**Title**

# Long-term vegetation change in species-rich *Nardus* grasslands of central Germany caused by eutrophication, recovery from acidification and management change

**Running head**

vegetation change in *Nardus* grasslands

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**Abstract**

*Questions*

The impact of environmental changes on species-rich *Nardus* grasslands has been documented from the Atlantic biogeographic region but not from Central Europe. Which patterns and trends of community change in species-rich *Nardus* grassland of the Continental biogeographic region occurred in past decades? Are patterns and trends similar across areas within the Continental biographic region of Germany? Do they correspond to identified changes in the Atlantic biogeographic region of Europe?

*Location*

East Hesse Highlands, Germany

*Methods*

In 2012/15, we re-surveyed vegetation relevés on quasi-permanent plots originally surveyed between 1971 and 1986/87 and re-measured soil parameters. We tested for differences in species frequency and abundance, mean Ellenberg indicator values, diversity measures and soil variables. Nitrogen and sulphur deposition data were analysed to evaluate effects of atmospheric pollutants. We used regression analyses to identify the contribution of environmental drivers to changes in species composition.

*Results*

We found significant increases in soil pH, Ellenberg R and N values, species of agricultural grasslands and grassland fallows. C:N ratio, *Nardus* grassland specialists and low-nutrient indicators declined, while changes in species composition relate to changes in pH and management. There was a strong decrease in sulphur and a moderate increase in nitrogen deposition. Local patterns in atmospheric depositions did not correlate with local changes in species composition and soil parameters.

*Conclusion*

The findings indicate significant overall eutrophication, a trend towards less acidic conditions, and insufficient management and abandonment. This is widely consistent across study areas and correspond to recent reports on vegetation changes and recovery from acidification in the Atlantic biogeographic region. We strongly assume reduction in 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 triggering changes in *Nardus* grasslands across Western and Central Europe.

**Keywords**

acid grasslands, environmental change, eutrophication, habitat management, long-term vegetation change, Nardus grasslands, nitrogen deposition, resurvey study, sulphur deposition

**Nomenclature**

The nomenclature follows the German taxonomic reference list (GermanSL version 1.3) of Jansen & Dengler (2008).

## Introduction

Semi-natural grasslands are of high importance for human well-being by providing important ecosystem services and high biodiversity (Dengler et al. 2014; Hejcman et al. 2013). They are, however, under increasing threat by effects of global change, e.g. land use change, nitrogen deposition and climate change (Sala et al. 2000). Recent decades brought increasing evidence for the important role of atmospheric depositions on grassland biodiversity, mainly nitrogen (N) and sulphur (S) (Bobbink et al. 1998; Dupré et al. 2010). 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 (*Nardetalia strictae*, Peppler-Lisbach & Petersen 2001) are typical semi-natural grasslands on strong to moderate acid soils in large parts of temperate Europe. In the European context, they are classified as the priority natural habitat H6230* (Species-rich *Nardus* grasslands on silicious substrates in mountain and submountain areas in Continental Europe) of the EU Habitats Directive (Directive 92/43/EEC, European Council 1992) and are assigned to several types in the EUNIS classification (e.g. E1.71, E1.72, E3.52, E4.31). Moreover, they are often also referred to as or included in the type 'acid grasslands' (e.g. Damgaard et al. 2011; Stevens et al. 2011b). Indicated by their high conservation status, *Nardus* grasslands are highly endangered due to global change drivers mentioned above, which apply to semi-natural grasslands in general. Among these drivers, abandonment and land-use intensification have mainly triggered the decline of *Nardus* grasslands in Central Europe since the late 19$^{th}$ century (Leuschner & Ellenberg 2017). Moreover, their preference for poorly buffered, nutrient-poor soils makes them particularly vulnerable to processes of eutrophication and acidification and thus to atmospheric depositions (Dupré et al. 2010; Helsen et al. 2014). This also applies to Atlantic heathlands (Bobbink et al. 1998; Southon et al. 2013), to which *Nardus* grasslands are floristically closely related. The goal of this study is to investigate long-term changes in *Nardus* grassland of the Continental biogeographic region and to assess the extent to which these drivers cause problems for the conservation of this endangered habitat type.

Eutrophication summarises the effects of nutrient enrichment, mainly of N or P and can be attributed to agricultural fertilisation and atmospheric deposition (Bobbink et al. 2010; Ceulemans et al. 2013). Eutrophication results in species losses due to competitive exclusion of light-demanding, low-productive species (Bobbink & Hicks 2014; Ceulemans et al. 2013; Hautier et al. 2009) and other changes in species and functional composition (Helsen et al. 2014).

Acidification is mainly driven by atmospheric deposition of N (NHy, NOx) and S (SOx), but is also modified by local factors, e.g. bedrock and soil characteristics (Roy et al. 2014). It results in decreasing pH values, leaching of base cations, $Al^{3+}$ mobilisation, and higher ratios of Al:Ca and $NH_4$:$NO_3$ (de Graaf et al. 2009; Stevens et al. 2009; Ross et al. 2012; Kleijn et al. 2008; Bobbink & Hicks 2014). These effects are considered to be responsible for the decline and regional extinction of small-growing *Nardus* grassland and heathland species (like *Arnica montana*) in the Netherlands (Fennema 1991; de Graaf et al. 1998). Additionally, soil acidification may lead to reduced nutrient availability preventing the effects of N deposition from being effective (Stevens et al. 2010b).

Studies analysing the effects of N deposition on acidic grasslands are predominantly from the Atlantic biogeographic region of Europe (European Council 1992). Most 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 (Damgaard et al. 2011; Field et al. 2014; Payne et al. 2017; Stevens et al. 2010a). Moreover, a decrease in forb and bryophyte cover and richness was found (Maskell et al. 2010; Stevens et al. 2006). Ellenberg N values increased with increasing N deposition (Henrys et al. 2011; Pakeman et al. 2016), whereas Ellenberg R values decreased due to N deposition-driven acidification (Maskell et al. 2010). Regarding environmental factors, soil pH was negatively correlated to N deposition rates, whereas C:N ratio showsed a significant positive relationship with N deposition (Stevens et al. 2006; Stevens et al. 2011a).

While S deposition, after peaking in the 1980/90s, decreased considerably over the last two decades in many European regions (Morecroft et al. 2009; Teufel et al. 1994), N deposition rates are still on a relatively high level (Dentener et al. 2006; Dupré et al. 2010), especially for NHy (Gauger et al. 2013). Morecroft et al. (2009) and McGovern et al. (2011) associated

decreasing SOx deposition with increasing pH values. At that time, both studies could not observe respective vegetation changes that reflect recovery from acidification. Hence, Stevens et al. (2016) assumed longer time scales for a recovery signal of the vegetation. Stevens et al. (2011a) highlight the effects of pH on soil NHy:NOx ratio and the specific consequences for the impact of N deposition. They predict a shift from stress-tolerant species (adapted to $Al^{3+}$ and $NH^{4+}$ toxicity) to more competitive species (preferring low NHy:NOx ratio and sensitive to $Al^{3+}$ and $NH_4$) with increasing soil pH. Indeed, more recent studies suggest that detectable recovery effects fulfil predicted changes in species composition of acid grasslands (Mitchell et al. 2018; Rose et al. 2016). Additionally, effects of changes in habitat management contribute to long-term N and S deposition driving vegetation changes in various species-rich grassland types (Humbert et al. 2016). Late or unregularly mowing and a low grazing intensity can promote dwarf shrubs and competitor species (Arens & Neff 1997; Armstrong et al. 1997).

The present study is based on investigations of Peppler-Lisbach & Könitz (2017), who analysed changes in *Nardus* grasslands (species composition and environmental factors) at local scale in a small central German area (Fulda-Werra-Bergland) within the Continental biogeographic region. The study revealed eutrophication effects (increase in species of managed grasslands and mean Ellenberg N values and a decline of *Nardus* grassland species), but no acidification during the time span of the resurvey study. Rather signs of recovery from acidification (increasing pH and Ellenberg R values) were found.

For the present study, we aimed to:

- confirm the validity of these results at the regional scale, specifically regarding the interrelations between eutrophication and recovery from acidification hypothesised by Peppler-Lisbach & Könitz (2017), by adding data of a second resurvey study from the Continental biogeographic region.

- detect common trends and spatial patterns between changes in deposition and species composition to gain insights into causal pathways from deposition to vegetation change via environmental factors, especially soil pH. For this purpose, spatially explicit data on N and S deposition were included.

- to test whether there is a regionally consistent recovery trend from acidification—as reported by Rose et al. (2016) and Mitchell et al. (2018) for the Atlantic biogeographic region—that applies to the Continental biogeographic region of Europe where no studies have addressed this topic yet.

