RESEARCH ARTICLE

Long-term vegetation changes in *Nardus* grasslands indicate eutrophication, recovery from acidification, and management change as the main drivers

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Abstract

Questions: Which trends and patterns of community change occurred in *Nardus* grasslands over recent decades in parts of the Continental biogeographic region of Germany? Are patterns and trends consistent across two study regions? Do impacts of environmental changes on *Nardus* grasslands in Central Europe correspond to those identified in the European Atlantic biogeographic region?

Location: East Hesse Highlands, Germany.

Methods: In 2012–2015, we re-surveyed quasi-permanent plots that had been initially surveyed between 1971 and 1987, and re-measured soil parameters. We tested for differences in species frequency and cover, mean Ellenberg indicator values, species richness, and soil variables. Nitrogen and sulphur deposition data were analysed to evaluate possible effects of atmospheric pollutants. We used regression and redundancy analyses to identify environmental drivers responsible for changes in species composition.

Results: Across regions, we found significant increases in soil pH, Ellenberg *R* and *N* indicator values, plant nutrient indicators, forbs, species of agricultural grasslands and of fallows. By contrast, the C:N ratio, *Nardus* grassland specialists, low-nutrient indicators, and graminoids declined. Changes in species composition were related to changes in pH and management. There was a strong decrease in sulphur and a moderate increase in nitrogen deposition, whose local-scale pattern did not correlate with changes in soil parameters. However, there was an effect of local NH_y changes on species composition.

Conclusions: The findings indicate significant overall eutrophication, a trend towards less acidic conditions and insufficient management, which are widely consistent across our study regions and correspond to recent reports of vegetation changes and recovery from acidification in the Atlantic biogeographic region. We assume the reduced sulphur deposition during recent decades to be a major driver of these changes, combined with increased nitrogen deposition and reduced management

intensity. This suggests a large-scale validity of processes that influenced changes in *Nardus* grasslands of Western and Central Europe.

1 | INTRODUCTION

Semi-natural grasslands are of high importance to human well-being, by providing important ecosystem services and high biodiversity (Hejcman *et al.*, 2013; Dengler *et al.*, 2014). They are, however, under threat by effects of global-change drivers (Sala *et al.*, 2000). Recent decades brought evidence for the important role of atmospheric depositions, mainly of nitrogen (N) and sulphur (S), on grassland biodiversity (Morecroft *et al.*, 2009). Consequences for European semi-natural grasslands are the loss of species diversity, a change in species composition, and a decline of ecosystem functions (Bobbink *et al.*, 2010; Phoenix *et al.*, 2012; Stevens *et al.*, 2004).

Nardus grasslands are typical semi-natural grasslands on acid soils in large parts of temperate Europe. They are often also referred to as "acid grasslands" (Damgaard *et al.*, 2011; Stevens *et al.*, 2011). *Nardus* grasslands are highly endangered by global-change drivers. Among these drivers, mainly abandonment and land-use intensification have driven the decline of *Nardus* grasslands in Central Europe since the late 19th century (Leuschner & Ellenberg, 2017). Moreover, their preference for poorly buffered, nutrient-poor soils makes them particularly vulnerable to processes of eutrophication and acidification (Duprè *et al.*, 2010; Helsen *et al.*, 2014). In the European context, species-rich *Nardus* grasslands are classified as a priority natural habitat (H6230*) of the EU Habitats Directive (Directive 92/43/ EEC, European Council, 1992). Thus, conservation efforts of the European community aim to protect these grasslands in a favourable conservation status. The goal of this study was to investigate long-term changes in *Nardus* grasslands in the Continental biogeographic region and to show the extent to which drivers of these changes hinder the conservation of this habitat type.

Eutrophication summarises the effects of nutrient enrichment, mainly of nitrogen or phosphorus, which can be attributed to both agricultural fertilisation and atmospheric deposition (Bobbink *et al.*, 2010; Ceulemans *et al.*, 2013). Eutrophication results in the loss of species due to competitive exclusion of light-demanding, poorly competitive species and other changes in species and functional composition (Bobbink & Hicks, 2014; Helsen *et al.*, 2014). Acidification is mainly driven by atmospheric deposition of N (NH_y, NO_x) and S (SO_x), but is also modified by local factors such as soil characteristics (Roy *et al.*, 2014). Acidification results in decreasing pH values, leaching of base cations, Al^{3+} mobilisation, and higher ratios of Al:Ca and $NH_4:NO_3$ (Kleijn *et al.*, 2008; Stevens & Dise, 2009; Ross *et al.*, 2012). These effects are considered to be responsible for the decline and regional extinction of low-growth *Nardus* grassland

and heathland species in The Netherlands (Fennema, 199; de Graaf *et al.*, 19981). Additionally, soil acidification may lead to reduced nutrient availability, preventing the effects of N deposition from being effective (Stevens *et al.*, 2010).

Studies on the effects of N deposition on acid grasslands were predominantly from the Atlantic biogeographic region of Europe. Commonly reported effects are a decrease in total species richness, a decline in typical acid grassland or heathland species adapted to low-nutrient availability, an increase in graminoid cover, but a decrease in graminoid richness (Stevens *et al.*, 2010; Damgaard *et al.*, 2011; Field *et al.*, 2014; Payne *et al.*, 2017). Moreover, decreases in forb and bryophyte cover and richness were found (Stevens *et al.*, 2006). Ellenberg indicator values for nitrogen (*N*) increased with increasing N deposition (Henrys *et al.*, 2011; Pakeman *et al.*, 2016), whereas Ellenberg indicator values for soil reaction (*R*) decreased due to N deposition-driven acidification (Maskell *et al.*, 2010). Regarding environmental factors, soil pH was negatively correlated with N deposition rates, whereas the C:N ratio showed a significant positive relationship with N deposition (Stevens *et al.*, 2006, 2011).

While S deposition, after peaking in the 1980/1990s, decreased considerably over the last two decades in many European regions (Teufel & Gauger, 1994; Morecroft *et al.*, 2009; Kirk et al., 2010), N deposition rates are still at a high level (Dentener *et al.*, 2006), especially for NH_y (Gauger *et al.*, 2013). Morecroft *et al.* (2009) and McGovern *et al.* (2011) associated decreasing SO_x deposition with increasing soil pH values, but did not observe any vegetation recovery from acidification. Hence, Stevens *et al.* (2016) assumed longer timescales for recovery signals of the vegetation. The predictions of Stevens *et al.* (2011) about the impacts of N deposition on soil (pH, $NH_y:NO_x$ ratio) and species shifts (from stress-tolerant species to more competitive species) were recently found to hold for acid grasslands (Rose *et al.*, 2016; Mitchell *et al.*, 2018).

The effects of land-use changes contribute additionally to long-term N and S deposition-driven vegetation changes in semi-natural grasslands (Humbert *et al.*, 2016). For example, infrequent mowing and low or reduced grazing intensity promote dwarf shrubs and tall tussock grass species due to the lower intensity of disturbance. Simultaneously, characteristic small-growing *Nardus* grassland specialists are outcompeted, and specific habitat structures, like increased litter or moss cover, are facilitated (Arens & Neff, 1997; Armstrong *et al.*, 1997). By contrast, an intensive management of *Nardus* grasslands by increased livestock grazing, and early, and more frequent, mowing favours highly competitive common grassland species and the homogenisation of community structures (Mariotte *et al.*, 2013).

This study is based on the local-scale investigations of Peppler-Lisbach and Könitz (2017), who detected long-term changes in *Nardus* grasslands in a small study area in Central Germany (Fulda–Werra Bergland). Eutrophication effects were revealed, but no acidification, during the time span of the re-survey and indeed indications were found of recovery from acidification. For the present study, we aimed to upscale findings from the local to a regional scale by considering and adding data from a second re-survey study from the Continental biogeographic region. Moreover, we aimed to detect common trends and spatial patterns between changes in deposition, soil parameters, and species composition, to gain insights into causal relationships between spatially explicit changes in N and S deposition regimes and vegetation change via environmental factors. Accordingly, we hypothesise that there have been considerable changes in N and S deposition rates between the initial survey and the re-survey in both study regions. As a result, we expected that changes in ecosystem-relevant depositions influenced changes in soil conditions, which can be identified exemplarily by a decrease in C:N ratio and an increase in soil pH, as indications for eutrophication and recovery from acidification, respectively. Hence, we assumed that both changes in soil chemical drivers and possible changes in management would have induced significant changes in vegetation composition of *Nardus* grasslands, not only within but also across regions. This would confirm recently observed long-term vegetation changes having a consistent pattern across regions, and would support a cross-territorial consistent recovery trend from acidification as reported by Rose *et al.* (2016) and Mitchell *et al.* (2018) from the Atlantic biogeographic region.

