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Nardus grasslands and wet heaths are affected differently by reintroduction of management and pH recovery

Borstgrasrasen und Feuchtheiden reagieren unterschiedlich auf die Wiederaufnahme von Nutzung und sich erholende pH-Werte

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Abstract

Semi-natural habitats in temperate regions are local hotspots of biodiversity, but multiple stressors such as land-use change and atmospheric deposition pose a threat to the existence and functioning of these ecosystems. We conducted a resurvey of *Nardus* grasslands and wet heaths in the Eifel mountains to monitor the development of these habitats under the influence of a long-term management regime and the above-mentioned stressors. Surveys of 50 plots of *Nardus* grasslands and 14 of wet heaths from 1986 were repeated in 2018. Prior to the first survey, the meadows had lain fallow for approx. 30 years. Shortly afterwards, they were re-entered into a management program with annual mowing from mid-July. We found significantly increased soil pH values from an average of 3.9 up to 4.6 since the 1980s, following the reduction in SO_2-depositions. Ellenberg indicator values for soil reaction and nutrients increased significantly in the wet heaths but stayed relatively stable in the *Nardus* grasslands. All meadows that were *Nardus* grasslands in 1986 could still be identified as such, with high total species numbers and a high proportion of character species. However, cover sums of these declined, while more species typical of agricultural grasslands and small sedge fens occurred. Low-competitive species (e.g. *Carex pilulifera*, *Pedicularis sylvatica*) profited, while species that can gain dominance in fallow situations (esp. *Molinia caerulea*) were pushed back. The consistent management of the sites contributed essentially to this outcome by effectively counteracting eutrophication. The relatively early date of mowing enabled a successful removal of nutrients and resulted in a characteristic structure and species composition. However, some quantitative changes indicate a risk of eutrophication and that continuing management will be crucial for a sustained conservation of *Nardus* grasslands. The same management, however, was not equally able to preserve wet heaths, which have largely been transformed into wet varieties of *Nardus* grasslands, small sedge-dominated swards or wet meadows with signs of eutrophication. Other management strategies (e.g. periodic top soil removal, possibly combined with extensive grazing) should be considered. In any case, we recommend further monitoring to secure the survival of these important remnants of historical land use.

Keywords: Eifel, eutrophication, long-term vegetation change, nitrogen deposition, resurvey, sulphur deposition

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Semi-natural habitats are local hotspots of biodiversity in temperate regions whose landscapes are severely affected by species loss (HABEL et al. 2013, DENGLER et al. 2014). They offer rare refuges for specialised species of nutrient-poor sites. Multiple stressors pose a threat to the existence and functioning of these habitats. Changed land-use practices have considerably reduced the extent of semi-natural and nutrient-poor ecosystems over the last century (LEUSCHNER & ELLENBERG 2017). The usage of suitable areas has been intensified by fertilising and drainage, while most less productive sites were abandoned or afforested (POSCHLOD et al. 2005). Global warming and atmospheric depositions, recently especially of nitrogen and in the past also of sulphur oxide, are additional drivers of vegetation change (SALA et al. 2000).

The habitats considered in this study are species-rich *Nardus* grasslands (*Nardetalia strictae* Preising 1950) and wet heaths (*Ericion tetralicis* Schwickerath 1933 and *Oxycocco-Ericion* Nordhagen 1936). They are protected under European law as FFH habitat types (No. 6230, prioritary, "Species-rich *Nardus* grasslands" and No. 4010, "Northern Atlantic wet heaths with *Erica tetralix*"). Their conservation status in Germany is stated as "unfavourable – bad" with a worsening trend (BFN 2019). Out of 105 species listed by ELLENBERG et al. (1992) as character species of *Nardus* grasslands and wet heaths, 64% are currently included as threatened in the Red List of Germany (METZING et al. 2018).

To our knowledge there are few long-term studies on current vegetation changes of *Nardus* grasslands, and even fewer for wet heaths. The available studies originate from different regions in Europe, but with a strong focus on the UK, and cover different time spans between the middle of the 20th century and the early 2000s. Some general trends were described in the majority of long-term resurvey studies: The diversity of the habitats was commonly described as degrading, with a decrease in the number of characteristic species and an increase in Ellenberg indicator values for nutrients (DUPRÈ et al. 2010, MCGOVERN et al. 2011, BRITTON et al. 2017, PEPPLER-LISBACH et al. 2020). In some cases, graminoid species have increased at the expense of forbs (DUPRÉ et al. 2010, MCGOVERN et al. 2011); in other cases, generalist and more competitive species have increased (BRITTON et al. 2017, PEPPLER-LISBACH et al. 2020). The main drivers of community changes were reported to be nitrogen and sulphur depositions, as well as the reduction of management intensity.