## Material and methods

### Study areas

The study areas (local scale: Fulda-Werra-Bergland, FWB, and Rhön Mountains, RHN), are parts of the East Hesse Highlands (regional scale) in the central German low mountain range and are about 100 km apart from each other. Both areas have a geological base predominantly built of Triassic sandstone, locally (FWB) or dominantly (RHN) covered by tertiary basalt. The altitudes of the study plots vary from 230 to 720 m a.s.l. (FWB) and 570 to 940 m a.s.l. (RHN). The climate is of a sub-oceanic character with a mean annual precipitation of 650-1000 mm and mean annual air temperature of 5-9°C (FWB) and <5-8°C (RHN) (Klink 1969; Bohn et al. 1996).

### Data collection

*Vegetation surveys*

The study is based on a resurvey of vegetation relevés of species-rich *Nardus* grasslands (*Nardetalia stricae*, *Violion caninae*) (Peppler-Lisbach & Petersen 2001). The plots (97 in total) were initially surveyed in 1971 by Borstel (1974) (n=10, RHN) and 1986/87 (n=87, RHN: 27, FWB: 60) by Peppler (1992), respectively. The plots at each study area were resurveyed in 2012 (FWB, Peppler-Lisbach & Könitz 2017) and 2014/2015 (RHN). Plot sizes were taken from the initial surveys and varied between 6 and 50 m² (mean 23.6 m², sd 8.2), which corresponds to the standard community's minimum relevé area (Dierschke 1994). To eliminate the influence of direct fertilisation, we excluded resurvey plots in RHN, which experienced agricultural intensification outside of nature reserves. Hence, all remaining plots either are within protected areas and managed according to schemes excluding fertilisers or were abandoned.

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). They were not permanently marked but could be relocated using precise hand-drawn maps and geographical coordinates, following the recommendations of Kapfer et al. (2017) to reduce the inherent error in the resurveyed data from these kind of plots.

*Soil sampling and analysis*

Mixed soil samples of the upper 0-10cm (auger diameter 5cm) were collected during the resurvey. Samples were thoroughly mixed to ensure homogeneity. The soil samples were sieved to <2mm for further processing. Soil pH was measured electrometrically in deionised water and 1 N KCl solution, respectively, depending on the method used for the initial analyses. That was KCl for the relevés of Borstel (1974) and water for the other relevés of Peppler (1992). Total C and N content of the soil was analysed using a CN element analyser (vario MAX CHN – Elementar Analysensysteme GmbH and Flash EA 2000 – Thermo Fischer Scientific; Germany).

*Data on sulphur and nitrogen deposition*

Deposition rates for both study areas were extracted for each plot from national modelling studies of airborne N (NHy, NOx, Ntotal) and S (SOx) pollution between 1987 and 2007 with a spatial resolution of 1x1 km (Gauger et al. 2000; Gauger et al. 2002; Gauger et al. 2008; Gauger 2010). These modelled data are the only nationwide available data about N and S deposition in Germany covering both study areas in the relevant period of comparison. Earlier modelled or measured data, to get cumulative deposition rates prior to the original survey (e.g. Mitchell et al. 2018), were not available.

**Data analysis**

Vegetation relevés were taxonomically harmonised. For this, some taxa had to be merged to aggregates, especially *Alchemilla vulgaris* agg. Some taxa were only aggregated for analyses including individual species information for both study areas (RHN and FWB), while otherwise kept on the original taxonomical rank for calculating variables of species group diversity and indicator values, e.g. *Festuca ovina* agg. and *Ranunculus polyanthemos* agg. Species were assigned to species groups (Supplementary Information S1): character species

(C, *Nardetalia* specialists in open habitats according to Peppler-Lisbach & Petersen 2001), other low-nutrient indicators (D, species of infertile grasslands, dry grasslands, fens with N indicator values ≤3, according to Ellenberg 1992), grassland species (G, species of agricultural grassland with Ellenberg N values >3) and fallow indicators (F, including all tree and shrub species and herbaceous species of forests and forest clearings). For each species group, species numbers and cumulative abundances were calculated for all the 194 old and new relevés, respectively. Moreover, we calculated the proportional abundances as well as proportional species numbers with respect to total species richness of Leguminosae and graminoid species (Poaceae, Cyperaceae, Juncaceae) in each of the relevés. For quantitative analyses of species abundances, original Braun-Blanquet cover codes were transformed to percentage values and subsequently square-root transformed.

For all relevés, unweighted mean Ellenberg indicator values (Ellenberg 1992) were calculated. Shannon diversity indices and Shannon-based evenness values were computed using the R-package "vegan" (Oksanen et al. 2015). We derived the differences of all variables (v, i.e. species numbers, cumulative abundances, environmental variables) between the initial recordings (t1) and the resurvey (t2) as $\Delta v = v(t2) - v(t1)$. General trends in $\Delta v$ were tested by paired Wilcoxon tests (R-package "exactRankTest", Hothorn & Hornik 2017).

To quantify changes in species composition between initial and resurvey relevé, we calculated the Sørensen distance (Legendre & Legendre 2012). Two other indices were calculated to quantify specifically species gains and losses: the species loss index (SLI = n.l/n[t1]) and the species gain index (SGI = n.g/n[t2]), where n.l is the number of species no longer occurring in the resurvey relevé, n.g is the number of new species in the resurvey relevé and n[t1], n[t2] are the numbers of species in the initial and resurvey relevé, respectively.

We calculated linear regression models for $\Delta v$ as the respective dependent variable and soil variables (initial pH and CN [$pH_i$, $CN_i$], $\Delta$ pH, $\Delta$ CN), changes in management ($\Delta$M, three categories: xF [continuously or recently fallow, reference category], FM [t1: fallow, t2: managed], MM [t1: managed, t2: managed]), altitude (a.s.l.) and region (FWB, RHN) as predictor variables. Initial pH values of ten RHN plots measured originally only in KCl were corrected by $pH_icorr = pHi + 0.895$, according to the mean difference between pH ($H_2O$) and

pH (KCl) of these plots measured in 2015. Dependent variables were Box-Cox transformed prior to the analyses to improve normality. Variable selection was done by stepwise selection based on Bayes Information Criterion (BIC). To test for statistical relationships between deposition data and environmental variables, vegetation variables (including indicator values), region and time, we used linear mixed models (R-package "lme4", Bates et al. 2015) with grid cell-ID as random effect. For all statistical analyses including soil and structural variables, the number of observations varied with the availability of reference data. For regression models, 80 plots remained after omitting all observations with missing values. All statistical analyses were conducted with the statistical software R 3.4.2 (R Core Team 2017).

## Results

*Changes in management*

Contrary to the general trend of increasing abandonment in the 1970s and 1980s with 58 (=60%) fallow plots, at the time of the resurvey most of the 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, in 1971/87 77% of the managed plots had been mown. Due to an increase in grazed plots, this proportion was reduced to 63% in 2012/15. At that time, the management in both study areas was generally characterised by late mowings dates (end of July to beginning of September) and low grazing intensity.

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**Table 1** Management changes between time periods and areas (FWB: Fulda-Werra-Bergland, RHN: Rhön Mountains).

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Overall, Δ M consisted of 17 plots classified as xF (i.e. fallow in 2012/15), 36 as MM (managed in 1971/87 and in 2012/15) and 44 as FM (managed, formerly fallow). The Δ M classes had an uneven altitudinal distribution (ANOVA: $F(2, 94)=13.18$, $P<0.001$), with MM concentrated at high altitudes (mean 732m, sd 172m), FM at intermediate altitudes (mean 558m, sd 143m)

and fallows at low altitudes (530m, sd 223m). However, there was only a significant difference between MM and the other two Δ M classes (Scheffé test: $P$ <0.001).

*Changes in sulphur and nitrogen depositions*

At the regional scale, there was a drastic decline in SOx depositions between 1987/89 and 2005/07 (Linear mixed model: $P$ <0.001), while NHy and Ntotal increased at the same time ($P$ <0.001), albeit less pronounced. Contrary to NHy, NOx decreased slightly over time. Although decreases in SOx and increases in NHy and Ntotal were significant in both study areas, there were marked differences in quantity. Reduction in SOx was higher in RHN, whereas increase in NHy and Ntotal was higher in FWB (Table 2). Regarding N deposition, there were also differences between NHy and NOx in the study areas. While there was a significant increase in NHy in both study areas, there was no change of NOx in FWB but a decrease in RHN (Table 2). Consequently, NHy:NOx ratio increased considerably ($P$ <0.001) in both study areas with no significant difference ($P$ =0.292). Hence, the net increase in Ntotal in both study areas can be attributed solely to the increase in NHy.

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**Table 2.** Sulphur and nitrogen deposition rates (kg ha-1 a-1) summarised for the plots in each study area (FWB: Fulda-Werra-Bergland, RHN: Rhön Mountains) (bold: significant differences, $P$: p-value for effect of study area in mixed linear models.

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*Changes in pH and C:N ratio*

At the regional scale, we found a significant increase in pH and a significant decrease in C:N ratio (Table 3). Out of 94 plots with pH reference measurements, 65 plots (69.1%) showed an increase in pH. However, a significant increase was found in the FWB plots ($P$ <0.001) but not in the RHN plots ($P$ =0.18). C:N ratio decreased in 52 plots (65%, n=80), resulting in a significant total decline that applies also when looking at both study areas separately (FWB: $P$ =0.006, RHN: $P$ =0.011).

