des Werra-Meißner-Gebietes (Hessen, Niedersachsen) nach 25 Jahren. *Tuexenia*, *37*, 201−228.

Perring, F. (1956). *Climatic and edaphic gradients of chalk grassland*. PhD Thesis, Queens College, Cambridge University, Cambridge, UK.

Perring, F. (1958). A theoretical approach to the study of chalk grassland. *Journal of Ecology*, *46*, 665−679. DOI: 10.2307/2257544

Perring, F. (1959). Topographical gradients of chalk grassland. *Journal of Ecology*, *47*, 447−481. DOI: 10.2307/2257376

Perring, F. (1960). Climatic gradients of chalk grassland. *Journal of Ecology*, *48*, 415−442. DOI: 10.2307/2257526

Plate, H. (1949). *Ein Beitrag zur Kenntnis der Grünlandvegetation in Stedingen und ihre Beziehungen zu den Grundwasserverhältnissen*. Unpubl. manuscript.

Puhl, L. E., Perelman, S. B., Batista, W. B., Burkart, S. E., & León, R. J. C. (2014). Local and regional long-term diversity changes and biotic homogenization in two temperate grasslands. *Journal of Vegetation Science*, *25*, 1278–1288. https://doi.org/10.1111/jvs.12179

Pykälä, J., Luoto, M., Heikkinen, R. K., & Kontula, T. (2005). Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic and Applied Ecology*, *6*, 25−33. https://doi.org/10.1016/j.baae.2004.10.002

R Core Team (2016). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Raehse, S. (1999). *Veränderungen der hessischen Grünlandvegetation seit Beginn der 50er Jahre am Beispiel ausgewählter Tal- und Bergregionen Nord- und Mittelhessens*. Dissertation, Universität Kassel, Germany.

Reinecke, J., Klemm, G., & Heinken, T. (2014). Vegetation change and homogenization of species composition in temperate nutrient-deficient Scots pine forests after 45 yr. *Journal of Vegetation Science*, *25*, 113−121. https://doi.org/10.1111/jvs.12069

Rich, T. C. G., Cooper, E. A., Rodwell, J. S. & Malloch, A. J. C. (1993). *Effects of climate change and air pollution on British calcicolous ecosystems*. Final report to UK Department of the Environment, UK.

Rosenthal, G. & Müller, J. (1988). Wandel der Grünlandvegetation im mittleren Ostetal - Ein Vergleich 1952-87. *Tuexenia*, *8*, 79–99.

Rosenthal, G., Hildebrand, J., Zöckler, C., Hengstenberg, M., Mossakowski, D., Lakomy, W., & Burfeindt, I. (1998). Feuchtgrünland in Norddeutschland: Ökologie, Zustand, Schutzkonzepte. *Angewandte Landschaftsökologie 15*, 1–291.

Schuch, S., Bock, J., Leuschner, C., Schaefer, M., & Wesche, K. (2011). Minor changes in orthopteran assemblages of Central European protected dry grasslands during the last 40 years. *Journal of Insect Conservation*, *15*, 811–822. https://doi.org/10.1007/s10841-011-9379-6

Seitz, B. (1994). Die Vegetation des Streesee-Beckens bei Biesenthal. *Verhandlungen des Botanischen Vereins von Berlin und Brandenburg*, *127*, 87–115.

Sengl, P., Magnes, M., Wagner, V., Erdös, L., & Berg, C. (2016). Only large and highly-connected semi-dry grasslands achieve plant conservation targets in an agricultural matrix. *Tuexenia*, *36*, 167–190. DOI: 10.14471/2016.36.008

Stevens, C. J., Dise, N. B., Mountford, J. O., & Gowing, D. J. G. (2004). Impacts of nitrogen deposition on the species richness of grasslands. *Science*, *303*, 1876–1879. DOI: 10.1126/science.1094678

Stevens, C. J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D. J. G., Bleeker, A., ..., Dise, N. B. (2011a). The impact of nitrogen deposition on acid grasslands in the Atlantic region of Europe. *Environmental Pollution, 159*, 2243–2250. https://doi.org/10.1016/j.envpol.2010.11.026