Deposited nitrogen levels currently exceed the threshold for critical loads from atmospheric deposition (10-20 kg N ha^{-1} a^{-1} for *Nardus* grasslands and wet heaths), in most parts of Europe (BOBBINK & HETTELINGH 2011). Typical effects of reactive nitrogen deposition are known to be a general loss of biodiversity, an increased graminoid: forb ratio (STEVENS et al. 2006, FIELD et al. 2014), a decrease in evenness, and an increase in more nutrient-demanding species of agricultural grasslands (DE GRAAF et al. 2009, BOBBINK et al. 2010, STEVENS et al. 2010, 2011, SOUTHON et al. 2013). As nitrogen-induced eutrophication facilitates higher productivity, species that are able to react to increased nutrient availability with high growth rates outcompete those adapted to nutrient-poor environments (BOBBINK et al. 1998, ROEM & BERENDSE 2000, DE GRAAF et al. 2009). Another effect of nitrogen deposition is acidification, especially due to ammonium (NH_4^+). As a consequence, rare species, which are often typical of intermediate pH values, decline, in favour of acid-resistant species that are more often grasses (BOBBINK et al. 1998, KLEIJN et al. 2008, MASKELL et al. 2010).

In contrast to nitrogen deposition, which persists on a high level, sulphur oxide emissions have been significantly reduced in the last decades due to effective air pollution policies (UBA 2019). As a consequence, pH levels have recently been found to be recovering (KIRK et al. 2010, McGovern et al. 2011, Mitchell et al. 2018, Peppler-Lisbach et al. 2020). McGovern et al. (2011) found that the vegetation response to recovery from acidification is lagging behind by decades, as soil parameters such as exchangeable cations still reflect an earlier, more acid, state. The more recent studies by Britton et al. (2017) and Peppler-Lisbach et al. (2020), however, found a significant increase of acid-sensitive species.

Here, we present the results of a resurvey of both the vegetation and the soil chemistry of plots first surveyed in 1986 in *Nardus* grasslands and wet heaths in the Eifel mountains in West-Germany. All of the study sites were mown for the last 30 years, with one cut from mid-July. The local conditions of the sites are very well controlled, with a strict conservation status, no drainage or fertilising, and a management regime in place that aims to maintain the typical vegetation structure and diversity. However, global and regional influences cannot be controlled. This study offers an opportunity to explore the long-term effects of well-planned and -conducted conservation practices in valuable habitats under the stress of global and regional drivers.

We expect a shift in species composition indicating eutrophication and less acidic conditions due to (1) recovery of pH values as a result of sulphur emissions that were high in the past but have been reduced for decades, and (2) eutrophication caused by ongoing high N-depositions. We further expect that (3) the implemented management regime of regular mowing has generally preserved the typical structure and species composition of vegetation.

2. Materials and Methods

2.1 Study area

The study area is located in the west of Germany in the Eifel Mountains, approx. 50 km south-west of the city of Bonn. It presents the northernmost part of the Rhenish Slate Mountains with predominantly siliceous bedrock (sandstone, clay shales, greywacke). These substrates weather to nutrient-poor soils with low pH values containing a water-retaining soil horizon due to their high clay content (Meynen & Schmitthüsen 1953). The altitude of the study plots varies from 500 to 605 m a.s.l. The climate is of a sub-oceanic character, with a mean annual precipitation of 800–900 mm and a mean annual air temperature of 7.7 °C (DWD CDC 2018). Individual relevés were from nine different meadow sites dispersed over an extent of approx. 18 km × 5 km and isolated from each other in the landscape. The size of the single sites ranges from 0.4 to 4.8 ha. All study sites are protected under federal law as nature reserves, and most of them additionally under European law as Natura 2000 sites (Kreis Euskirchen 2003, 2005). Except for one site, there is no intensive agricultural use taking place in the direct vicinity i.e. there is no or no strong input of fertiliser from agricultural sites and a low chance of species of intensively used grasslands to invade the swards. In most cases, the sites were surrounded by coniferous forest. At the time of the initial survey in 1986, the meadows had been abandoned for approx. 30 years (Ludwig 1987). Soon afterwards, all sites were entered into a management program with contractual nature conservation, and have since been mown once a year from mid-July (Schumacher et al. 2007, BioStation 2019b). Additionally, two EU-funded projects for the maintenance of heaths and *Nardus* grasslands were conducted in the area (BioStation 2018, 2019a). They comprised measures such as clearing shrubs and blocking off ditches to restore a more natural water regime. The reactive nitrogen deposition level, currently 11–12 kg N ha^{-1} a^{-1} (UBA 2020), lies in the range of critical loads that have been described for acid grassland and wet heath.