2 | METHODS

2.1 | Study regions

The study regions (Fulda–Werra Bergland, FWB, and Rhön Mountains, RHN) are parts of the East Hesse Highlands in the Central German low mountain range and are about 100 km apart from each other. Both areas have a bedrock predominantly built of Triassic sandstone, which is locally (FWB) or dominantly (RHN) covered by Tertiary basalt. The elevation of the study plots varies from 230 m to 720 m a.s.l. (FWB) and 570 m to 940 m a.s.l. (RHN). The climate is sub-oceanic, with a mean annual precipitation of 650–1,000 mm and a mean annual temperature of 5–9°C (Klink, 1969; Bohn *et al.*, 1996).

2.2 | Data collection

2.2.1 | Vegetation surveys

The study is based on a re-survey of vegetation plots of *Nardus* grasslands (*Nardetalia strictae*, *Violion caninae*) (Peppler-Lisbach & Petersen, 2001). Plots (97 in total) were initially surveyed in 1971 by von Borstel (1974) ($n = 10$, RHN) and in 1986/87 ($n = 87$; RHN: 27,

FWB: 60) by Peppler (1992), respectively. The plots in each of the study regions were re-surveyed in 2012 (FWB) and 2014/15 (RHN) and could be re-localized to a precision of five to ten meters. Plot sizes were taken from the initial surveys and varied between 6 m^2 and 50 m^2 (mean 23.6 m^2, *SD* 8.2 m^2). Woody plant specimens with a height between 0.5 m and 5 m were assigned to the shrub layer, those >5 m to the tree layer. To eliminate influences of direct fertilisation and succession, we excluded re-survey plots in RHN that had experienced agricultural intensification, and plots that experienced advanced, undisturbed, secondary succession since the initial survey (i.e. shrub/tree layer >60% cover). Hence, all remaining plots are either within protected areas or managed according to agri-environment schemes without fertilisers. Species cover/abundance values were harmonised on the standard Braun-Blanquet scale (r, +, 1–5). The plots can be classified as "quasi-permanent plots" (Kapfer *et al.*, 2017), as they were not permanently marked but could be re-localized using precise hand-drawn maps and geographical coordinates. The recommendations of Kapfer *et al.* (2017) to reduce the inherent error in this source of re-surveyed data were followed.

2.2.2 | Soil sampling and analysis

Mixed soil samples of the upper 0–10 cm (auger diameter 5 cm, taken from three sample points) were collected during the re-survey. Samples were thoroughly mixed to ensure homogeneity and were sieved to <2 mm for further processing. Soil pH was measured electrometrically in deionised water (relevés of Peppler, 1992) and 1 N KCl solution (relevés of von Borstel, 1974). To examine the C:N ratio (CN), the total C and N content of all soil samples was analysed using a CN element analyser (vario MAX CHN; Elementar Analysensysteme GmbH, Langenselbold, Germany and Flash EA 2000; Thermo Fisher Scientific, Dreieich, Germany).

2.2.3 | Data on sulphur and nitrogen deposition

Deposition rates for both study regions were extracted for each plot from national modelling studies of airborne N (NH_y, NO_x, N_{total}) and S (SO_x) pollution between 1987 and 2007, with a spatial resolution of 1 km × 1 km (Gauger *et al.*, 2000, 2002; Gauger & Kölbe, 2008; Gauger, 2010). Our plots were situated within 40 different grid cells (FWB: 21, RHN: 19). These modelled data are, nationwide, the only available data on N and S deposition in Germany that cover both study regions in the relevant period of comparison. Earlier modelled or measured data, to provide cumulative deposition rates prior to the initial survey, were not available.

2.3 | Data analysis

Vegetation relevés were taxonomically harmonised. For doing so, some taxa had to be merged to aggregates (*Alchemilla vulgaris*

agg., *Festuca ovina* agg. [including the character species *Festuca filiformis*], and *Ranunculus polyanthemos* agg.). Species were assigned to species groups according to three criteria (Appendix S1). Sociological groups based on their occurrence in certain syntaxa were:

- Character species (C, *Nardetalia* specialists in open habitats including heathland species according to Peppler-Lisbach & Petersen, 2001)
- Other low-productive grassland species (D, species of anthropo-zoogenic heathlands/grasslands according to Ellenberg *et al.*, 2001 with an Ellenberg *N* indicator value of <4)
- Species of agricultural grasslands (G, species of anthropo-zoogenic heathlands/grasslands and an Ellenberg *N* indicator value of ≥4)
- Species of fallows (F, species of forests, forest clearings and fringes according to Ellenberg *et al.*, 2001, including trees and shrubs)

Functional groups consist of graminoids (Poaceae, Cyperaceae, and Juncaceae) and forbs (all other herbaceous, non-graminoid species). Ecological groups were defined according to species Ellenberg *R* and *N* indicator values: nutrient indicators ($N > 5$), basiphytic low-nutrient indicators ($N < 4$ and $R > 5$) and acidophytic low-nutrient indicators ($N < 4$ and $R < 4$). For each sociological and ecological species group, species numbers and cumulative cover were calculated for all the 194 initial and re-survey relevés. For functional groups, we calculated the proportional richness and cover in relation to all species (trees and shrubs excluded), and the grass:forb ratio. For quantitative analyses of species cover values, original Braun-Blanquet cover codes were transformed to percentage values. For all relevés, cover-weighted and unweighted (presence/absence) mean indicator values were calculated.

We derived the differences for all variables (*v*, i.e. species numbers, cumulative cover, environmental variables) between the initial survey (t_1) and the re-survey (t_2) as $\Delta v = v(t_2) - v(t_1)$. To quantify changes in deposition rates, we averaged deposition rates for the modelling period 1987–1989 (representing t_1) and 2005–2007 (representing t_2). ΔSO_x, ΔNH_y and ΔNO_x were calculated accordingly. General trends in Δv were tested by one-sample Wilcoxon tests (equivalent to a paired two-sample Wilcoxon test, package "exactRankTest" Hothorn & Hornik, 2017). To test for differences between study regions, we used two-sample exact Wilcoxon tests on Δv and with study region as the grouping variable. Changes in soil variables, management, richness, and species groups were tested for the plot-based dataset with $80 \leq n \leq 97$, depending on data availability.

To test for effects of environmental drivers and study regions, we calculated linear regression models for Δv as the dependent variable and differences in soil variables (ΔpH, ΔCN), changes in management (ΔM, three categories: xF [continuously or recently fallow, reference category], FM [t_1: fallow, t_2: managed], MM [t_1: managed, t_2: managed]), elevation (m a.s.l.), and study region as predictor variables. To improve normality, dependent variables were Box–Cox

transformed prior to the analyses. The selection of variables was by stepwise selection based on the Bayesian Information Criterion.

To analyse the effects of changes in N and S deposition on species composition, we pooled plot values (vegetation data, soil variables, management) per grid cell to account for pseudo-replication caused by plots situated within the same grid cell of the deposition data set ($n = 40$). As pooled values per grid cell, we used means ($\Delta cover$, ΔpH, ΔCN), medians ($\Delta presence/absence$), or the management category (ΔM). Median $\Delta presence/absence$ values of 0.5/−0.5 were assigned to 1 and −1, respectively, to re-transform data to integer values.

As a complementary approach to test for effects of drivers (ΔpH, ΔCN, ΔM, ΔSO_x, ΔNH_y, ΔNO_x) and study area on the entire species composition, we employed redundancy analyses (RDA) of species differences ($\Delta sqrt[cover]$ or $\Delta presence/absence$) and tested with permutation tests (R package "vegan," Oksanen et al., 2015. These analyses were performed at the plot level ($n = 80$), or, when including deposition changes, with the pooled dataset ($n = 40$). For deposition variables, we conducted single-variable RDAs with study area as the first constraining variable, the relating deposition change variable as the second constraining variable and, additionally, their interaction with study region. Study region was taken as the first constraining variable to partial out local differences in species composition that could have been caused by other study region-specific factors.