Stevens, C. J., Duprè, C., Gaudnik, C., Dorland, E., Dise, N. B., Gowing, D. J. G., ..., Diekmann, M. (2011b). Changes in species composition of European acid grasslands observed along a gradient of nitrogen deposition. *Journal of Vegetation Science*, *22*, 207–215. https://doi.org/10.1111/j.1654-1103.2010.01254.x

Stevens, D. P., Smith, S. L. N., Blackstock, T. H., Bosanquet, S. D. S., & Stevens, J. P. (2010). *Grasslands of Wales: A survey of lowland species-rich grasslands, 1987–2004*. University of Wales Press, Cardiff.

Sutorius, M. (1979). *Erfassung und Kartierung der Pflanzengesellschaften im Bereich des Naturschutzgebietes Hohe Sieben, des Naturschutzgebietes Dümmer/Vogelwiese und der Teichwiesen im Randbereich des Dümmer*. Unpubl. manuscr., Hannover, Germany.

Timmermann, A., Damgaard, C., Strandberg, M. T., & Svenning, J. C. (2015). Pervasive early 21st-century vegetation changes across Danish semi-natural ecosystems: more losers

than winners and a shift towards competitive, tall-growing species. *Journal of Applied Ecology*, *52*, 21–30. https://doi.org/10.1111/1365-2664.12374

Török, P., & Dengler, J. (2018). Palaearctic grasslands in transition: Overarching patterns and future prospects. In V. R. Squires, J. Dengler, H. Feng & L. Hua (Eds.), *Grasslands of the world: diversity, management and conservation* (pp. 15–26). Boca Raton, US: CRC Press.

van den Berg, L. J. L., Vergeer, P., Rich, T. C. G., Smart, S. M., Guest, D., & Ashmore, M. R. (2011). Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. *Global Change Biology*, *17*, 1871–1883. https://doi.org/10.1111/j.1365-2486.2010.02345.x

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., ..., Verstraeten, G. (2012). Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*, *100*, 352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Verheyen, K., De Frenne, P., Baeten, L., Waller, D. M., Hédl, R., Perring, M. J., ..., Bernhard-Römermann, M. (2017). Combining biodiversity resurveys across regions to advance global change research. *Bioscience*, *67*, 73–83. https://doi:10.1093/biosci/biw150

Wesche, K., Krause, B., Culmsee, H. & Leuschner, C. (2009). Veränderungen in der Flächen-Ausdehnung und Artenzusammensetzung des Feuchtgrünlandes in Norddeutschland seit den 1950er Jahren. *Berichte der Reinhold-Tüxen-Gesellschaft*, *21*, 196–210.

Wesche, K., Krause, B., Culmsee, H. & Leuschner, C. (2012). Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. *Biological Conservation*, *150*, 76–85. http://dx.doi.org/10.1016/j.biocon.2012.02.015

Wilson, B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: the world records. *Journal of Vegetation Science*, *23*, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Wittig, B., Waldmann, T. & Diekmann, M. (2007). Veränderungen der Grünlandvegetation im Holtumer Moor über vier Jahrzehnte. *Hercynia*, *40*, 285–300.

Zeeman, B. J., McDonnell, M. J., Kendal, D., & Morgan, J. W. (2017). Biotic homogenization in an increasingly urbanized temperate grassland ecosystem. *Journal of Vegetation Science*, *28*, 550–561. https://doi.org/10.1111/jvs.12507

Zelený, D. & Schaffers, A. P. (2012). Too good to be true: pitfalls of usingmean Ellenberg indicator values in vegetation analyses. *Journal of Vegetation Science*, *23*, 419–431. https://doi.org/10.1111/j.1654-1103.2011.01366.x

Zielonkowski, W. (1973). Wildgrasfluren der Umgebung Regensburgs. Vegetationskundliche Untersuchungen an einem Beitrag zur Landespflege. *Hoppea*, *31*, 1–183.