*Changes in indicator value variables*

There was a general increase in mean R and N values (Table 3). Out of 97 plots, 78 plots (80.4 %) showed an increase in mean N values and 68 plots (70.1 %) an increase in mean R values. While the increase of mean N values was due to both an increase in high-nutrient indicators and a decrease in low-nutrient indicators, the increase in mean R values was only due to a decline of acidophytes. Indicators of base rich conditions did not show a significant overall increase. Regarding the other indicator values, there was only a moderate decrease in mean light values. Mean values for temperature, continentality and soil moisture did not change significantly (Table 3).

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**Table 3** Differences of soil chemical variables (a) and Ellenberg indicator value variables (b) summarised for both study areas (bold: significant differences, *P*: p-value Wilcoxon-Test).

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*Changes in vegetation structure, species diversity and species groups*

Overall, there were significant increases in cover of the shrub and moss layer (Table 4). There were no significant overall changes in herb layer cover, evenness, Shannon diversity and total richness. We detected significant overall changes in each of the species groups, both qualitatively and quantitatively. *Nardus* sward specialists and other low-nutrient species declined in number and abundance, whereas characteristic species of both agricultural and abandoned grasslands showed an overall increase (Table 4). The proportion of graminoids decreased, while the proportion of Leguminosae increased.

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**Table 4** Differences of vegetation structure variables (a), species diversity variables (b) and species groups summarised for both study areas (bold: significant differences, *P*: p-value Wilcoxon-Test).

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*Changes of individual species: winners and losers*

A considerable number of species showed either a significant total increase (20 spp.) or a decrease (34 spp.) in frequency and/or abundance (Supplementary Information S2). Declining species belonged mainly 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 pulegoides, Carex panicea*). Mean R and N values of decreasing species were 3.8 and 2.5, respectively. Increasing species were notably agricultural grassland species (e.g. *Taraxacum* sect. Ruderalia, *Trifolium pratense* and *T. repens*) or indifferent species (e.g. *Veronica chamaedrys, Rhytidiadelphus squarrosus, Anemone nemorosa*) with higher R and N values; mean 5.0 and 4.8, respectively. Seven species with significant changes differed between study areas with respect to magnitude of change. Only two species (*Agrostis capillaris, Vicia cracca)* displayed different directions of change, as they increased in FWB and decreased in RHN.

*Shifts in species composition: regression models*

The results of the regression models show which environmental variables had an influence on changes in species composition (detailed in Supplementary Information S3). The most important predictor was Δ pH as it influenced various dependent variables in a positive (+) or negative (-) way: total richness (+), richness and abundance of other low-nutrient indicators and grassland species (+); proportional richness of Leguminosae (+), proportional richness and abundance of graminoids (-); Shannon-index and evenness (+); Sørensen distance (+) and SGI (+); mean R value (+), proportion of basiphytic species (+) and acidophytic species (-).

Interestingly, there was no statistical effect of Δ pH on character species, fallow indicators, SLI, mean N values, N indicators and cover of vegetation layers. Apart from Δ pH, initial pH influenced some of the dependent variables additionally, e.g. grassland species (+), proportional abundances of graminoids (-), Shannon index (+), mean R value (+), proportion of basiphytic (+) and acidophytic (-) species. Initial CN and Δ CN had only a minor influence in the regression models, whereas ongoing abandonment was a significant driver for species losses (SLI) and had a positive effect on richness and abundance of fallow indicators and

shrub cover. Hence, species gains were mainly driven by changes in pH, while losses were rather due to lack of management.

Significant species composition differences between study areas were rarely found. Apart from herb layer cover, the cumulative abundance of character species and other low-nutrient indicators (all showing a stronger decline in RHN), measures of beta-diversity showed significant differences between the study areas: Sørensen index, as well as species gains and losses and their respective proportions, displayed higher values in the Rhön Mountains.

*Effects of sulphur and nitrogen depositions on environmental variables and species composition*

Despite drastic changes in S and N deposition in the long term, we found almost no significant correlations between S or N depositions and environmental or vegetation variables (Supplementary Information S4). However, we found correlations with regard to beta diversity measures (Sørensen distance, SGI, SLI). These indices showed significant differences between the study areas in the regression models (see Supplementary Information S3).

## Discussion

Our results indicate a strong tendency towards eutrophication and less acidic conditions of *Nardus* grasslands of the Continental biogeographic region over the past decades. Eutrophication was indicated by increased Ellenberg N values (changes in means, increase in proportion of nutrient indicators, decrease in low-nutrient indicators), associated with a decline in C:N ratio. In the FWB plots, a reduction in the thickness of the organic surface (Of-)layer was an additional indicator for enhanced mineralisation (Peppler-Lisbach & Könitz 2017). Less acidic conditions and the increase in pH were floristically reflected by an increase in mean Ellenberg R values and a decline of acidophytes. Consistently in both study areas, Δ pH proved to be the most important predictor for changes in species composition, particularly the increase in total species richness, agricultural grassland species, Leguminosae and a decrease in graminoids. However, the significant decline in character species was not related to Δ pH, neither at local nor at regional scale. Character species declined only with decreasing thickness of the Of-layer in FWB.

There are several possible explanations for eutrophication. In our case, direct fertilisation can be ruled out because all plots were either situated within nature reserves and therefore managed without fertilising or had been abandoned. Therefore, other reasons have to be taken into account. Firstly, reduced management intensities (e.g. late mowing dates, undergrazing) support 'auto-eutrophication' (Leuschner & Ellenberg 2017), i.e. the promotion of tall growing, N-demanding species with an internal nutrient cycling resulting in less nutrient losses through biomass removal. Secondly, the increase of airborne N deposition is a source of eutrophication: The total N deposition exceeded the critical loads for *Nardus* grasslands from 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 pH. On the contrary, increased N deposition would expect further acidification, for example indicated by declining pH values (Stevens et al. 2011b). This is especially true for NHy depositions, which particularly increased in the study areas 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 soil reaction, e.g. many agricultural grassland species (Stevens et al. 2011c).

The presented results show the opposite picture: according to the increased soil pH, sites became more favourable for species of agricultural and calcareous grasslands with higher Ellenberg Rand N indicator values while acidophytic species declined. A crucial driver for recent changes in soil pH is the decrease in SOx deposition rates because there is a close correlation between atmospheric acid depositions and topsoil pH (Stevens et al. 2009). Several studies report effects of declined SOx deposition rates in Europe since the 1990s on soil properties and more recent on species composition of semi-natural grasslands (McGovern et al. 2011; Mitchell et al. 2018; Morecroft et al. 2009; Rose et al. 2016). Changes in soil pH imply changes in N availability and soil $NH_4$:$NO_3$ ratio (Stevens et al. 2011c). Stevens et al. (2011a) predicted that with increasing soil pH, NHy deposition inputs will be progressively converted into the non-toxic $NO_3$ form and by this 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 study areas this process is overruled by the soil buffering capacity. Following Rose et al. (2016), Peppler-Lisbach & Könitz (2017) and Mitchell et al. (2018), we assume therefore that the

observed changes in this study are significantly triggered by recovery from acidification due to decreasing SOx depositions. This interpretation would explain the combined pattern of decreasing acidification and eutrophication.

Contrary to our expectations, the local patterns of changes in species composition and soil parameters were not related to the local patterns of N and S depositions. The only indication that there was an effect of diverse deposition rates were the more pronounced floristic changes in RHN compared to FWB that might have been caused by the significantly higher reduction of SOx in RHN. However, studies covering a wider geographical extent were able to detect common patterns of N deposition and floristic change (Dupré et al. 2010). Reason for that poor influence of local deposition patterns could be that the overall magnitudes of atmospheric deposition change is a master factor that overcompensates relatively low local variabilities. Hence, deposition changes might have triggered the general pattern of floristic changes but cannot explain local differences (Damgaard et al. 2011).

The results show widely consistent long-term changes in *Nardus* grasslands of both study areas, confirming the previous findings of Peppler-Lisbach & Könitz (2017) at local scale (FWB). Differences between the study areas concern some quantitative aspects of community change with a generally higher species-turnover in RHN than in FWB. At the species level, most species with significant changes displayed the same trend (increase or decrease) in both study areas. Only indicators of base-rich soils (e.g. *Thymus pulegioides, Koeleria pyramidata, Cirsium acaule*) or of higher altitudes (e.g. *Luzula luzuloides, Phyteuma spicatum*) showed significant differences between the study areas with a stronger decline in RHN as compared to FWB (Peppler 1992). This can be attributed to differences in bedrock proportions and altitudinal range between the study areas. Generally, a minimum level of inaccuracy in resurveying quasi-permanent plots cannot be excluded entirely and minor differences between study areas could be possibly linked to this methodological issue (Kapfer et al. 2017). However, the ecological consistency of the results suggests that a possible pseudo-turnover plays a minor role in this resurvey study (Ross et al. 2010; Verheyen et al. 2018).