For all statistical analyses that included soil and structural variables, the number of observations varied with the availability of reference data and can be found in the results tables. All statistical analyses were conducted with the statistical software R 3.6.1 (R Core Team, 2017). The nomenclature follows the German taxonomic reference list (GermanSL version 1.3) of Jansen and Dengler (2008).

3 | RESULTS

3.1 | Changes in management

Contrary to the generally high number of abandoned plots of the initial survey, with 58 (i.e. 60%) fallow plots, at the time of the re-survey, most plots (80, i.e. 82%) were managed (Table 1). Only three plots in the RHN and none in the FWB had been abandoned after the first survey. Concerning management type, mowing was realised in 77% and grazing in 33% of all managed plots in the initial survey. This proportion changed due to an increase of grazed plots to 63% and 37%, respectively, in 2012–2015. At that time, plots were managed either by late mowing (August or September) or by low-intensity grazing. Unfortunately, there was no consistent information available about the management of the plots between the two surveys and, in particular, about exact dates of re-introduced management on initially fallow plots.

Management change (ΔM) was translated into three categories: 17 plots were categorised as xF (i.e. fallow or managed in 1971–1987, fallow in 2012–2015), 36 as MM (managed in both periods), and 44 as FM (fallow-managed). The ΔM categories had an uneven altitudinal distribution (ANOVA: $F_{2,94} = 13.18$, $p < 0.001$), with MM

concentrated at high elevations (mean 732 m a.s.l., *SD* 172 m a.s.l.), FM at intermediate elevations (mean 558 m a.s.l., *SD* 143 m a.s.l.) and xF at low elevations (mean 530 m a.s.l., *SD* 223 m a.s.l.). However, only the difference between MM and the other two ΔM classes was significant (Scheffé test: $p < 0.001$).

3.2 | Changes in sulphur and nitrogen depositions

Across both regions, there was a drastic decline in SO_x deposition between 1987 and 2007 in both regions (Table 2, Appendix S2), while NH_y and N_{total} increased at the same time, albeit less prominently. In contrast to NH_y, NO_x decreased slightly over time, with no significant change in FWB. Although decreases in SO_x and increases in NH_y were significant in both regions, there were marked differences in quantities. The reduction in SO_x was greater in RHN, whereas the increase in NH_y was greater in FWB. The NH_y:NO_x ratio increased considerably in both regions, with no difference across the regions. Hence, the net increase in N_{total} for the regions can be

attributed solely to the increase in NH_y. Changes in deposition rates of all components showed a highly significant negative correlation with elevation (ΔSO_x: $r_p = -0.92$, ΔNH_y: $r_p = -0.67$, ΔNO_x: $r_p = -0.89$ and ΔN_{total}: $r_p = -0.82$, all $p < 0.001$). Thus, within the re-survey period there were stronger declines of deposition rates at lower elevations than at higher elevations. ΔNH_y:NO_x was, however, not correlated with elevation ($r_p = 0.10$, $p = 0.56$).

3.3 | Changes in pH and C:N ratio, mean indicator values and vegetation structure

Across both regions, we found an increase in soil pH and a decrease in CN (Table 3). However, the increase in pH was only statistically significant in FWB and not in RHN. ΔpH was negatively correlated with the initial pH ($r = -0.59$, $p < 0.001$, $n = 94$). CN decreased in 52 of 80 plots, resulting in a decline in both regions. These changes coincide with general increases in mean *R* and *N* indicator values (Table 3). Out of 97 plots, 78 plots showed an increase in mean Ellenberg *N* values and 68 plots an increase in mean Ellenberg *R* values. This trend occurred across regions, although increases of presence/absence-based mean *R* and *N* were not statistically significant in RHN. There were increases in cover of the shrub and moss layer, with a significant difference between the regions, but we found no overall change in the herb layer cover across regions (Table 3). Trends of shrub and herb layers were different between regions: In FWB there was an increase in shrub and herb layer cover, whereas the shrub layer remained stable and the herb layer decreased in RHN.

3.4 | Changes in total species richness and species groups

We did not detect significant changes in total species richness. This also applies to the richness of vascular plants and bryophytes when analysed separately (results not shown). However, we detected overall qualitative and quantitative changes in almost every

TABLE 1 Management changes between time periods and regions (FWB: Fulda–Werra Bergland, RHN: Rhön Mountains)

Management		Management change category	Region		
1971–1987	2012–2015		FWB	RHN	*n*
Fallow	Fallow	xF	13	1	17
Mown	Fallow	xF	0	2	
Grazed	Fallow	xF	0	1	
Fallow	Mulched	FM	1	0	44
Fallow	Mown	FM	15	4	
Fallow	Grazed	FM	21	3	
Mown	Mown	MM	6	19	36
Mown	Grazed	MM	1	2	
Grazed	Mown	MM	2	3	
Grazed	Grazed	MM	1	2	

TABLE 2 Deposition rates of SO_x, NH_y and NO_x across regions (overall) and within regions (FWB: Fulda–Werra Bergland, RHN: Rhön Mountains)

	(a) Means						(b) Differences				*n*
	Overall		FWB		RHN						
	t_1	t_2	t_1	t_2	t_1	t_2	Δoverall	ΔFWB	ΔRHN	FWB:RHN	
SO_x	21.1	8.0	17.7	8.3	24.8	7.6	↓***	↓***	↓***	***	40/21/19
NH_y	8.7	12.5	7.7	12.2	9.7	12.7	↑***	↑***	↑***	***	40/21/19
NO_x	10.7	10.2	10.1	10.2	11.4	10.1	↓***	–	↓***	***	40/21/19
N_{total}	19.4	22.6	17.8	22.5	21.1	22.8	↑***	↑***	↑***	***	40/21/19
NH_y: NO_x	0.8	1.2	0.8	1.2	0.9	1.3	↑***	↑***	↑***	ns	40/21/19

Notes: (a) Means for 1987 (t_1) and 2007 (t_2), and (b) results of exact Wilcoxon tests: one-sample tests on ΔSO_x, ΔNH_y, ΔNO_x and FWB:RHN: two-sample tests on differences between regions. ↑ or ↓ indicate trends of change, while – indicates no change. Significance levels are indicated by: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns, not significant. *n*, number of plots (overall/FWB/RHN). See Appendix S2 for detailed results.
Units: SO_x: kg S/ha a^{-1}; NH_y, NO_x, N_{total}: kg N/ha a^{-1}

TABLE 3 Soil variables, Ellenberg indicator values and structural variables across regions (overall) and within regions (FWB: Fulda–Werra Bergland, RHN: Rhön Mountains)

	(a) Means						(b) Differences				n
	Overall		FWB		RHN					FWN: RHN	
	t_1	t_2	t_1	t_2	t_1	t_2	Δoverall	ΔFWB	ΔRHN		
Soil parameters											
Soil pH	4.49	4.80	4.40	4.65	4.73	5.16	↑***	↑***	–	*	94/58/36
Soil C:N ratio	14.06	13.42	14.65	13.85	12.55	12.30	↓***	↓***	↓***	ns	80/51/29
Ellenberg indicator values											
Mean R (cover-weighted)	3.01	3.57	3.01	3.43	3.00	3.92	↑***	↑***	↑***	ns	97/60/37
Mean R (presence/absence)	3.52	3.73	3.48	3.59	3.64	4.07	↑***	↑***	↑·	ns	97/60/37
Mean N (cover-weighted)	2.71	3.05	2.70	3.00	2.72	3.20	↑***	↑***	↑***	ns	97/60/37
Mean N (presence/absence)	2.94	3.30	2.90	3.20	3.07	3.55	↑***	↑***	↑·	ns	97/60/37
Structural variables											
Cover shrub layer (%)	0.00	2.04	0.00	2.84	0.00	0.00	↑***	↑***	–	*	87/60/27
Cover herb layer (%)	90.35	90.59	89.31	91.31	93.00	88.75	–	↑***	↓***	***	87/60/27
Cover moss layer (%)	23.01	43.65	19.98	36.94	30.75	60.75	↑***	↑***	↑***	ns	87/60/27