Supporting information

Appendix 1. List of wet grassland specialists

Appendix 2. Comparison of species richness of old and new, non-traceable plots of wet grasslands from Germany

Appendix 3. Mean Ellenberg indicator values of plots in the 23 original surveys of grasslands

Appendix 4. Mean response ratios and confidence intervals for the differences in mean Ellenberg L, T and K values between re-surveyed and original plots

Appendix 5. Within-data set Jaccard dissimilarity of old plots and new plots

Appendix 6. List of dry grassland specialists

TABLE 1 Data sources for the meta-analysis of vegetation changes in semi-natural grasslands. The studies are divided into different grassland types and, within grassland type, ordered according to the number of years between original and re-survey.

Study number / Reference of re-survey	Year(s) of re-survey	Plot size of re-survey [m²]	Reference of original survey	Year(s) of original survey	Plot size of original survey [m²]	No. of plots	Country	Region
Wet grasslands (Molinietalia)								
(1) Immoor et al. (2017)	2015	20	Plate (1949)	1948	unknown	52	Germany	Stedinger Land NW Bremen, Niedersachsen
(2) Wittig et al. (2007)	2006	25	Dierschke (1969, 1979)	1963-64	10-100	109	Germany	Holtumer Moor SE Bremen, Niedersachsen
(3) Raehse (1999) – Table VI.II	1990	25	Unpublished	1950-66	unknown	34	Germany	Hessen
(4) Raehse (1999) – Table VI.III	1990	25	Unpublished	1950-63	unknown	56	Germany	Hessen
(5) Raehse (1999) – Table VI.I	1990	25	Unpublished	1950-66	unknown	34	Germany	Hessen
(6) Rosenthal & Müller (1988)	1987	4	Lenski (1953)	1952	4	27	Germany	Ostetal E Bremen, Niedersachsen
(7) Raehse (1999) – Table V	1990-91	25	Unpublished	1950-73	unknown	29	Germany	Hessen

(8) Blüml et al. (2012)	2008	25	Sutorius (1979)	1979	25	34	Germany	Lake Dümmer, Niedersachsen
(9) Frese (1994)	1993	20-30	Meisel (1967)	1964	20-30	264	Germany	Ostetal E Bremen, Niedersachsen
(10) Luka (2014)	2013	25	Meißner (1992)	1991-92	25	18	Germany	Lange Damm Wiesen, Brandenburg
(11) Blüml et al. (2012)	2008	25	Ganzert & Pfadenhauer (1988)	1987	mostly 50-60	60	Germany	Lake Dümmer, Niedersachsen
(12) Unpublished	2016	25	Blüml et al. (2012)	1995	25	29	Germany	Lake Dümmer, Niedersachsen
(13) Fanigliulo (2014)	2011	mostly 16	Seitz (1994)	1992	mostly 16	44	Germany	Streeseebecken bei Biesenthal, Brandenburg

Dry grasslands (Festuco-Brometea)

(14) Newton et al. (2012)	2009	2 h survey	Good (1937)	1931-36	1 h survey	69	United Kingdom	Dorset, S England
(15) Hagen (1996)	1989-91	4-100 (mostly 25)	Gauckler (1938)	1931-36	6-100 (mostly 25)	36	Germany	Fränkischer Jura, Bayern
(16) Bennie et al. (2006)	2001-03	*ca* 50	Perring (1956, 1958, 1959,	1952-53	*ca* 50	92	United Kingdom	East Anglia (27 plots), Kent (7), Dorset (43),

								Yorkshire Wolds (15)
			1960)					
(17) Hagen (1996)	1989-91	4-80 (mostly 25)	Zielonkowski (1973)	1968-70	6-50 (mostly 25)	47	Germany	Fränkischer Jura, Bayern
(18) Hahn et al. (2013)	2012	1-16	Andres (1994)	1993	1-16	134	Germany	Kyffhäuser Mountains, Thüringen
(19) Van den Berg et al. (2011)	2006-09	144	Rich et al. (1993)	1990-93	144	48	United Kingdom	Across Great Britain