2.2 Data sampling

The resurvey is based on relevés made in 1986 by Gerhard Ludwig (LUDWIG 1987). This data basis was very well suited for a revisitation study. The methods of the original study were well documented and the author could be won as co-author for the resurvey study. In 2018, 50 relevés of *Nardus* grasslands (*Violion caninae* Schwickerath 1944: *Violenion caninae* Peppler-Lisbach & Petersen 2001, *Juncenion squarrosi* Peppler-Lisbach & Petersen 2001 and *Galium-saxatile-Nardus-stricta* community, Peppler-Lisbach & Petersen 2001) and 14 plots of groundwater-influenced wet heaths (*Ericion tetralicis* Schwickerath 1933 and *Oxycocco-Ericion* Nordhagen ex Tx.1937) were resampled. Precisely drawn maps with a thorough documentation of plot locations were used (scale 1:5000, pseudo-permanent following KAPFER et al. 2017). These were geo-referenced with ArcGIS (ESRI 2012). The resulting coordinates were located in the field using a differential GPS with an accuracy of up to 2 cm. While resampling, we avoided small-scale heterogeneity created by vehicle lanes or small depressions, to obtain homogeneous plots (as this has been done in the initial study in the same way). In the case of five plots overgrown by shrubs, the original location was shifted by a few meters. The plots sampled in 2018 were permanently marked by magnets in two diagonal corners. The plot size was 20 m². Species cover values were estimated using a modified Braun-Blanquet scale in which the lower classes "r", "+", and "1" were classified based only on percent cover and not on number of individuals (LUDWIG 1987).

Mixed soil samples from 1–10 cm depth were taken from every plot and soil pH was measured in deionised water. Additional data on ortho-phosphate were available for 22 plots. In 1986, these had been measured directly in soil water extracted by suction cups. Direct extraction of soil water was not possible in 2018 due to dry weather conditions; we therefore created an equilibrium soil solution from soil samples as a substitute (RICHARDS 1954, BLUME et al. 2011). Ortho-phosphate was measured with a photometer, with a measuring range of 15–1000 µg P l^{-1} after filtering the soil solution with a mesh width of 0.45 µm.

2.3 Data analysis

All data was organised with Turboveg (HENNEKENS & SCHAMINÉE 2001), the analyses were conducted with R and Rstudio (RSTUDIO TEAM 2016, R CORE TEAM 2020), including the packages vegdata (JANSEN & DENGLER 2010), vegan (OKSANEN et al. 2019), hier.part (NALLY & WALSH 2004), exactRankTests (HOTHORN & HORNIK 2019), car (FOX & WEISBERG 2019), nortest (GROSS & LIGGES 2015), ggplot2 (WICKHAM 2016) and reshape2 (WICKHAM 2007). All species names were harmonised according to the GermanSL1.3 (JANSEN & DENGLER 2008, 2010). A few taxa that were identified to different levels in the two surveys were merged to aggregates: *Festuca rubra* agg., *Centaurea jacea* agg. and *Dactylorhiza maculata* agg.

To account for initial floristic differences between plots in 1986, which might have influenced subsequent changes, we classified the plots into *Nardus* grassland (syntaxon N) and wet heath (syntaxon WH).

For all relevés, mean presence-absence based and community weighted (after square root transformation of cover) Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR), and soil nitrogen (mN) were calculated (ELLENBERG et al. 1992).

We classified species into seven groups according to their habitat preference (Supplement E1), following ELLENBERG et al. (1992) and for moss species DIERSSEN (1982) unless indicated otherwise: 1. NardG, character species of *Nardus* grasslands (class *Calluno-Ulicetea* Br.-Bl. et Tüxen 1943 ex Klika et Hadač 1944, according to PEPPLER-LISBACH & PETERSEN 2001); 2. WetH, character species of wet heaths (*Oxycocco-Sphagnetea* Br.-Bl. & Tx. ex Westhoff et al. 1946); 3. SSF, character species of small sedge fens (*Scheuchzerio-Caricetea nigrae* Tx. 1937); 4. AgriG, species of agricultural grasslands (*Molinio-Arrhenatheretea* Tx. 1937, with N.EIV values > 3); 5. PoorG, other species of nutrient-poor grasslands with N.EIV values <= 3 not included in NardG; 6. Aban, abandonment indicators like trees, bushes, and typical understorey species; 7. I, indifferent species. All species were additionally classified into groups according to taxonomy and growth form: 1. dicotyl herbs, 2. graminoids, 3. trees/bushes, 4. dwarf shrubs, 5. monokotyle herbs, 6. mosses.