The overall results from both study areas in the continental biographical region show that changes in species-rich *Nardus* grasslands follow a general trend across Europe. The detected pattern of eutrophication and recovery from acidification is widely consistent with findings

from the Atlantic biogeographical region (Rose et al. 2016; Mitchell et al. 2018). However, beside atmospheric depositions land-use change is still another important trigger (Rose et al. 2016). Low management intensities (abandonment, late mowing or insufficient grazing) seemingly increased species losses and indirectly supported eutrophication and the spread of agricultural grassland generalists (Peppler-Lisbach & Könitz 2017).

## Conclusion

The findings of this study highlight the risk of eutrophication as a long-term cross-regional threat for species-rich *Nardus* grasslands, which ranges from the Atlantic into the Continental biogeographic region of Europe. Furthermore, they illustrate that both changes in management and the deposition regime of air pollutants have contributed to the detected species turnover. Due to a higher eutrophication pressure, an adapted management becomes an increasingly challenging issue. Measures like regular management, earlier dates of mowing and higher grazing intensities could become increasingly important to compensate for N depositions and more favourable mineralization conditions. This underpins the importance of increased conservation efforts to protect the high biodiversity value of *Nardus* grassland under future global change (Stevens et al. 2016). Moreover, the study illustrates the relevance of long-term data in combination with resurveys to build the consistent understanding of environmental driver interactions and their impacts on biodiverse semi-natural grasslands.

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## Author contributions

CPL, NK, NS and GR designed the study and conducted the vegetation resurvey; 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 gave critical comments and revisions. All authors gave their final approval for publication.

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## Supplementary Information

**Supplementary Information S1.** Assignment of species to species groups.

**Supplementary Information S2.** Differences of single species between time steps.

**Supplementary Information S3.** Linear regression models for differences in species composition.

**Supplementary Information S4.** Results of single variable linear mixed models of deposition variables.

720 **Tables with legends**

721 **Table 1** Management changes between time periods and areas (FWB: Fulda-Werra-Bergland,
722 RHN: Rhön Mountains).

| Management | | Management change category | Study area | | n |
|---|---|---|---|---|---|
| 1971-1987 | 2012-15 | | FWB | RHN | |
| 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 | |

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**Table 2** Sulphur and nitrogen deposition rates (kg ha-1 a-1) summarised for the plots in each study area (FWB: Fulda-Werra-Bergland, RHN: Rhön Mountains) (bold: significant differences, *P*: p-value for effect of study area in mixed linear models.

| Deposition parameter | FWB mean | FWB sd | RHN mean | RHN sd | *P* |
|---|---|---|---|---|---|
| **SOx 1987-89** | **17.71** | **1.83** | **24.95** | **1.65** | **0.000** |
| **SOx 2005-07** | **8.18** | **0.47** | **7.67** | **0.36** | **0.000** |
| **Δ SOx** | **-9.53** | **1.76** | **-17.28** | **1.37** | **0.000** |
| **SOx cum. 1987-2007** | **351.97** | **18.03** | **337.66** | **14.63** | **0.004** |
| **NHy 1987-89** | **7.73** | **0.65** | **9.73** | **0.63** | **0.000** |
| **NHy 2005-07** | **12.19** | **0.70** | **12.74** | **0.69** | **0.031** |
| **Δ NHy** | **4.46** | **0.28** | **3.01** | **0.74** | **0.000** |
| **NOx 1987-89** | **10.09** | **0.70** | **11.44** | **0.58** | **0.000** |
| NOx 2005-07 | 10.13 | 0.52 | 10.12 | 0.47 | 0.485 |
| **Δ NOx** | **0.04** | **0.55** | **-1.32** | **0.26** | **0.000** |
| **Ntotal 1987-89** | **17.82** | **1.35** | **21.17** | **1.18** | **0.000** |
| Ntotal 2005-07 | 22.31 | 1.16 | 22.86 | 1.01 | 0.292 |
| **Δ Ntotal** | **4.50** | **0.75** | **1.69** | **0.76** | **0.000** |
| **Ntotal cum. 1987-2007** | **460.11** | **26.75** | **481.93** | **26.14** | **0.022** |

730 **Table 3** Differences of soil chemical variables (a) and Ellenberg indicator value variables (b)

731 summarised for both study areas (bold: significant differences, *P*: p-value Wilcoxon-Test).

| | min diff | max diff | mean diff | median diff | *P* | n |
|---|---|---|---|---|---|---|
| (a) | | | | | | |
| **Δ pH** | **-0.720** | **2.030** | **0.262** | **0.180** | **0.000** | 94 |
| **Δ CN** | **-4.600** | **4.300** | **-0.811** | **-0.960** | **0.000** | 80 |
| (b) | | | | | | |
| **Δ mean L** | **-0.639** | **0.825** | **-0.056** | **-0.059** | **0.048** | 97 |
| Δ mean T | -1.329 | 1.500 | 0.014 | 0.043 | 0.815 | 97 |
| Δ mean K | -1.251 | 1.248 | 0.019 | 0.019 | 0.771 | 97 |
| Δ mean F | -2.277 | 1.808 | 0.055 | 0.056 | 0.066 | 97 |
| **Δ mean R** | **-1.056** | **1.486** | **0.188** | **0.160** | **0.001** | 97 |
| **Δ mean N** | **-0.627** | **1.622** | **0.370** | **0.317** | **0.000** | 97 |
| Δ prop. basophytes (R>5) | -0.267 | 0.341 | 0.017 | 0.000 | 0.217 | 97 |
| **Δ prop. acidophytes (R<5)** | **-0.434** | **0.232** | **-0.049** | **-0.029** | **0.000** | 97 |
| **Δ prop. nutrient indicators (N>5)** | **-0.118** | **0.267** | **0.046** | **0.045** | **0.000** | 97 |
| **Δ prop. low nutrient indicators (N<5)** | **-0.337** | **0.184** | **-0.076** | **-0.060** | **0.000** | 97 |

732 Abbreviation: prop. – number of species as proportion of total species richness

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735 **Table 4** Differences of vegetation structure variables (a), species diversity variables (b) and
736 species groups summarised for both study areas (bold: significant differences, *P*: p-value
737 Wilcoxon-Test).

| | min diff | max diff | mean diff | median diff. | *P* | n |
|---|---|---|---|---|---|---|
| (a) | | | | | | |
| **Δ cover shrubs** | **0.000** | **55.000** | **1.690** | **0.000** | **0.000** | 87 |
| Δ cover herbs | -25 | 40 | 0.598 | 0.000 | 0.765 | 87 |
| **Δ cover mosses** | **-75** | **100** | **18.690** | **13.000** | **0.000** | 87 |
| (b) | | | | | | |
| Δ evenness | -0.335 | 0.212 | 0.005 | -0.001 | 0.417 | 97 |
| Δ Shannon | -1.241 | 1.598 | -0.007 | -0.028 | 0.631 | 97 |
| Δ total species richness | -27 | 41 | 0.361 | 0.000 | 0.929 | 97 |
| (c) | | | | | | |
| **Δ ri. character species** | **-10** | **8** | **-1.60** | **-1** | **0.000** | 97 |
| **Δ ri. other low-nutrient indicators** | **-14** | **11** | **-1.57** | **-2** | **0.000** | 97 |
| **Δ ri. grassland species** | **-9** | **17** | **1.52** | **1** | **0.004** | 97 |
| **Δ ri. fallow indicators** | **-10** | **9** | **0.57** | **0** | **0.001** | 97 |
| **Δ abund. character species** | **-33.61** | **14.93** | **-5.16** | **-4.20** | **0.000** | 97 |
| **Δ abund. other low-nutrient indicators** | **-24.63** | **15.02** | **-3.16** | **-2.91** | **0.001** | 97 |
| **Δ abund. grassland species** | **-21.35** | **29.36** | **2.58** | **3.15** | **0.002** | 97 |
| **Δ abund. fallow indicators** | **-14.78** | **17.33** | **0.98** | **0.00** | **0.001** | 97 |
| (d) | | | | | | |
| **Δ prop. ri. graminoids** | **-0.455** | **0.181** | **-0.040** | **-0.026** | **0.023** | 97 |
| **Δ prop. abund. graminoids** | **-0.507** | **0.347** | **-0.044** | **-0.030** | **0.003** | 97 |
| **Δ prop. ri. leguminosae** | **-0.105** | **0.179** | **0.011** | **0.000** | **0.014** | 97 |
| **Δ prop. abund. leguminosae** | **-0.095** | **0.183** | **0.014** | **0.000** | **0.001** | 97 |

738 Abbreviations: ri. – richness (species number), abund. – cumulative abundance of a species group,
739 prop. abund. – cumulative abundance of species group as proportion of total cumulative abundance.;
740 prop. ri - number of species as proportion of total species richness.

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# Supplementary Information to the paper Peppler-Lisbach, C. et al.: Long-term vegetation change in species-rich *Nardus* grasslands of central Germany caused by eutrophication, recovery from acidification and management change. *Applied Vegetation Science*.