Other types of grasslands

(20) Raehse (1999) – Table II; *Nardetalia*	1990-91	25	Unpublished	1950-73	unknown	30	Germany	Hessen
(21) Peppler-Lisbach & Könitz (2017); *Nardetalia*	2012	4-30	Peppler (1987)	1986-87	4-30	66	Germany	Hessen, Niedersachsen
(22) Raehse (1999) – Table VIII; *Trisetion*	1990-91	25	Unpublished	1950-73	unknown	46	Germany	Hessen
(23) Raehse (1999) – Table IX; *Arrhenatherion*	1990-91	25	Unpublished	1950-73	unknown		Germany	Hessen

TABLE 2 Relationship between mean Jaccard dissimilarity (total and separately for the replacement and nestedness components) between all pairs of original and re-surveyed plots in a study and the time between surveys, response ratios of mean Ellenberg indicator values, and response ratios of species richness of the corresponding study, calculated for the 13 studies of wet grasslands. Pearson correlation coefficients (*r*) and *p* values (in bold when < 0.05) are given.

	Total dissimilarity		Replacement		Nestedness	
	r	*p*	*r*	*p*	*r*	*p*
Years between surveys	0.720	**0.006**	0.653	**0.016**	0.186	0.453
Response ratio for						
mean Ellenberg F value	-0.482	0.095	-0.426	0.147	-0.159	0.604
mean Ellenberg R value	0.780	**0.002**	0.671	**0.012**	0.325	0.279
mean Ellenberg N value	0.837	**<0.001**	0.771	**0.002**	0.190	0.535
Total species richness	-0.928	**<0.001**	-0.843	**<0.001**	-0.248	0.415
Number of habitat specialists	-0.826	**<0.001**	-0.771	**0.002**	-0.155	0.613