Notes: (a) Means for initial survey (t_1) and re-survey (t_2) and (b) results of exact Wilcoxon tests: one-sample tests on differences of variables ($\Delta v_{(t2-t1)}$) and FWB:RHN: two-sample tests on differences between regions. ↑ or ↓ indicate trends of change, while – indicates no change. Significance levels are indicated by: ·, $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns: not significant. n, number of plots (overall/FWB/RHN). See Appendix S3 for detailed results.

species group (Table 4). Regarding sociological groups, character species and other low-productive grassland species declined in number and abundance, whereas species of agricultural grasslands and fallows showed an overall increase. The latter groups increased significantly only in FWB. Other low-productive grassland species declined in cover only in RHN, but not in FWB. For ecological groups, there was a general increase of nutrient indicators and a significant decrease of acidophytic and basiphytic low-nutrient indicators in both richness and cover. Regarding functional groups, graminoids decreased proportionally in cover but not in richness, whereas forbs increased both quantitatively and qualitatively. The grass:forb ratio showed a decrease across regions, but qualitatively only in RHN.

3.5 | Changes in individual species: winners and losers

A considerable number of species showed either a significant total increase (14 species) or a decrease (19 species) in frequency and/or abundance (Appendix S4). Declining species mainly belonged to the groups of character species (e.g. *Arnica montana*, *Danthonia decumbens*, *Nardus stricta*, *Calluna vulgaris*) and other low-nutrient indicators (e.g., *Festuca ovina* agg., *Briza media*, *Thymus pulegioides*, *Carex panicea*). Ellenberg R (mean 3.4) and N (mean 2.5) indicator values of decreasing species were low. Increasing species

were notably those of agricultural grasslands (e.g. *Holcus lanatus*, *Trifolium pratense*, *T. repens*) or indifferent species (e.g. *Taraxacum* Sect. *Ruderalia*, *Veronica chamaedrys*, *Rhytidiadelphus squarrosus*) with higher Ellenberg R (mean 5.3) and N (mean 4.9) values. Only five species showed different changes between regions; four of them occurred only in either FWB or RHN, whilst *Campanula rotundifolia*, which occurred in both regions, showed a significantly stronger decline in FWB than in RHN.

3.6 | Drivers of floristic change: regression models

The results of the regression models indicate which environmental variables had an influence on changes in species composition at the plot level (Table 5, Appendix S5). The most important predictor was ΔpH, which influenced most of the dependent variables positively. Only richness of graminoids was negatively related to ΔpH.

Contrary to our expectations, we found no effect of ΔpH on mean N indicator values, acidophytic low-nutrient indicators, character species, or on the grass:forb ratio. ΔCN had a minor influence, with a partially negative effect on graminoids. Ongoing abandonment had a significantly positive effect on richness and abundance of fallow species. Region had no significant influence, except on the cover of character species, cover of other low-productive grassland species, cover of species of agricultural grasslands, and cover of

TABLE 4 Total species richness, richness, and cumulative cover of species groups across regions (overall) and within regions (FWB: Fulda–Werra Bergland, RHN: Rhön)

| | (a) Means | | | | | | (b) Differences | | | | |
| | Overall | | FWB | | RHN | | | | | FWN: | |
	t_1	t_2	t_1	t_2	t_1	t_2	Δoverall	ΔFWB	ΔRHN	RHN	n
Species richness											
Total species richness	30.61	32.10	29.59	30.71	33.20	35.65	–	–	–	ns	97
Sociological species groups											
Richness of character species	9.13	7.52	9.16	7.86	9.05	6.65	↓***	↓***	↓*	ns	97/60/37
Cover of character species	82.77	62.41	75.00	66.22	102.60	52.70	↓***	↓*	↓***	ns	97/60/37
Richness of other low-productive grassland species	8.32	7.10	8.10	6.84	8.90	7.75	↓***	↓***	↓*	ns	97/60/37
Cover of other low-productive grassland species	36.14	31.90	33.68	36.59	42.40	19.95	↓*	–	↓***	***	97/60/37
Richness of species of agricultural grasslands	6.80	9.04	6.33	7.92	8.00	11.90	↑**	↑***	–	ns	97/60/37
Cover of species of agricultural grasslands	32.55	44.58	33.14	48.86	31.05	33.65	↑**	↑***	–	***	97/60/37
Richness of species of fallows	0.90	1.69	1.02	2.04	0.60	0.80	↓***	↓***	–	*	97/60/37
Cover of species of fallows	2.80	6.14	2.73	7.88	3.00	1.70	↓**	↓***	–	**	97/60/37
Ecological species groups											
Richness of nutrient indicators	1.10	2.30	1.02	2.00	1.30	3.05	↑***	↑***	↑**	ns	97/60/37
Cover of nutrient indicators:	2.82	6.23	2.41	6.24	3.85	6.20	↑***	↑***	–	ns	97/60/37
Richness of basiphytic low-nutrient indicators	1.54	1.01	1.43	0.86	1.80	1.40	↓***	↓***	↓*	ns	97/60/37
Cover of basiphytic low-nutrient indicators	4.68	3.28	4.53	3.37	5.05	3.05	↓***	↓**	↓**	ns	97/60/37
Richness of acidophytic low-nutrient indicators	8.63	7.38	8.59	7.55	8.75	6.95	↓***	↓**	↓*	ns	97/60/37
Cover of acidophytic low-nutrient indicators	75.04	54.54	69.86	57.00	88.25	48.25	↓***	↓**	↓***	*	97/60/37
Functional species groups											
Proportional richness of graminoides	0.43	0.40	0.44	0.43	0.40	0.33	↓·	–	↓·	ns	97/60/37
Proportional cover of graminoids	0.58	0.53	0.57	0.54	0.60	0.50	↓**	↓*	↓·	ns	97/60/37
Proportional richness of forbs	0.51	0.56	0.49	0.53	0.55	0.64	↑***	↑**	↑**	ns	97/60/37
Proportional cover of forbs	0.35	0.40	0.36	0.38	0.32	0.44	↑**	↑*	↑**	ns	97/60/37
Grass:Forb ratio (presence/absence)	1.20	1.00	1.26	1.15	1.05	0.64	↓*	–	↓*	ns	97/60/37
Grass:Forb ratio (cover)	2.72	2.13	2.49	2.18	3.31	2.03	↓*	–	–	ns	97/60/37

Notes: (a) Means for initial survey (t_1) and re-survey (t_2) and (b) results of exact Wilcoxon tests: one-sample tests on differences of variables ($\Delta v_{(t2-t1)}$) and FWB:RHN: two-sample tests on differences between regions. ↑ or ↓ indicate trends of change, while – indicates no change. Significance levels are indicated by: ·, $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns, not significant. n, number of plots (overall/FWB/RHN). See Appendix S3 for detailed results.

TABLE 5 Multiple linear regression models of environmental change drivers (ΔpH, ΔCN, management change, ΔM) and region on changes in species composition at the plot scale

	R^2	ΔpH	ΔCN	ΔM: FM	ΔM: MM	RHN
Ellenberg indicator value						
Δmean R value (cover-weighted)	0.16***	↑***				
Δmean R value (presence/absence)	0.24***	↑***				
Δmean N value (cover-weighted)	ns					
Δmean N value (presence/absence)	ns					
Species richness						
Δtotal richness	0.20***	↑***				
Sociological species groups						
Δrichness of character species	ns					
Δcover of character species	0.14**					↓**
Δrichness of other low-productive grassland species	0.29***	↑***				
Δcover of other low-productive grassland species	0.20***	↑***				↓***
Δrichness of species of agricultural grasslands	0.15***	↑***				
Δcover of species of agricultural grasslands	0.14**	↑**				↓*
Δrichness of species of fallows	0.12**				↓**	
Δcover of species of fallows	0.19***			↓**	↓***	
Ecological species groups						
Δrichness of nutrient indicators	0.08*	↑*				
Δcover of nutrient indicators	ns					
Δrichness of basiphytic low-nutrient indicators	0.21***	↑***				
Δcover of basiphytic low-nutrient indicators	0.09**	↑**				
Δrichness of acidophytic low-nutrient indicators	ns					
Δcover of acidophytic low-nutrient indicators	0.11**					↓*
Functional species groups						
Δproportional richness of graminoids	0.14**	↓**	↓*			
Δproportional cover of graminoids	0.07**		↓*			
Δproportional richness of forbs	0.12**	↑**				
Δproportional cover of forbs	0.08**	↑**				
Δgrass:forb ratio (presence/absence)	ns					
Δgrass:forb ratio (cover)	ns					

Notes: R^2 and overall significance level of the model. RHN: region Rhön Mountains in contrast to region FWB, ΔM categories: fallow to managed (FM) and continuously managed (MM) in contrast to fallow. ↑ or ↓ indicate trends of regression coefficients. Significance levels are indicated by: ·, $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns, not significant. See Appendix S5 for detailed results.

acidophytic low-nutrient indicators. All these groups showed significantly greater decreases in RHN than in FWB.