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## Supplementary Information S1. Assignment of species to species groups

### Legend

C – character species (*Nardetalia* specialists in open habitats) (Peppler-Lisbach & Petersen 2001)

D – other low-nutrient indicators (species of infertile grassland (dry grassland, fens) with Ellenberg N indicator values ≤3 (Ellenberg 1992)

G – grassland species (species of cultural grassland with Ellenberg N indicator values >3) (Ellenberg 1992)

F – fallow indicators (all tree and shrub species and herbaceous species of forests and forest clearings) (Leuschner & Ellenberg 2017)

All other species: indifferent

| Species full name | Species group |
|---|---|
| Acer pseudoplatanus | F |
| Achillea millefolium | G |
| Agrostis canina | D |
| Agrostis capillaris | G |
| Agrostis gigantea | G |
| Agrostis stolonifera | G |
| Alchemilla glaucescens | D |
| Alchemilla vulgaris agg. | G |
| Alopecurus pratensis | G |
| Antennaria dioica | D |
| Anthriscus sylvestris | G |
| Arnica montana | C |
| Arrhenatherum elatius | G |
| Betonica officinalis | G |
| Betula pendula | F |
| Betula pubescens | F |
| Bistorta officinalis | G |
| Briza media | D |

| | |
|---|---|
| Calluna vulgaris | C |
| Caltha palustris | G |
| Campanula rotundifolia | D |
| Cares pilulifera | C |
| Carex canescens | D |
| Carex caryophyllea | D |
| Carex echinata | D |
| Carex nigra | D |
| Carex ovalis | C |
| Carex pallescens | C |
| Carex panicea | D |
| Carex pulicaris | D |
| Carlina acaulis | D |
| Carlina vulgaris | D |
| Centaurea jacea | D |
| Centaurea nigra ssp. nemoralis | D |
| Cerastium holosteoides | G |
| Cirsium acaule | D |
| Cirsium palustre | G |
| Colchicum autumnale | G |
| Crataegus laevigata | F |
| Crataegus monogyna | F |
| Crepis mollis | G |
| Crepis paludosa | G |
| Cynosurus cristatus | G |
| Dactylorhiza majalis | G |
| Danthonia decumbens | C |
| Deschampsia flexuosa | C |
| Dianthus superbus | D |
| Dryopteris carthusiana | F |
| Dryopteris filix-mas | F |
| Epilobium angustifolium | F |
| Equisetum arvense | F |
| Eriophorum angustifolium | D |
| Eriophorum vaginatum | D |
| Euphrasia officinalis ssp. rostkoviana | G |
| Euphrasia stricta | D |
| Festuca ovina agg. | D |
| Festuca rubra agg. | G |
| Filipendula ulmaria | G |
| Frangula alnus | F |
| Fraxinus excelsior | F |
| Galeopsis tetrahit | F |
| Galium album | G |
| Galium boreale | D |
| Galium pumilum | D |
| Galium saxatile | C |
| Galium uliginosum | D |
| Galium verum | D |

| | |
|---|---|
| Genista tinctoria | D |
| Geranium sylvaticum | G |
| Geum rivale | G |
| Helianthemum nummularium | D |
| Helictotrichon pratense | D |
| Helictotrichon pubescens | G |
| Heracleum sphondylium | G |
| Hieracium lachenalii | D |
| Hieracium lactucella | C |
| Hieracium laevigatum | D |
| Hieracium pilosella | D |
| Holcus lanatus | G |
| Hypericum maculatum | D |
| Hypnum jutlandicum | C |
| Hypochaeris maculata | D |
| Hypochaeris radicata | D |
| Juncus acutiflorus | D |
| Juncus conglomeratus | D |
| Juncus effusus | G |
| Juncus filiformis | D |
| Juncus squarrosus | C |
| Juniperus communis | F |
| Knautia arvensis | G |
| Koeleria pyramidata | D |
| Lathyrus linifolius | C |
| Lathyrus pratensis | G |
| Leontodon autumnalis | G |
| Leontodon hispidus | G |
| Leucanthemum ircutianum | G |
| Lotus corniculatus | D |
| Lotus pendunculatus | G |
| Lupinus polyphyllus | F |
| Luzula campestris | C |
| Luzula luzuloides | F |
| Luzula multiflora | C |
| Maianthemum bifolium | F |
| Molinia caerulea | D |
| Myosotis nemorosa | G |
| Nardus stricta | C |
| Pedicularis sylvatica | C |
| Phyteuma nigrum | G |
| Phyteuma orbiculare | D |
| Picea abies | F |
| Pimpinella major | G |
| Pimpinella saxifraga | D |
| Pinus sylvestris | F |
| Plantago lanceolata | G |
| Pleurozium schreberi | C |
| Poa pratensis | G |

| | |
|---|---|
| Poa trivialis | G |
| Polygala serpyllifolia | C |
| Polygala vulgaris | C |
| Populus tremula | F |
| Potentilla erecta | D |
| Potentilla palustris | D |
| Potentilla tabernaemontani | D |
| Prunella grandiflora | D |
| Prunella vulgaris | G |
| Quercus robur | F |
| Ranunculus acris | G |
| Ranunculus flammula | D |
| Ranunculus repens | G |
| Rhinanthus minor | G |
| Roa canina | F |
| Rubus idaeus | F |
| Rumex acetosa | G |
| Rumex acetosella | D |
| Salix aurita | F |
| Salix caprea | F |
| Salix x multinervis | F |
| Sanguisorba officinalis | G |
| Saxifraga granulata | D |
| Senecio jacobaea | G |
| Serratula tinctoria | D |
| Silene flos-cuculi | G |
| Silene otites | D |
| Sorbus aucuparia | F |
| Succisa pratensis | D |
| Taraxacum sect. Ruderalia | G |
| Tephroseris helenitis | D |
| Thesium pyrenaicum | D |
| Thymus pulegioides | D |
| Trientalis europaea | F |
| Trifolium dubium | G |
| Trifolium pratense | G |
| Trifolium repens | G |
| Trifolium spadiceum | D |
| Trisetum flavescens | G |
| Trollius europaeus | G |
| Vaccinium myrtillus | C |
| Vaccinium oxycoccus | D |
| Vaccinium vitis-idaea | C |
| Valeriana dioica | G |
| Veronica officinalis | C |
| Viburnum opulus | F |
| Vicia cracca | G |
| Viola canina | C |
| Viola palustris | D |

| | |
|---|---|
| Viola tricolor | G |

**TABLE S1.** Assignment of species to species groups.

## References


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# Supplementary Information to the paper Peppler-Lisbach, C. et al.: Long-term vegetation change in species-rich Nardus grasslands of central Germany caused by eutrophication, recovery from acidification and management change. *Applied Vegetation Science*.

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## Supplementary Information S2. Differences of single species between 1971-1987 (t1) and 2012/15 (t2)

**Temporal changes (abundance / frequency) for both study areas:**

p Wilcox abund.: *P*-value paired Wilcoxon test abundance 1974-87 vs. 2012/15

p Wilcox p/a: *P*-value paired Wilcoxon test p/a 1974-87 vs. 2012/15

**Differences depending on study areas:**

p Wilcox abund.: *P*-value paired Wilcoxon test differences in abundance

p Wilcox p/a: *P*-value paired Wilcoxon test p/a differences

Highlighted in bold: Significant differences between study areas (*P*-value < 0.05)