Variable changes were calculated as Δvariable = var_{2018} – var_{1986}. Tests on the significance of parameter changes (e.g., ΔpH, Δcover sums of character species) were conducted using a Wilcoxon signed rank test. Changes of individual species (abundance and cover) were also tested for significance, with p-values corrected for the number of species considered (controlling the false discovery rate, fdr) (BENJAMINI & HOCHBERG 1995). Only species that occurred at least 10 times in the dataset were included.

Species "gain" and "loss", as indices for species turnover, were calculated with:

$gain = newspec / specnum_{2018}$ and $loss = lostspec / specnum_{1986}$,

where *newspec* is the number of species in a 2018 relevé that were not present in the corresponding plot in 1986 and *lostspec* is the number of species in a 1986 relevé that were no longer found in the corresponding plot in 2018. *Specnum* is the total number of species in the respective years. Evenness was calculated as a measure for the dominance structure of species in the relevés (PIELOU 1966). Sørensen dissimilarities based on presence/absence data, as well as cover values, were also computed (BORCARD et al. 2018). A fallow index for each plot was calculated as a sum of square-root transformed cover values of all fallow indicator species (species group Aban) and *Molinia caerulea* as a species gaining dominance in abandoned meadows.

A DCA of all relevés from 1986 and 2018 was performed with the function "decorana" (package vegan) from presence/absence data, without down-weighting of rare species. We calculated the best multiple linear regression models for changes in species richness (total, vascular, and bryophytes), Sørensen dissimilarity (quantitative and qualitative), ΔmR and ΔmN, as well as changes in frequency and cover sums of the species groups NardG, SSF, AgriG and PoorG as dependent variables. Explaining variables included in the full model were: pH_{1986}, ΔpH, $fallow\text{-}index_{1986}$, and site. Models for ΔmR and ΔmN also included mF_{1986} and ΔmF as a surrogate for soil moisture. F- and R- or N-values of the present species were not correlated, i.e. species of wetter sites did not have higher or lower R- or N-values. Interaction terms with syntaxon (wet heath/*Nardus* grassland) were included for all variables except site. Nitrogen or sulphur-oxide deposition were not included as predictor variables, because they are largely uniform across the study region and therefore cannot explain local differences. The same applies to the management regime. Variables were selected by stepwise elimination with the "step"-function based on Bayes Information Criterion (BIC). Dependent variables of models whose residuals did not follow a normal distribution were rank-transformed (ΔSSF.pa, Δspecnum.bryo). Models for ΔmR and ΔmN showed an outlier outside the "Cook's distance" metric of 0.5, which has an extreme ΔpH of 2.4 that might be a measurement error, and in one case the influence of one single species with very high N-value (*Epilobium angustifolium*, $n = 8$). This outlier data point was removed for the final model.

To examine variable effects on overall vegetation change, we conducted a Permanova based on Euclidean distances of a matrix of species differences between the years. For this, we used the rda function of the package vegan, including permutation testing, as it offers automatic variable selection. To obtain the species-differences matrix, square-root transformed cover values of species per plot in 1986 were subtracted from the respective values in 2018. The same procedure was used for presence/absence data.

3. Results

3.1 Soil variables and mean indicator values

Across all sites, between 1986 and 2018, the mean pH value showed a significant increase from 3.87 to 4.62 (Fig. 1). The range in which aluminium toxicity plays a role ($pH < 4.5$, SCHEFFER & SCHACHTSCHABEL 2010) was reached for 98% of the plots in 1986, while this was only the case for 22% in 2018. The change in pH values was negatively dependent on initial pH values (estimate: -0.72, R^2: 0.33, $p < 0.001$), i.e. the more acid the soils were in 1986, the more the pH values increased until 2018. Additionally, increasing soil