3.7 | Drivers of floristic change: redundancy analysis

Significant effects of ΔpH and ΔM on species composition (cover-weighted and presence/absence plot dataset with $n = 80$) were revealed by the RDA models (with single predictive variables), whereas ΔCN had no effect (Table 6). In most models, study region had a partial effect on species composition, reflecting the different a priori species compositions of the two regions. However, study region had no additional effect on presence/absence data of species when ΔM

was the constraining variable. An interaction effect with study region was found only for ΔM in cover-weighted species data.

Based on these results, we calculated the minimal adequate multiple RDA models on cover-weighted and presence/absence species data, which included both ΔpH and FF (as the only significant factor level of ΔM) as constraining variables and study area as conditioning variable. In both ordinations, axis 1 reflects species composition shifts connected to changes in soil pH, and axis 2 composition shifts connected to management changes, which were, however, mainly restricted to FWB (Appendix S6). Species arrows and correlations with species group changes indicate a positive response of nutrient indicators and/or basiphytes (e.g., *Plantago lanceolata*, *Rumex acetosa*, *Thymus pulegioides*) to increasing pH, and a negative response

	P (v)	P (SR)	P (v:SR)	Total variance	Constrained variance	%-explained
(a) Changes in soil parameters and management (plot dataset, $n = 80$)						
Cover-weighted species data						
ΔpH	**0.002**	**0.001**	0.176	139.68	10.24	7.33
ΔCN	0.589	**0.001**	0.102	139.68	8.03	5.75
Δmanagement	**0.003**	**0.005**	**0.010**	139.68	14.34	10.26
Presence/absence species data						
ΔpH	**0.001**	**0.003**	0.113	24.62	1.55	6.30
ΔCN	0.918	**0.004**	0.692	24.62	1.01	4.09
Δmanagement	**0.006**	0.123	0.288	24.62	1.89	7.67
(b) Changes in deposition (grid cell-pooled dataset, $n = 40$)						
Cover-weighted species data						
ΔSO$_x$	0.091	**0.001**	0.208	139.68	8.58	6.14
ΔNH$_y$	0.130	**0.001**	0.081	139.68	8.72	6.24
ΔNO$_x$	0.152	**0.001**	**0.002**	139.68	9.04	6.47
Presence/absence species data						
ΔSO$_x$	**0.004**	**0.036**	0.300	24.62	1.23	4.98
ΔNH$_y$	**0.003**	**0.007**	0.481	24.62	1.25	5.07
ΔNO$_x$	**0.003**	0.052	**0.006**	24.62	1.39	5.64

TABLE 6 Results of single-variable RDA models of cover-weighted and presence/absence species data including interaction with study region

Notes: (a) Soil parameters and management change and (b) deposition data. Given are the results (p values, significant values with $p < 0.05$ set in bold) of permutation tests on additional effects of the respective variable (v), effects of the study region (SR), and interactions.

of acidophytic species (e.g., *Nardus stricta*, *Vaccinium myrtillus*, acidophytic bryophytes). Woody species, *Molinia caerulea* and *Galeopsis tetrahit*, increased on fallow sites, whereas many low-productive grassland species declined.

3.8 | Effects of sulphur and nitrogen deposition on environmental variables and species composition

Regression analyses showed no significant effects of S or N deposition changes (ΔSO$_x$, ΔNH$_y$, ΔNO$_x$) on pooled ΔpH and ΔCN (results not shown). In the RDAs, none of the deposition change variables showed additional effects on cover-weighted species change when study area was the first constraining variable (Table 6). In contrast, we found significant effects of ΔNH$_x$ and, though less pronounced, ΔSO$_x$ for the presence/absence species change, irrespective of study region. For ΔNO$_x$, an interaction effect was detected indicating that the effect on species composition was restricted to one of the regions (i.e. RHN).

To combine effects of soil and deposition change (ΔpH and ΔNH$_y$), while taking into account other factors that influence species composition and the deposition regime, we calculated a multiple RDA model for presence/absence species data with ΔpH and ΔNH$_y$ as constraining variables and ΔM, elevation and study region as conditioning variables. The ordination diagram indicates the floristic pattern reflecting the influence of NH$_y$ change (Appendix S6). We interpret the first axis as a combined eutrophication effect of

ΔpH and ΔNH$_y$, with negative axis 1 scores linked to increasingly occurring nutrient-demanding species, a higher proportion of forbs, and increasing mean N and R indicator values. Character species and acidophytes react in the reverse manner. Axis 2 summarises remaining contrasting effects of both predictor variables, which probably reflect local acidification effects of NH$_y$. This component corresponds to a local spatial windward/leeward pattern of the plots in the Rhön Mountains, with more wind-exposed plots in the northwestern part (high axis 2 scores) and leeward southwestern plots (low axis 2 scores).

4 | DISCUSSION

Our results indicate strong eutrophication and less acidic conditions of *Nardus* grasslands in parts of the Continental biogeographic region over the past decades. In the vegetation, eutrophication was indicated by increased N indicator values (changes in means, increase in proportion of nutrient indicators, decrease in low-nutrient indicators) and a decrease in CN. The vegetation response to less acidic conditions, indicated by the increase in soil pH, was an increase in mean R indicator values and a decline of acidophytes. Consistently in both regions, ΔpH was seen to be the most important predictor for changes in total species richness and species composition on the one hand, particularly for the increase of forbs, basiphytes, and species of agricultural grasslands, and on the other hand the decrease of graminoid richness. Unexpectedly,

the significant decline of character species was not related to ΔpH, neither within nor across regions. Instead, the decline of character species for plots in FWB was related to a reduced fermented organic matter (Of) layer of the top soil (Peppler-Lisbach & Könitz, 2017).

There are several possible causes for eutrophication effects. Direct fertilisation can be ruled out in our study, because all plots were either situated within nature reserves, and therefore managed without fertilisation, or fallow. Therefore, other reasons must be taken into account. We see three potential drivers for eutrophication: firstly, increased airborne N deposition; secondly, reduced SO_x deposition with subsequent changes in nutrient availability in soils; and, thirdly, reduced management intensities with processes of auto-eutrophication and insufficient nutrient removal.

The increase of airborne N deposition can be a possible source of eutrophication in *Nardus* grasslands, since total N deposition exceeded the critical loads for this grassland type (10 to 20 kg N ha^{-1} a^{-1}), at which the community is expected to lose its stability (Bobbink & Hettelingh, 2011). However, high N deposition rates cannot explain the significant increase in soil pH. On the contrary, increased N deposition should theoretically lead to further acidification by decreasing pH values (Stevens *et al*., 2011). This is particularly true for NH_y depositions, which increased across regions during the past decades. Expected changes in species composition would be an increase of acid-tolerant species and a decline of species adapted to moderately acid to neutral soils, e.g., many species of agricultural grasslands (Stevens *et al*., 2011). Our findings show, however, the opposite picture: according to the increased soil pH, sites became more favourable for species of agricultural grasslands with higher *R* and *N* indicator values, while acidophytic species and low-nutrient indicators declined. The relevant driver for recent changes in soil pH is hence the decrease in SO_x deposition rates, particularly as there is a strong correlation between atmospheric acid depositions and topsoil pH (Stevens et al., 2009; Kirk et al., 2010). Several other studies reported effects on soil properties of declined SO_x deposition rates in Europe since the 1990s, and more recently on species composition of semi-natural grasslands (e.g. Morecroft *et al*., 2009; McGovern *et al*., 2011). Changes in soil pH also result in changes in N availability and soil $NH_4:NO_3$ ratio (Stevens *et al*., 2011). Stevens *et al*. (2011) predicted that with increasing soil pH, NH_y inputs would be progressively converted into nitrate and thus favour N-demanding, acid-intolerant species like those from agricultural grasslands. Although nitrification processes potentially bear the risk of soil acidification, increased pH values indicate that in our case, this process was overruled by decreasing SO_x depositions and the soil buffering capacity. Following Rose *et al*. (2016), Peppler-Lisbach and Könitz (2017) and Mitchell *et al*. (2018), we suggest therefore that the changes observed during this study are governed significantly by recovery from acidification due to decreasing SO_x depositions. This interpretation would explain the combined pattern of decreasing acidification and eutrophication.