| Species name | Species group | R value | N value | Temporal changes: Abundance | | | | | Temporal changes: Frequency (p/a) | | | | | Differences depending on study areas | | | | | | Presence in only one study area | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | Abundance | | | Frequency (p/a) | | | | |
| | | | | mean tot. | mean t1 | mean t2 | diff mean | p Wilcox abund. | freq. tot. | freq. t1 | freq. t2 | diff freq | p Wilcox p/a | diff FWB | diff RHN | p Wilcox abund. | diff p/a FWB | diff p/a RHN | p Wilcox p/a | | |
| **decreasing species** | | | | | | | | | | | | | | | | | | | | | |
| Danthonia decumbens | C | 3 | 2 | 2.1 | 2.4 | 1.9 | -0.5 | 0.002 | 58.2 | 73.2 | 43.3 | -29.9 | 0.000 | -0.15 | -1.16 | 0.182 | -0.23 | -0.41 | 0.136 | | qualitative |
| Arnica montana | C | 3 | 2 | 2.3 | 2.7 | 1.8 | -0.9 | 0.000 | 32.0 | 44.3 | 19.6 | -24.7 | 0.000 | -0.85 | -1.11 | 0.654 | -0.23 | -0.27 | 0.643 | | and |
| Festuca ovina agg. | D | | | 5.0 | 6.4 | 3.7 | -2.7 | 0.003 | 74.2 | 86.6 | 61.9 | -24.7 | 0.000 | **-0.68** | **-6.00** | **0.017** | -0.22 | -0.30 | 0.408 | | quantitative |
| Calluna vulgaris | C | 1 | 1 | 2.3 | 3.0 | 1.5 | -1.5 | 0.011 | 37.6 | 49.5 | 25.8 | -23.7 | 0.000 | -0.43 | -3.22 | 0.346 | -0.22 | -0.27 | 0.530 | | decrease |
| Briza media | D | x | 2 | 0.4 | 0.6 | 0.2 | -0.4 | 0.002 | 16.5 | 25.8 | 7.2 | -18.6 | 0.000 | -0.35 | -0.51 | 0.684 | -0.18 | -0.19 | 0.968 | | |
| Campanula rotundifolia | D | x | 2 | 1.3 | 1.6 | 1.0 | -0.6 | 0.000 | 49.5 | 58.8 | 40.2 | -18.6 | 0.000 | **-0.17** | **-1.22** | **0.002** | **-0.10** | **-0.32** | **0.014** | | |
| Thymus pulegioides | D | x | 1 | 0.5 | 0.7 | 0.3 | -0.4 | 0.001 | 19.1 | 27.8 | 10.3 | -17.5 | 0.001 | **-0.22** | **-0.78** | **0.005** | **-0.10** | **-0.30** | **0.028** | | |
| Polytrichum commune | | 2 | | 1.8 | 2.7 | 0.8 | -1.9 | 0.002 | 17.0 | 24.7 | 9.3 | -15.5 | 0.002 | -0.90 | -3.62 | 0.811 | -0.17 | -0.19 | 0.817 | | |
| Nardus stricta | C | 2 | 2 | 23.6 | 30.6 | 16.6 | -14.0 | 0.000 | 89.2 | 95.9 | 82.5 | -13.4 | 0.002 | -12.48 | -16.49 | 0.687 | -0.10 | -0.19 | 0.268 | | |
| Carex panicea | D | x | 4 | 1.1 | 1.3 | 0.9 | -0.4 | 0.009 | 21.6 | 27.8 | 15.5 | -12.4 | 0.004 | 0.02 | -1.05 | 0.093 | -0.08 | -0.19 | 0.179 | | |
| Plagiomnium affine | | 7 | | 0.6 | 1.2 | 0.1 | -1.1 | 0.002 | 10.8 | 16.5 | 5.2 | -11.3 | 0.007 | | | | | | | FWB | |
| Solidago virgaurea | | x | 4 | 0.2 | 0.3 | 0.1 | -0.2 | 0.004 | 7.7 | 12.4 | 3.1 | -9.3 | 0.004 | -0.10 | -0.38 | 0.049 | -0.05 | -0.16 | 0.066 | | |
| Galium pumilum | D | 4 | 2 | 0.4 | 0.5 | 0.3 | -0.2 | 0.015 | 13.9 | 18.6 | 9.3 | -9.3 | 0.049 | **0.10** | **-0.70** | **0.015** | **-0.02** | **-0.22** | **0.014** | | |
| Lophocolea bidentata | | 5 | | 0.2 | 0.3 | 0.1 | -0.2 | 0.041 | 7.2 | 11.3 | 3.1 | -8.2 | 0.022 | -0.27 | -0.08 | 0.170 | -0.12 | -0.03 | 0.159 | | |
| Ptilidium ciliare | | 2 | | 0.1 | 0.2 | 0.0 | -0.2 | 0.016 | 3.6 | 7.2 | 0.0 | -7.2 | 0.016 | -0.13 | -0.19 | 0.766 | -0.07 | -0.08 | 0.791 | | |
| Vaccinium vitis-idaea | C | 2 | 1 | 0.3 | 0.5 | 0.1 | -0.3 | 0.005 | 9.8 | 13.4 | 6.2 | -7.2 | 0.039 | -0.10 | -0.65 | 0.065 | -0.03 | -0.14 | 0.092 | | |
| Dicranum polysetum | | 5 | | 0.5 | 1.0 | 0.0 | -1.0 | 0.031 | 3.1 | 6.2 | 0.0 | -6.2 | 0.031 | | | | | | | RHN | |
| Koeleria pyramidata | D | 7 | 2 | 0.1 | 0.2 | 0.1 | -0.1 | 0.016 | 6.2 | 9.3 | 3.1 | -6.2 | 0.031 | **-0.03** | **-0.32** | **0.007** | **-0.02** | **-0.14** | **0.019** | | |
| Vaccinium myrtillus | C | 2 | 3 | 6.3 | 6.6 | 6.0 | -0.6 | 0.073 | 56.7 | 70.1 | 43.3 | -26.8 | 0.000 | **1.50** | **-4.05** | **0.006** | -0.23 | -0.32 | 0.302 | | qualitative |
| Hieracium pilosella | D | x | 2 | 1.3 | 1.4 | 1.2 | -0.2 | 0.089 | 35.6 | 44.3 | 26.8 | -17.5 | 0.002 | 0.07 | -0.57 | 0.787 | -0.20 | -0.14 | 0.632 | | decrease only |
| Genista tinctoria | D | 6 | 1 | 0.6 | 0.7 | 0.6 | -0.1 | 0.133 | 16.0 | 21.6 | 10.3 | -11.3 | 0.013 | -0.12 | -0.08 | 0.220 | -0.17 | -0.03 | 0.078 | | |
| Hieracium lactucella | C | 4 | 2 | 0.6 | 0.6 | 0.6 | 0.0 | 0.139 | 20.6 | 25.8 | 15.5 | -10.3 | 0.041 | 0.05 | -0.16 | 0.624 | -0.12 | -0.08 | 0.658 | | |
| Pohlia nutans | | 2 | x | 0.1 | 0.2 | 0.1 | -0.1 | 0.145 | 4.6 | 8.2 | 1.0 | -7.2 | 0.039 | -0.13 | -0.03 | 0.773 | -0.07 | -0.08 | 0.790 | | |
| Cirsium acaule | D | 8 | 2 | 0.3 | 0.5 | 0.1 | -0.4 | 0.000 | 10.3 | 14.4 | 6.2 | -8.2 | 0.057 | **-0.10** | **-0.92** | **0.010** | -0.03 | -0.16 | 0.075 | | quantitative |
| Deschampsia flexuosa | C | 2 | 3 | 8.4 | 11.8 | 5.0 | -6.8 | 0.000 | 66.5 | 70.1 | 62.9 | -7.2 | 0.230 | -5.12 | -9.51 | 0.861 | -0.13 | 0.03 | 0.139 | | decrease only |
| Antennaria dioica | D | 3 | 2 | 0.2 | 0.5 | 0.0 | -0.4 | 0.010 | 5.7 | 9.3 | 2.1 | -7.2 | 0.065 | | | | | | | RHN | |
| Trollius europaeus | G | 6 | 5 | 0.2 | 0.3 | 0.1 | -0.2 | 0.014 | 11.3 | 14.4 | 8.2 | -6.2 | 0.146 | -0.15 | -0.30 | 0.569 | -0.07 | -0.05 | 0.917 | | |
| Juncus squarrosus | C | 1 | 1 | 0.2 | 0.4 | 0.0 | -0.4 | 0.031 | 4.1 | 7.2 | 1.0 | -6.2 | 0.070 | -0.62 | 0.00 | 0.085 | -0.10 | 0.00 | 0.092 | | |
| Galium verum | D | 7 | 3 | 0.4 | 0.6 | 0.3 | -0.3 | 0.031 | 14.9 | 17.5 | 12.4 | -5.2 | 0.302 | -0.32 | -0.22 | 0.607 | -0.05 | -0.05 | 0.911 | | |
| Pimpinella saxifraga | D | x | 2 | 0.6 | 0.7 | 0.5 | -0.2 | 0.015 | 25.8 | 27.8 | 23.7 | -4.1 | 0.388 | -0.20 | -0.30 | 0.841 | -0.03 | -0.05 | 0.765 | | |
| Luzula luzuloides | F | 3 | 4 | 0.7 | 1.1 | 0.4 | -0.8 | 0.006 | 19.1 | 19.6 | 18.6 | -1.0 | 1.000 | **-0.03** | **-1.95** | **0.005** | 0.00 | -0.03 | 0.741 | | |
| Sanguisorba officinalis | G | x | 5 | 1.4 | 1.8 | 0.9 | -0.9 | 0.021 | 28.4 | 28.9 | 27.8 | -1.0 | 1.000 | -0.35 | -1.87 | 0.084 | 0.00 | -0.03 | 0.690 | | |
| Phyteuma spicatum | | 6 | 5 | 0.6 | 0.8 | 0.4 | -0.4 | 0.027 | 26.8 | 26.8 | 26.8 | 0.0 | 1.000 | **-0.05** | **-1.00** | **0.014** | 0.00 | 0.00 | 1.000 | | |
| | mean: | 3.8 | 2.5 | | | | | | | | | | | | | | | | | | |
| **increasing species** | | | | | | | | | | | | | | | | | | | | | |
| Rhytidiadelphus squarrosus | | 5 | x | 14.7 | 3.3 | 26.0 | 22.7 | 0.000 | 55.2 | 37.1 | 73.2 | 36.1 | 0.000 | 15.77 | 32.54 | 0.210 | 0.30 | 0.35 | 0.597 | | qualitative |
| Veronica chamaedrys | | x | x | 1.4 | 0.6 | 2.1 | 1.5 | 0.000 | 38.7 | 24.7 | 52.6 | 27.8 | 0.000 | 1.65 | 1.30 | 0.199 | 0.22 | 0.38 | 0.101 | | and |
| Taraxacum sect. Ruderalia | G | x | 8 | 0.2 | 0.0 | 0.4 | 0.3 | 0.000 | 11.3 | 2.1 | 20.6 | 18.6 | 0.000 | **0.15** | **0.57** | **0.016** | **0.10** | **0.32** | **0.006** | | quantitative |
| Holcus lanatus | G | x | 5 | 1.1 | 0.8 | 1.4 | 0.7 | 0.000 | 39.2 | 29.9 | 48.5 | 18.6 | 0.001 | 0.62 | 0.73 | 0.181 | 0.15 | 0.24 | 0.363 | | increase |
| Trifolium repense | G | 6 | 6 | 0.8 | 0.1 | 1.4 | 1.2 | 0.000 | 14.9 | 6.2 | 23.7 | 17.5 | 0.000 | 1.75 | 0.43 | 0.524 | 0.18 | 0.16 | 0.897 | | |
| Stellaria graminea | | 4 | 3 | 0.6 | 0.4 | 0.8 | 0.4 | 0.010 | 27.3 | 18.6 | 36.1 | 17.5 | 0.001 | 0.57 | 0.08 | 0.127 | 0.22 | 0.11 | 0.316 | | |
| Trifolium pratense | G | x | x | 0.7 | 0.2 | 1.2 | 1.1 | 0.000 | 16.5 | 8.2 | 24.7 | 16.5 | 0.001 | 1.55 | 0.24 | 0.331 | 0.18 | 0.14 | 0.706 | | |
| Rhinanthus minor | G | x | 3 | 0.9 | 0.6 | 1.1 | 0.5 | 0.007 | 25.3 | 18.6 | 32.0 | 13.4 | 0.007 | 0.65 | 0.35 | 0.713 | 0.12 | 0.16 | 0.504 | | |
| Hypochaeris radicata | D | 4 | 3 | 0.3 | 0.1 | 0.4 | 0.3 | 0.005 | 11.3 | 5.2 | 17.5 | 12.4 | 0.002 | 0.38 | 0.14 | 0.490 | 0.13 | 0.11 | 0.715 | | |