FIGURE 1 Mean response ratios (*RR*) and 95% confidence intervals (CI) for the difference in species richness between re-surveyed and original plots in 13 studies of wet grasslands from Germany, related against the time (in years) between the two surveys. CI not overlapping with the dashed line at $RR = 0$ indicate significant changes (at $p < 0.05$). The left panel shows the results for total species richness, the right panel those for the number of habitat specialists for wet grasslands.
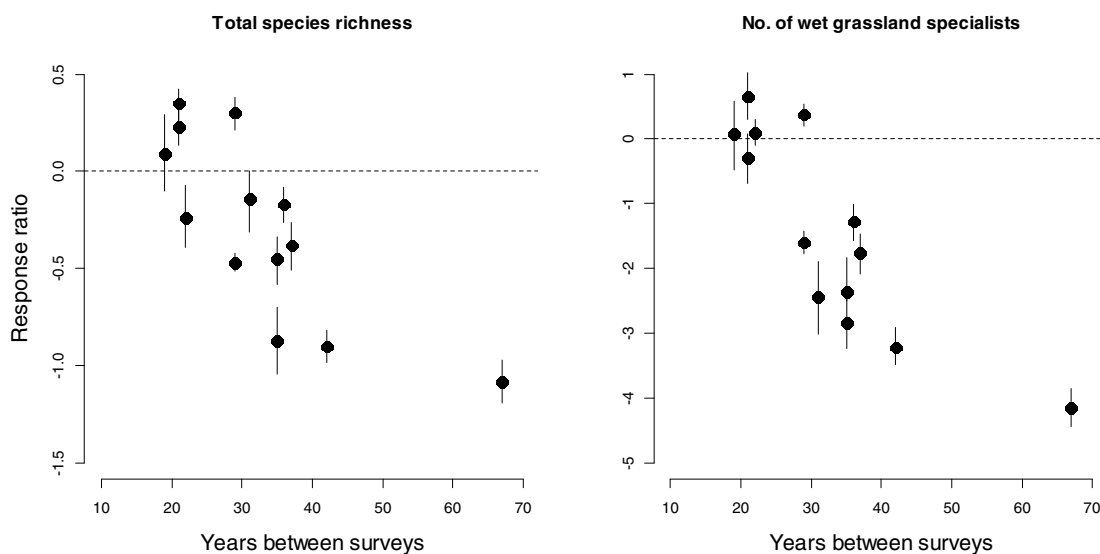
FIGURE 2 (a) Mean response ratios (*RR*) and 95% confidence intervals (CI) for the difference in mean Ellenberg indicator values for soil moisture (mF, left panel) and soil nitrogen (mN, right panel) between re-surveyed and original plots in 13 studies of wet grasslands from Germany, related against the time (in years) between the two surveys. The "2" indicates an overlap of the means and CI of two studies. CI not overlapping with the dashed line at *RR* = 0 indicate significant changes (at *p* < 0.05). (b) Relationship between the response ratios (*RR*) for total species richness and mean Ellenberg values for soil moisture (mF, left panel) and soil nitrogen (mN, right panel).