Contrary to our expectations, local patterns of changes in soil parameters were not related to local patterns of N and S deposition. However, we detected an effect of NH_y and SO_x deposition change on local patterns of floristic change in the RHN, which may also be the case for differences in floristic changes between FWB and RHN, as deposition rates changed differently between regions and across elevations. We were not able to separate deposition effects from other drivers differing between the study regions. Other studies covering a wider geographical range detected significant common patterns of N deposition and floristic change (Duprè *et al*., 2010). The reason for the relatively low influence of the local deposition change patterns in our study could be that the overall magnitudes of change in atmospheric deposition acted as a master factor that overcompensated local variations. Hence, deposition changes might have governed the general pattern of floristic changes, but can only poorly explain local differences (Damgaard *et al*., 2011).

Another factor that contributes to eutrophication is reduced management intensity supporting "auto-eutrophication," i.e. the promotion of tall-growing, N-demanding species with an internal nutrient cycling resulting in less nutrient losses through biomass removal (Leuschner & Ellenberg, 2017). The lack of detailed information on temporal management changes between the two surveys, and the unbalanced design, limit the interpretation of inter-correlations between management history and vegetation change. Nevertheless, on fallow sites we can confirm that fallow indicator species were favoured and that small herbaceous species declined accordingly. This pattern has been reported in several studies of secondary succession in *Nardus* grasslands (Schwabe *et al*., 2019). Interestingly, fallow species not only increased in fallow plots, they were still present in former fallow plots in which management had been re-established prior to the re-survey. This could be due to legacy effects of the fallow period that were still detectable despite the re-introduced management (Arens & Neff, 1997; Hansson & Fogelfors, 2000), or, alternatively, to insufficient suppression of fallow species by current late and low-intensity management (Schiefer, 1982; Scheidel & Bruelheide, 2004). Generally, we have no indication of mediating effects by management on the identified soil and vegetation change, which indicates that the deposition-related drivers and management act rather independently.

The results show widely consistent long-term changes in *Nardus* grasslands across our study regions and confirm the local-scale findings of Peppler-Lisbach and Könitz (2017). We were hardly able to detect any contrasting results, except that total herb cover increased in FWB but decreased in RHN. Differences in quantity or significance between regions relate mainly to changes of some sociological species groups. For example, changes in the species of agricultural grasslands might not have been significant in RHN because some sociologically indifferent taxa with a significant increase, such as *Taraxacum* sect. *Ruderalia* or *Veronica chamaedrys*, were not classifiable to this group. Moreover, an unbalanced distribution of management change classes was mainly responsible for differing significance between study regions. At the species level, most species with significant changes displayed the same trend in both regions,

and significant differences could largely be explained by the lack of the relevant species in the species composition in one of the study regions. The fact that pH did not increase significantly in RHN fits in the general pattern that soils with high initial pH show a less pronounced pH recovery than more acidic soils (Kirk *et al.*, 2010), which were more frequent in FWB. Moreover, the RHN plots included a few plots with organic soils, which tend to show a weak pH recovery due to a lack of weatherable minerals (Kirk *et al.*, 2010).

Generally, a minimum level of inaccuracy in re-surveying quasi-permanent plots cannot be entirely excluded, and minor variations between the regions could be linked to this methodological issue, although the re-localisation accuracy was similar in both study regions (Kapfer *et al.*, 2017). However, the ecological consistency of the results suggests that a possible pseudo-turnover plays a minor role in our re-survey study (Ross *et al.*, 2010; Verheyen *et al.*, 2018).

In light of other European studies, our overall results across regions suggest that changes in *Nardus* grasslands follow a general trend across Europe. The patterns of eutrophication and recovery from acidification in the Continental biogeographic region are widely consistent with findings from the Atlantic biogeographic region (Stevens *et al.*, 2011; Mitchell *et al.*, 2018). However, beside atmospheric depositions, change in land use is still an important driver. Low management intensities seem to increase species losses and indirectly support eutrophication and the spread of grassland generalists (Rose *et al.*, 2016). Conservation should therefore consider these corresponding drivers in defining their efforts and measures to counteract attested biodiversity losses.

5 | CONCLUSIONS

The findings of this study highlight the risk of eutrophication as a long-term, cross-territorial, threat for species-rich *Nardus* grasslands, which range from the Atlantic into the Continental biogeographic region of Europe. Furthermore, they illustrate that both changes in the deposition regime of air pollutants and in management have contributed to species turnover. Due to the constantly high eutrophication pressure, appropriate management becomes a challenging issue. To compensate for N depositions and more favourable mineralisation conditions, measures such as regular management, earlier mowing dates, and moderately increased grazing intensities could become increasingly important. This underpins the importance of expanded conservation efforts to protect the high biodiversity of *Nardus* grassland under future global change (Stevens *et al.*, 2016). Moreover, this study highlights the relevance of long-term data, in combination with re-surveys, to support a consistent understanding of environmental driver interactions and their impacts on biodiverse, semi-natural grasslands.

AUTHOR CONTRIBUTIONS
CPL, NK, NS, and GR designed the study and conducted the re-survey; CPL and NS analysed the vegetation and environmental data; all authors contributed to the interpretation of the results and discussed them; CPL and NS drafted the manuscript, on which GR and NK gave critical comments and revisions. All authors gave their final approval for publication.

DATA ACCESSIBILITY STATEMENT
The data (vegetation, site and habitat characteristics) of the plots from the initial survey and re-survey that support the findings of this study are available in Zenodo.org at https://doi.org/10.5281/zenodo.3928271

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REFERENCES
Arens, R. and Neff, R. (1997). *Experimental Studies on the Conservation of Low-Intensively Managed Grasslands* (German). Bonn-Bad Godesberg: Schriftenreihe Angewandte Landschaftsökologie: H. 13.

Armstrong, R. H., Grant, S. A., Common, T. G. and Beattie, M. M. (1997) Controlled grazing studies on Nardus grassland: Effects of between-tussock sward height and species of grazer on diet selection and intake. *Grass and Forage Science*, *52*(3), 219–231. https://doi.org/10.1111/j.1365-2494.1997.tb02352.x

Bobbink, R. and Hettelingh, J.-P. (2011) *Review and Revision of Empirical Critical Loads and Dose-Response Relationships: Proceedings of an expert workshop, Noordwijkerhout, 23–25 June 2010.* Bilthoven: RIVM.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M. et al (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Bobbink, R. and Hicks, W. K. (2014). Factors Affecting Nitrogen Deposition Impacts on Biodiversity: An Overview. In M. A. Sutton, K. E. Mason, L. J. Sheppard, H. Sverdrup, R. Haeuber, & W. K. Hicks (Eds.), *Nitrogen Deposition, Critical Loads and Biodiversity.* Dordrecht: Springer, Netherlands, pp. 127–138. https://doi.org/10.1007/978-94-007-7939-6_14

Bohn, U., Korneck, D., & Meisel, K. (1996). *Vegetation map of the Federal Republic of Germany, map CC 5518 Fulda* (German) (2nd ed). Schriftenreihe für Vegetationskunde: Vol. 15. Bonn-Bad Godesberg: BfN.