| | | | | Temporal changes: Abundance | | | | | Temporal changes: Frequency (p/a) | | | | | Differences depending on study areas | | | | | | Presence in only one study area | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | Abundance | | | Frequency (p/a) | | | | |
| Species name | Species group | R value | N value | mean tot. | mean t1 | mean t2 | diff mean | p Wilcox abund. | freq. tot. | freq. t1 | freq. t2 | diff freq | p Wilcox p/a | diff FWB | diff RHN | p Wilcox abund. | diff p/a FWB | diff p/a RHN | p Wilcox p/a | | |
| Vicia cracca | G | x | x | 0.3 | 0.2 | 0.4 | 0.2 | 0.004 | 13.4 | 7.2 | 19.6 | 12.4 | 0.004 | **0.42** | **-0.03** | **0.029** | **0.20** | **0.00** | **0.015** | | |
| Ceratodon purpureus | | x | | 0.2 | 0.0 | 0.4 | 0.4 | 0.002 | 5.2 | 0.0 | 10.3 | 10.3 | 0.002 | | | | | | | FWB | |
| Geranium sylvaticum | G | 6 | 7 | 0.2 | 0.0 | 0.4 | 0.4 | 0.007 | 6.2 | 1.0 | 11.3 | 10.3 | 0.006 | | | | | | | RHN | |
| Picea abies | | x | x | 0.1 | 0.0 | 0.2 | 0.1 | 0.016 | 5.7 | 1.0 | 10.3 | 9.3 | 0.004 | 0.22 | 0.03 | 0.147 | 0.13 | 0.03 | 0.081 | | |
| Platanthera bifolia | | 7 | x | 0.1 | 0.0 | 0.1 | 0.1 | 0.004 | 4.6 | 0.0 | 9.3 | 9.3 | 0.004 | 0.10 | 0.14 | 0.294 | 0.07 | 0.14 | 0.261 | | |
| Arrhenatherum elatius | G | 7 | 7 | 0.1 | 0.0 | 0.2 | 0.2 | 0.016 | 3.6 | 0.0 | 7.2 | 7.2 | 0.016 | 0.05 | 0.32 | 0.056 | 0.03 | 0.14 | 0.061 | | |
| Polygala serpyllifolia | C | 2 | 2 | 0.1 | 0.0 | 0.3 | 0.3 | 0.016 | 3.6 | 0.0 | 7.2 | 7.2 | 0.016 | 0.35 | 0.14 | 0.843 | 0.07 | 0.08 | 0.791 | | |
| Plantago lanceolata | G | x | x | 1.3 | 1.0 | 1.5 | 0.5 | 0.040 | 37.6 | 35.1 | 40.2 | 5.2 | 0.458 | 0.37 | 0.76 | 0.129 | 0.00 | 0.14 | 0.213 | | |
| Agrostis capillaris | G | 4 | 4 | 6.8 | 5.6 | 8.1 | 2.5 | 0.025 | 80.4 | 78.4 | 82.5 | 4.1 | 0.503 | **4.43** | **-0.60** | **0.009** | 0.08 | -0.03 | 0.253 | | |
| Anemone nemorosa | | x | 1.6 | 1.7 | 1.6 | 0.0 | 0.338 | 31.4 | 24.7 | 38.1 | 13.4 | 0.019 | 0.17 | -0.38 | 0.244 | 0.17 | 0.08 | 0.415 | | | qualitative |
| Leontodon autumnalis | G | 5 | 5 | 0.3 | 0.2 | 0.5 | 0.3 | 0.123 | 13.4 | 8.2 | 18.6 | 10.3 | 0.041 | 0.40 | 0.05 | 0.321 | 0.12 | 0.08 | 0.736 | | increase only |
| | mean: | 5.0 | 4.8 | | | | | | | | | | | | | | | | | | |

**Tab S2.1.** Differences of single species between 1971-1987 (t1) and 2012/15 (t2).

# Supplementary Information to the paper Peppler-Lisbach, C. et al.: Long-term vegetation change in species-rich Nardus grasslands of central Germany caused by eutrophication, recovery from acidification and management change. *Applied Vegetation Science*.

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## Supplementary Information S3. Linear regression models for differences in species composition.

In columns, model $R^2$, overall *P*-value, intercept, regression coefficients of variables and their respective *P*-values:
pHi, CNi: initial values of pH and CN
Δ pH, Δ CN: changes in pH and CN
Δ M: changes in management (reference category fallow); FM: fallow changed to managed, MM: continuously managed
Study area RHN: study area Rhön Mountains, reference category FWB (Fulda-Werra-Bergland)
n.s. = not significant