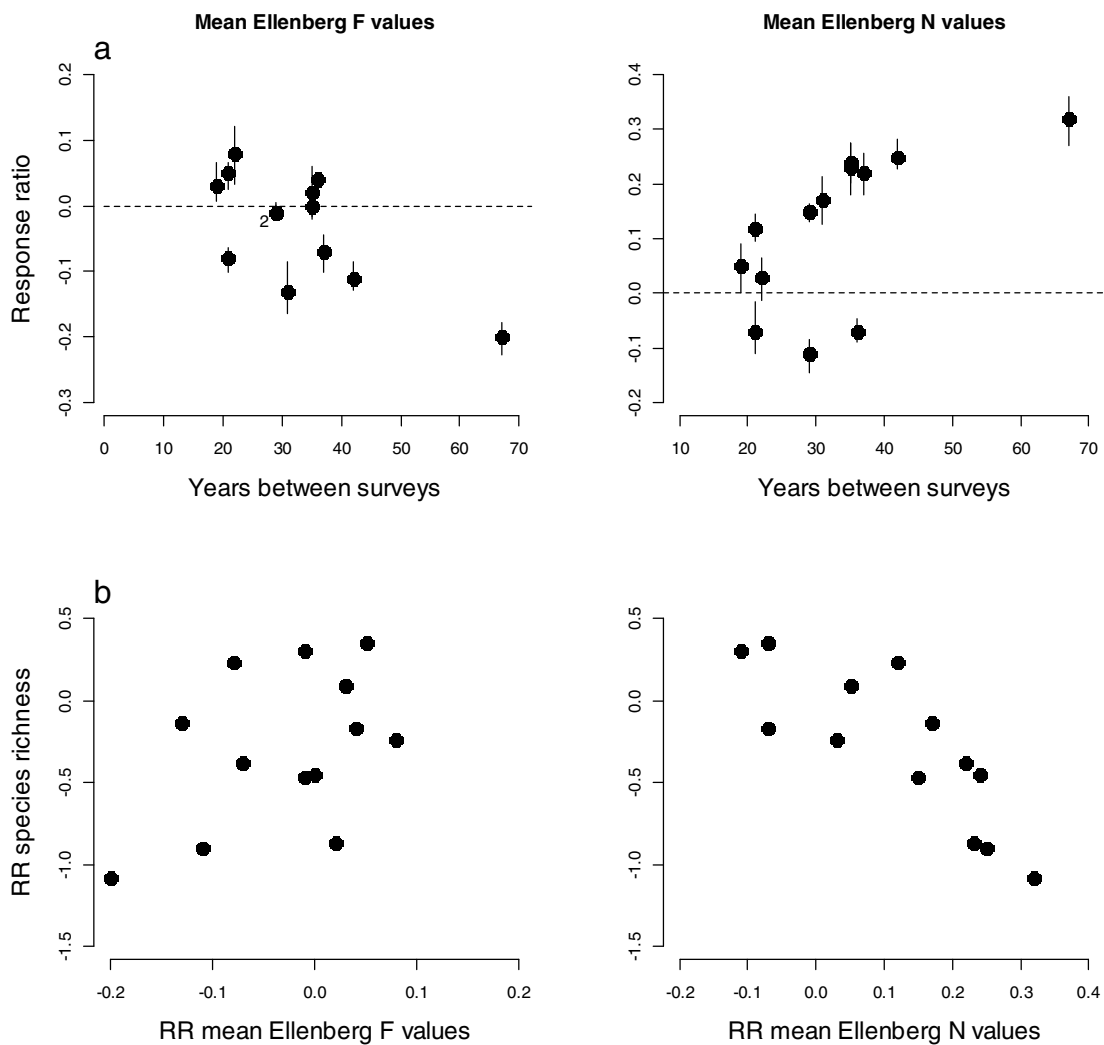
FIGURE 3 Mean response ratios (*RR*) and 95% confidence intervals (CI) in relation to time (in years) between the two surveys of six studies of dry grasslands, given (a) for the difference in species richness (total and the number of dry grassland specialists) between re-surveyed and original plots, and (b) for the temporal change in mean Ellenberg indicator values (for soil moisture (mF) and nitrogen (mN)). CI not overlapping with the dashed line at *RR* = 0 indicate significant changes (at $p < 0.05$).
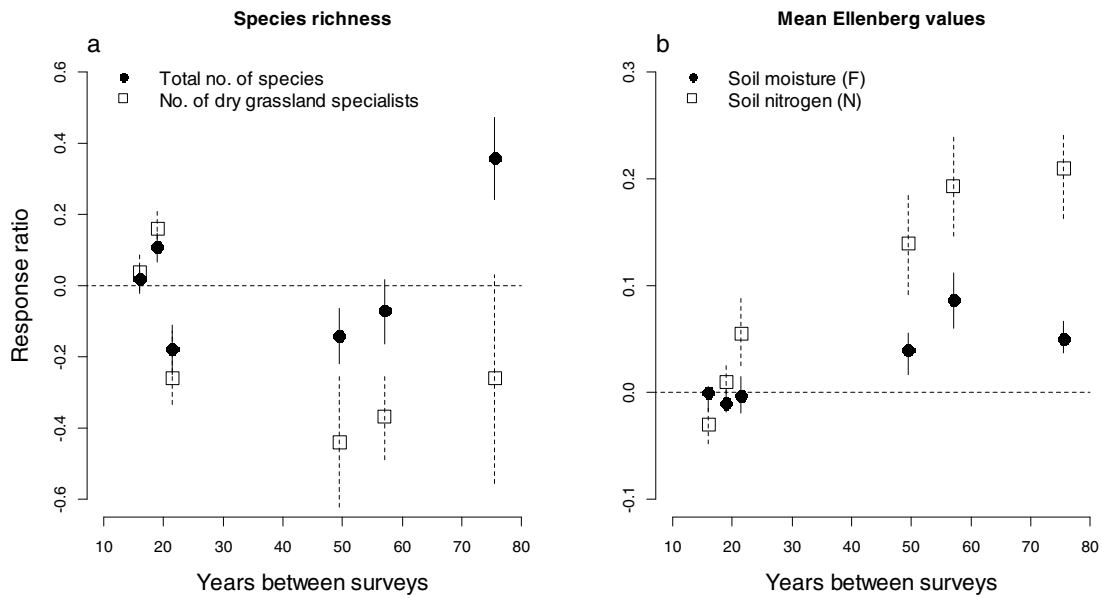
FIGURE 4 Mean response ratios (*RR*) and 95% confidence intervals (CI) of four studies of semi-natural grasslands (two data sets with *Nardetalia* plots, and one each with *Trisetion* and *Arrhenatherion* grasslands), given (a) for the difference in species richness (total and the number of habitat specialists) between re-surveyed and original plots, and (b) for the temporal change in mean Ellenberg indicator values (for soil reaction (mR) and nitrogen (mN)). CI not overlapping with the dashed line at *RR* = 0 indicate significant changes (at *p* < 0.05).