Ceulemans, T., Merckx, R., Hens, M. and Honnay, O. (2013) Plant species loss from European semi-natural grasslands following nutrient enrichment - is it nitrogen or is it phosphorus? *Global Ecology and Biogeography*, *22*(1), 73–82. https://doi.org/10.1111/j.1466-8238.2012.00771.x

Damgaard, C., Jensen, L., Frohn, L. M., Borchsenius, F., Nielsen, K. E., Ejrnæs, R. and Stevens, C. J. (2011) The effect of nitrogen deposition on the species richness of acid grasslands in Denmark: A comparison

with a study performed on a European scale. *Environmental Pollution*, 159(7), 1778–1782. https://doi.org/10.1016/j.envpol.2011.04.003

De Graaf, M. C. C., Bobbink, R., Roelofs, J. G. M. and Verbeek, P. J. M. (1998) Differential effects of ammonium and nitrate on three heathland species. *Plant Ecology*, 135(2), 185–196. https://doi.org/10.1023/A:1009717613380

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

Dentener, F., Drevet, J., Lamarque, J. F., Bey, I., Eickhout, B., Fiore, A. M. et al (2006) Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation. *Global Biogeochemical Cycles*, 20(4), n/a-n/a. https://doi.org/10.1029/2005GB002672

Duprè, C., Stevens, C. J., Ranke, T., Bleeker, A., Peppler-lisbach, C., Gowing, D. J. G. et al (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(1), 344–357. https://doi.org/10.1111/j.1365-2486.2009.01982.x

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V. and Werner, W. (2001). *Indicator Values of Plants in Central Europe (German)* (3rd ed.). Scripta geobotanica: Vol. 18. Göttingen: Goltze.

European Council. (1992) *The EU Habitats Directive (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora)*. Available at: https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A31992L0043

Fennema, F. (1991) SO2 and NH3 deposition as possible causes for the extinction of *Arnica montana* L. *Water, Air, & Soil Pollution*, 62(3), 325–336. https://doi.org/10.1007/BF00480264

Field, C. D., Dise, N. B., Payne, R. J., Britton, A. J., Emmett, B. A., Helliwell, R. C. et al (2014) The Role of Nitrogen deposition in widespread plant community change across semi-natural habitats. *Ecosystems*, 17(5), 864–877. https://doi.org/10.1007/s10021-014-9765-5

Gauger, T. (2010). Mapping of the deposition loads between 2004 and 2007, Appendix XI: Text and result statistics of the MAPESI project (Modelling of Air Pollutants and EcoSystem Impact - Detection, projection and assessment of pollutants and their effects in Germany) (German). Abschlussbericht im Auftrag des Umweltbundesamtes BMU/UBA 3707 64 200, UBA-Texte 42/2011. Dessau-Roßlau.

Gauger, T., Anshelm, F., Schuster, H., Erisman, J. W., Vermeulen, A. T., Draaijers, G. P. J., Nagel, H.-D. (2002) *Mapping of ecosystem specific long-term trends in deposition loads and concentrations of air pollutants in Germany and their comparison with Critical Loads and Critical Levels*. Berlin: Final Report on behalf of Federal Environmental Agency (Umweltbundesamt), BMU/UBA FE-No 299 42 210.

Gauger, T., Haenel, H. D., Rösemann, C., Dämmgen, U., Bleeker, A., Erisman, J. W., and Duyzer, J. H. (2008). National Implementation of the UNECE Convention on Long-range Transboundary Air Pollution (Effects), Part 1: Deposition Loads: Methods, modelling and mapping results, trends. (German): BMU/UBA 204 63 252. UBA-Texte 38/08 (1).

Gauger, T., Kölbe, R. and Anshelm, F. (2000) *Critical concentration levels and deposition loads and their exceedance in agricultural-, forest- and other nonforest semi natural-ecosystems, Part 1: Deposition Loads. Part 2: Critical Levels (German)*. Forschungsvorhaben im Auftrag des BMU/UBA, FE-Nr. 297 85 079. Universität Stuttgart, Institute of Navigation.

Gauger, T., Nagel, H.-D., Schlutow, A. and Scheuchner, T. (2013) *Generation of a Methodologically Consistent Time Series of Pollutants and Their Effects in Germany, Part 2 Final report (German)*. Dessau-Roßlau: Umweltbundesamt.

Hansson, M. and Fogelfors, H. (2000) Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. *Journal of Vegetation Science*, 11(1), 31–38. https://doi.org/10.2307/3236772

Hejcman, M., Hejcmanova, P., Pavlu, V. and Benes, J. (2013) Origin and history of grasslands in Central Europe - a review. *Grass and Forage Science*, 68(3), 345–363. https://doi.org/10.1111/gfs.12066

Helsen, K., Ceulemans, T., Stevens, C. J. and Honnay, O. (2014) Increasing soil nutrient loads of European semi-natural grasslands strongly alter plant functional diversity independently of species loss. *Ecosystems*, 17(1), 169–181. https://doi.org/10.1007/s10021-013-9714-8

Henrys, P. A., Stevens, C. J., Smart, S. M., Maskell, L. C., Walker, K. J., Preston, C. D. et al (2011) Impacts of nitrogen deposition on vascular plants in Britain: An analysis of two national observation networks. *Biogeosciences*, 8(12), 3501–3518. https://doi.org/10.5194/bg-8-3501-2011

Hothorn, T., & Hornik, K. (2017). exactRankTests: Exact Distributions for Rank and Permutation Tests. R package version 0.8-29 [Computer software]. Available at: https://CRAN.Rproject.org/package=exactRankTests

Humbert, J.-Y., Dwyer, J. M., Andrey, A. and Arlettaz, R. (2016) Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: A systematic review. *Global Change Biology*, 22(1), 110–120. https://doi.org/10.1111/gcb.12986

Jansen, F. and Dengler, J. (2008) GermanSL – A universal taxonomic reference list for phytosociological databases in Germany (German). *Tuexenia*, 28, 239–253.

Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F. H. and Grytnes, J.-A. (2017) Resurveying historical vegetation data - opportunities and challenges. *Applied Vegetation Science*, 20(2), 164–171. https://doi.org/10.1111/avsc.12269

Kirk, G. J. D., Bellamy, P. H. and Murray Lark, R. (2010) Changes in soil pH across England and Wales in response to decreased acid deposition. *Global Change Biology*, 16(11), 3111-3119. https://doi.org/10.1111/j.1365-2486.2009.02135.x

Kleijn, D., Bekker, R. M., Bobbink, R., de Graaf, M. C. C. and Roelofs, J. G. M. (2008) In search for key biogeochemical factors affecting plant species persistence in heathland and acidic grasslands: A comparison of common and rare species. *Journal of Applied Ecology*, 45(2), 680–687. https://doi.org/10.1111/j.1365-2664.2007.01444.x

Klink, H.-J. (1969) *The physical regions on map 112 Kassel, Geographical survey of Western Germany in the scale 1:200,000 (German)*. Bonn, Bad Godesberg: Bundesforschungsanstalt für Landeskunde und Raumordnung.

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

Mariotte, P., Buttler, A., Kohler, F., Gilgen, A. K. and Spiegelberger, T. (2013) How do subordinate and dominant species in semi-natural mountain grasslands relate to productivity and land-use change? *Basic and Applied Ecology*, 14(3), 217–224. https://doi.org/10.1016/j.baae.2013.02.003

Maskell, L. C., Smart, S. M., Bullock, J. M., Thompson, K. and Stevens, C. J. (2010) Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, 16(2), 671–679. https://doi.org/10.1111/j.1365-2486.2009.02022.x

McGovern, S., Evans, C. D., Dennis, P., Walmsley, C. and McDonald, M. A. (2011) Identifying drivers of species compositional change in a semi-natural upland grassland over a 40-year period. *Journal of Vegetation Science*, 22(2), 346–356. https://doi.org/10.1111/j.1654-1103.2011.01256.x

Mitchell, R. J., Hewison, R. L., Fielding, D. A., Fisher, J. M., Gilbert, D. J., Hurskainen, S. et al (2018) Decline in atmospheric sulphur deposition and changes in climate are the major drivers of long-term change in grassland plant communities in Scotland. *Environmental Pollution*, 235, 956–964. https://doi.org/10.1016/j.envpol.2017.12.086