Dependent variables Box-Cox transformed prior to analysis

| | R2 | *P* | Intercept | *P* | $pH_i$ | *P* | Δ pH | *P* | $CN_i$ | *P* | Δ CN | *P* | Δ M:FM | *P* | Δ M:MM | *P* | Study area RHN | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Alpha-Diversity** | | | | | | | | | | | | | | | | | | |
| Δ total richness | 0.188 | 0.000 | 10.878 | 0.000 | | | 3.899 | 0.000 | | | | | | | | | | |
| Δ Shannon index | 0.369 | 0.000 | -2.397 | 0.006 | 0.431 | 0.001 | 0.743 | 0.000 | 0.102 | 0.000 | 0.055 | 0.034 | | | | | | |
| Δ evenness | 0.133 | 0.001 | 0.454 | 0.000 | | | 0.151 | 0.001 | | | | | | | | | | |
| **Beta-Diversity** | | | | | | | | | | | | | | | | | | |
| Sørensen distance | 0.335 | 0.000 | -1.342 | 0.000 | | | 0.197 | 0.033 | | | | | | | | | 0.475 | 0.000 |
| species loss index (SLI) | 0.390 | 0.000 | -0.328 | 0.156 | | | | | -0.032 | 0.029 | | | -0.335 | 0.001 | -0.344 | 0.003 | 0.380 | 0.000 |
| species gain index (SGI) | 0.249 | 0.000 | -1.036 | 0.000 | | | 0.262 | 0.001 | | | | | | | | | 0.227 | 0.001 |
| **Species groups** | | | | | | | | | | | | | | | | | | |
| Δ richness character species | | n.s. | | | | | | | | | | | | | | | | |
| Δ richness other low-nutrient indicators | 0.215 | 0.000 | 11.327 | 0.000 | | | 4.455 | 0.000 | | | | | | | | | | |
| Δ richness grassland species | 0.189 | 0.000 | -1.611 | 0.533 | 1.330 | 0.018 | 2.409 | 0.000 | | | | | | | | | | |
| Δ richness fallow indicators | 0.148 | 0.002 | 22.336 | 0.000 | | | | | | | | | -3.766 | 0.014 | -5.587 | 0.000 | | |
| Δ abundance character species | 0.056 | 0.035 | 68.601 | 0.000 | | | | | | | | | | | | | -12.508 | 0.035 |
| Δ abundance other low-nutrient indicators | 0.298 | 0.000 | 26.485 | 0.000 | | | 9.765 | 0.000 | | | | | | | | | -8.179 | 0.000 |
| Δ abundance grassland species | 0.115 | 0.002 | 14.209 | 0.000 | | | 3.989 | 0.002 | | | | | | | | | | |
| Δ abundance fallow indicators | 0.213 | 0.000 | 17.823 | 0.000 | | | | | | | | | -3.852 | 0.000 | -4.790 | 0.000 | | |
| **Proportion of graminoids and Leguminosae** | | | | | | | | | | | | | | | | | | |
| Δ prop. no. graminoid species | 0.103 | 0.004 | -0.379 | 0.000 | | | -0.048 | 0.004 | | | | | | | | | | |
| Δ prop. abund. graminoid species | 0.234 | 0.000 | -0.223 | 0.011 | -0.049 | 0.011 | -0.102 | 0.000 | | | | | | | | | | |
| Δ prop. no. Leguminosae species | 0.057 | 0.033 | 0.212 | 0.000 | | | 0.023 | 0.033 | | | | | | | | | | |
| Δ prop. abund. Leguminosae species | | n.s. | | | | | | | | | | | | | | | | |
| **Structural parameters** | | | | | | | | | | | | | | | | | | |
| Δ cover shrubs | 0.409 | 0.000 | -0.047 | 0.605 | | | | | 0.017 | 0.004 | | | -0.161 | 0.000 | -0.178 | 0.000 | | |
| Δ cover herbs | 0.088 | 0.012 | 31.451 | 0.000 | | | | | | | | | | | | | -7.591 | 0.012 |
| Δ cover mosses | | n.s. | | | | | | | | | | | | | | | | |

| | R2 | *P* | Intercept | *P* | $pH_i$ | *P* | Δ pH | *P* | $CN_i$ | *P* | Δ CN | *P* | Δ M:FM | *P* | Δ M:MM | *P* | Study area RHN | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Ellenberg indicator values** | | | | | | | | | | | | | | | | | | |
| Δ mean R value | 0.318 | 0.000 | -1.478 | 0.008 | 0.322 | 0.007 | 0.721 | 0.000 | | | | | | | | | | |
| Δ mean N value | | n.s. | | | | | | | | | | | | | | | | |
| Δ basiphytic species (R > 5) | 0.284 | 0.000 | -0.085 | 0.350 | 0.066 | 0.001 | 0.109 | 0.000 | | | | | | | | | | |
| Δ acidophytic species (R < 5) | 0.201 | 0.000 | 1.414 | 0.000 | -0.164 | 0.010 | -0.282 | 0.000 | | | | | | | | | | |
| Δ nutrient indicators (N > 5) | | n.s. | | | | | | | | | | | | | | | | |
| Δ low-nutrient indicators (N < 5) | | n.s. | | | | | | | | | | | | | | | | |

**TABLE S3.1.** Linear regression models for differences in species composition.

# Supplementary Information to the paper Peppler-Lisbach, C. et al.: Long-term vegetation change in species-rich Nardus grasslands of central Germany caused by eutrophication, recovery from acidification and management change. *Applied Vegetation Science*.

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## Supplementary Information S4. Results of single variable linear mixed models of deposition variables (fixed effect) on environmental variables (a), Ellenberg indicator values (b), species diversity (c) and species groups (d).

**Legend of table head**

Random effect: grid cell of deposition data. Given are regression coefficients and respected *P*-values. Bold: significant coefficients

Ntotal cum. 1987-2007 – cumulative total nitrogen (NHy + NOx) deposition between 1987 and 2007

SOx cum. 1987-2007 – cumulative total sulphur (SOx) deposition between 1987 and 2007

Δ Ntotal – Change in total nitrogen (NHy + NOx) deposition within 1987 and 2007

Δ SOx – Change in sulphur (Sox) deposition within 1987 and 2007

ri. – richness (species number)

abund. – cumulative abundance of a species group

prop. abund. – cumulative abundance of species group as proportion of total cumulative abundance

prop. ri - number of species as proportion of total species richness

| Response variable | Ntotal cum. 1987-2007 | *P* | SOx cum. 1987-2007 | *P* | Δ Ntotal | *P* | Δ SOx | *P* |
|---|---|---|---|---|---|---|---|---|
| a) Environmental variables | | | | | | | | |
| Δ pH | -0.002 | 0.275 | -0.003 | 0.331 | 0.001 | 0.980 | 0.004 | 0.764 |
| Δ CN | 0.008 | 0.312 | 0.015 | 0.235 | -0.049 | 0.733 | -0.019 | 0.724 |
| b) Ellenberg indicator values | | | | | | | | |
| Δ mean R | 0.002 | 0.422 | 0.000 | 0.924 | -0.024 | 0.527 | -0.013 | 0.372 |
| Δ prop. basophytes (R>5) | 0.000 | 0.733 | -0.001 | 0.364 | -0.006 | 0.437 | -0.003 | 0.327 |
| Δ prop. acidophytes (R<5) | -0.001 | 0.410 | 0.000 | 0.689 | 0.014 | 0.181 | 0.006 | 0.138 |
| Δ mean N | 0.002 | 0.363 | -0.001 | 0.648 | -0.041 | 0.182 | -0.017 | 0.154 |
| Δ prop. nutrient indicators (N>5) | 0.001 | 0.106 | 0.001 | 0.312 | -0.008 | 0.207 | -0.003 | 0.211 |
| Δ prop. low-nutrient indicators (N<5) | -0.001 | 0.245 | 0.000 | 0.717 | 0.013 | 0.098 | 0.006 | 0.072 |
| c) Species diversity indices | | | | | | | | |
| Δ total species richness | -0.023 | 0.613 | -0.038 | 0.588 | -0.107 | 0.893 | -0.119 | 0.698 |
| Δ evenness | 0.000 | 0.736 | 0.000 | 0.815 | -0.004 | 0.604 | -0.003 | 0.392 |
| Δ Shannon | -0.001 | 0.536 | -0.001 | 0.778 | 0.015 | 0.717 | 0.002 | 0.912 |
| Sørensen distance | 0.000 | 0.499 | **-0.003** | **0.010** | **-0.032** | **0.006** | **-0.013** | **0.004** |
| Species loss index (SLI) | 0.001 | 0.247 | -0.002 | 0.060 | **-0.034** | **0.009** | **-0.014** | **0.007** |
| Species gain index (SGI) | 0.000 | 0.809 | **-0.003** | **0.007** | **-0.024** | **0.048** | **-0.010** | **0.042** |
| d) Species groups | | | | | | | | |
| Δ ri. character species | -0.015 | 0.367 | -0.007 | 0.781 | -0.075 | 0.794 | -0.009 | 0.937 |
| Δ abund. character species | -0.070 | 0.165 | 0.020 | 0.803 | 0.704 | 0.412 | 0.401 | 0.226 |
| Δ ri. other low-nutrient indicators | -0.013 | 0.527 | 0.001 | 0.972 | 0.400 | 0.250 | 0.143 | 0.288 |
| Δ abund. other low-nutrient indicators | -0.051 | 0.204 | 0.045 | 0.480 | **1.837** | **0.006** | **0.740** | **0.004** |
| Δ ri. grassland species | 0.020 | 0.420 | 0.011 | 0.763 | -0.019 | 0.962 | -0.126 | 0.428 |
| Δ abund. grassland species | 0.005 | 0.908 | 0.043 | 0.493 | 0.747 | 0.280 | 0.093 | 0.726 |
| Δ ri. fallow indicators | -0.022 | 0.082 | 0.014 | 0.454 | 0.149 | 0.476 | 0.132 | 0.102 |
| Δ abund. fallow indicators | -0.037 | 0.072 | 0.023 | 0.471 | 0.334 | 0.341 | 0.256 | 0.058 |
| Δ prop. ri. graminoids | 0.000 | 0.636 | 0.000 | 0.573 | 0.002 | 0.841 | 0.001 | 0.792 |
| Δ prop. abund. graminoids | 0.000 | 0.702 | 0.000 | 0.935 | 0.009 | 0.285 | 0.004 | 0.211 |
| Δ prop. ri. Leguminosae | 0.000 | 0.724 | 0.000 | 0.600 | 0.001 | 0.877 | 0.000 | 0.980 |
| Δ prop. abund. Leguminosae | 0.000 | 0.691 | 0.000 | 0.644 | 0.001 | 0.735 | 0.000 | 0.893 |

**TABLE S4.1.** Detailed results of single variable linear mixed models of deposition variables.