Morecroft, M. D., Bealey, C. E., Beaumont, D. A., Benham, S., Brooks, D. R., Burt, T. P. et al (2009) The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities

and the physical environment. *Biological Conservation*, *142*(12), 2814–2832. https://doi.org/10.1016/j.biocon.2009.07.004

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., … Wagner, H. (2015). vegan: Community Ecology Package. R package version 2.3-1 [Computer software]. Available at: https://CRAN.R-project.org/package=vegan

Pakeman, R. J., Alexander, J., Brooker, R., Cummins, R., Fielding, D., Gore, S. et al (2016) Long-term impacts of nitrogen deposition on coastal plant communities. *Environmental Pollution*, *212*, 337–347. https://doi.org/10.1016/j.envpol.2016.01.084

Payne, R. J., Dise, N. B., Field, C. D., Dore, A. J., Caporn, S. J. M. and Stevens, C. J. (2017) Nitrogen deposition and plant biodiversity: Past, present, and future. *Frontiers in Ecology and the Environment*, *15*(8), 431–436. https://doi.org/10.1002/fee.1528

Peppler, C. (1992) *The Nardus Grassland Communities (Nardetalia) of Western Germany (German)*. Dissertationes botanicae 193. Dissertationes botanicae. Vol 193. Göttingen, Berlin: Cramer.

Peppler-Lisbach, C. and Könitz, N. (2017) Vegetation changes in Nardus grasslands of the Werra-Meissner region (Hesse, Lower Saxony, Central Germany) after 25 years. *Tuexenia*, *37*, 201–228. https://doi.org/10.14471/2017.37.001

Peppler-Lisbach, C. and Petersen, J. (2001). Calluno-Ulicetea (G3), Part 1: Nardetalia strictae - Borstgrasrasen (German). Synopsis der Pflanzengesellschaften Deutschlands: H. 8. Göttingen.

Phoenix, G. K., Emmett, B. A., Britton, A. J., Caporn, S. J. M., Dise, N. B., Helliwell, R. et al (2012) Impacts of atmospheric nitrogen deposition: Responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Global Change Biology*, *18*(4), 1197–1215. https://doi.org/10.1111/j.1365-2486.2011.02590.x

R Core Team. (2017) *R: A language and environment for statistical computing [Computer software]*. Vienna, Austria: R Foundation for Statistical Computing. Available at: http://www.R-project.org/

Rose, R., Monteith, D. T., Henrys, P., Smart, S., Wood, C., Morecroft, M. et al (2016) Evidence for increases in vegetation species richness across UK Environmental Change Network sites linked to changes in air pollution and weather patterns. *Ecological Indicators*, *68*, 52–62. https://doi.org/10.1016/j.ecolind.2016.01.005

Ross, L. C., Woodin, S. J., Hester, A. J., Des Thompson, B. A. and Birks, H. J. B. (2010) How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? *Plant Ecology & Diversity*, *3*(1), 1–8. https://doi.org/10.1080/17550871003706233

Ross, L. C., Woodin, S. J., Hester, A. J., Des Thompson, B. A., Birks, H. J. B. and Wildi, O. (2012) Biotic homogenization of upland vegetation: Patterns and drivers at multiple spatial scales over five decades. *Journal of Vegetation Science*, *23*(4), 755–770. https://doi.org/10.1111/j.1654-1103.2012.01390.x

Roy, P.-O., Azevedo, L. B., Margni, M., van Zelm, R., Deschenes, L. and Huijbregts, M. A. J. (2014) Characterization factors for terrestrial acidification at the global scale: A systematic analysis of spatial variability and uncertainty. *The Science of the Total Environment*, *500*, 270–276. https://doi.org/10.1016/j.scitotenv.2014.08.099

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Wall, D. H. (2000) Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Scheidel, U. and Bruelheide, H. (2004) Experimental studies on the effect of cattle grazing of montane meadows in the Harz Mountains. *(German)*. *Hercynia N.F.*, *37*, 87–101.

Schiefer, J. (1982) Influence of the litter decomposition on the vegetation development of fallow grassland communities (German). *Tuexenia*, *2*, 209–218.

Schwabe, A., Tischew, S., Bergmeier, E., Garve, E., Härdtle, W., Heinken, T., Dierschke, H. (2019) Plant community of the year 2020: Mat

grassland (Nardus stricta grassland). *Tuexenia*, *39*, 287–308. https://doi.org/10.14471/2019.39.017

Stevens, C. J., Dise, N. B. and Gowing, D. J. G. (2009) Regional trends in soil acidification and exchangeable metal concentrations in relation to acid deposition rates. *Environmental Pollution*, *157*(1), 313–319. https://doi.org/10.1016/j.envpol.2008.06.033

Stevens, C. J., Dise, N. B., Gowing, D. J. G. and Mountford, J. O. (2006) Loss of forb diversity in relation to nitrogen deposition in the UK: Regional trends and potential controls. *Global Change Biology*, *12*(10), 1823–1833. https://doi.org/10.1111/j.1365-2486.2006.01217.x

Stevens, C. J., Dise, N. B., Mountford, J. O. and Gowing, D. J. G. (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science*, *303*(5665), 1876–1879. https://doi.org/10.1126/science.1094678

Stevens, C. J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D. J. G., Bleeker, A. et al (2010) Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental Pollution*, *158*(9), 2940–2945. https://doi.org/10.1016/j.envpol.2010.06.006

Stevens, C. J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D. J. G., Bleeker, A. et al (2011) The impact of nitrogen deposition on acid grasslands in the Atlantic region of Europe. *Environmental Pollution*, *159*(10), 2243–2250. https://doi.org/10.1016/j.envpol.2010.11.026

Stevens, C., Duprè, C., Gaudnik, C., Dorland, E., Dise, N., Gowing, D. et al (2011) Changes in species composition of European acid grasslands observed along a gradient of nitrogen deposition. *Journal of Vegetation Science*, *22*(2), 207–215. https://doi.org/10.1111/j.1654-1103.2010.01254.x

Stevens, C. J., Manning, P., van den Berg, L. J. L., de Graaf, M. C. C., Wamelink, G. W. W., Boxman, A. W. et al (2011) Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats. *Environmental Pollution*, *159*(3), 665–676. https://doi.org/10.1016/j.envpol.2010.12.008

Stevens, C. J., Payne, R. J., Kimberley, A. and Smart, S. M. (2016) How will the semi-natural vegetation of the UK have changed by 2030 given likely changes in nitrogen deposition? *Environmental Pollution*, *208*, 879–889. https://doi.org/10.1016/j.envpol.2015.09.013

Stevens, C. J., Thompson, K., Grime, J. P., Long, C. J. and Gowing, D. J. G. (2010) Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Functional Ecology*, *24*(2), 478–484. https://doi.org/10.1111/j.1365-2435.2009.01663.x

Teufel, J., Gauger, T. and Braun, B. (1994) *Influence of immissions and depositions of air pollution on Nardus grasslands in the Federal Republic of Germany (German)*. Stuttgart. (Final report of the research project No 108 02 101).

Verheyen, K., Bažány, M., Chećko, E., Chudomelová, M., Closset-Kopp, D., Czortek, P. et al (2018) Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science*, *29*(5), 812–823. https://doi.org/10.1111/jvs.12673

Von Borstel, U. O. (1974) *Studies on the vegetation development of ecologically different grassland and agricultural fallow sites in mountain ranges of Hesse (Westerwald, Rhön Mountains, Vogelsberg) (German)*. Dissertation at the Institut für Grünlandwirtschaft der Hessischen Lehr- und Forschungsanstalt für Grünlandwirtschaft und Futterbau, Eichhof. Gießen: Bad Hersfeld.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Assignment of species to species groups

Appendix S2. Detailed results of tests on differences in deposition rates

Appendix S3. Detailed results of tests on differences in soil variables, structural variables, Ellenberg indicator values, total species richness, species richness, and cover of species groups

Appendix S4. Detailed results of tests on differences in species frequency and cover

Appendix S5. Multiple linear regression models of differences in species composition and Ellenberg indicator values on environmental drivers, management change, and study region

Appendix S6. Detailed results and graphics of RDA analyses of species differences (cover-weighted and presence/absence species data)