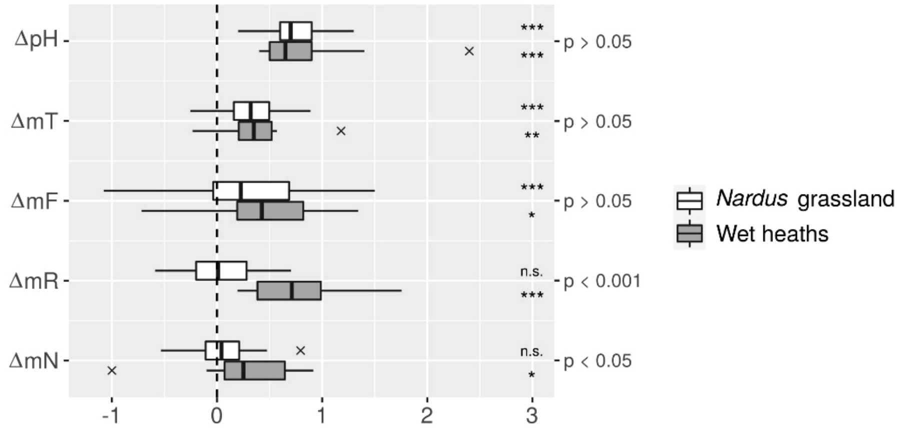

Fig. 1. Changes (Δ) of pH and presence/absence-based Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR) and soil nutrients (mN). Significance symbols (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. $p > 0.05$) indicate differences in indicator values between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abb. 1. Veränderung (Δ) von pH-Wert und ungewichteten Ellenberg-Zeigerwerten für Temperatur (mT), Bodenfeuchte (mF), Bodenreaktion (mR) und Nährstoffe (mN). Sternchen (*** $p < 0{,}001$; ** $p < 0{,}01$; * $p < 0{,}05$; n.s. $p > 0{,}05$) geben das Signifikanz-Niveau von Unterschieden der Zeigerwerte zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden in der Veränderung zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

moisture, estimated as difference in mean mF, had a positive effect on the change in pH values (estimate: 0.23, R^2: 0.13, $p = 0.002$). Wet heaths had lower pH values than *Nardus* grasslands in both survey years but the increase in pH did not differ between the syntaxa. mN and mR values showed significant differences between both community types in 1986, but not in 2018 (Supplement E2). Mean ortho-phosphate levels in soil water decreased significantly over time. Over all sites, they were on average 154 µg P l^{-1} in 1986. In 2018, 10 out of the 22 samples were under the detection limit of 15 µg P l^{-1}, the remaining 12 samples having an average of 27 µg P l^{-1}.

Mean unweighted indicator values for soil reaction and nutrients showed significant increases in the wet heath plots, while those of *Nardus* grassland remained comparatively stable over the study period (Fig. 1). The increases in mR and mN in *Nardus* grasslands were only significant for cover-weighted indicators (Supplement E3). Although the increase in pH values did not differ significantly between the syntaxa, the increase in mR and mN was significantly higher in the wet heath plots (Fig. 1). Mean unweighted indicator values for temperature and moisture showed significant increases across all plots, from a mean $mF_{1986} = 5.8$ to a mean $mF_{2018} = 6.1$, and a mean $mT_{1986} = 4.2$ to a mean $mT_{2018} = 4.5$.

3.2 Biodiversity and vegetation structure

All *Nardus* grasslands from 1986 were still typical *Nardus* grasslands in 2018, with high total species numbers (mean 34.3 / 20 m^2), and a high proportion of character species (on average 40% of total species, with 31% share of total cover). Total species numbers did not change significantly (Fig. 2). Broken down into vascular plants and bryophytes, vascular

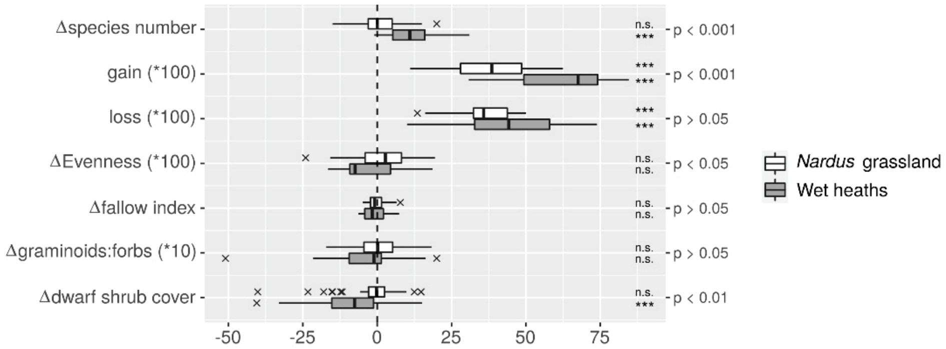

Fig. 2. Changes (Δ) in parameters describing biodiversity and structure between 1986 and 2018. Significance symbols (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. $p > 0.05$) indicate differences in variables between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abb. 2. Veränderungen (Δ) in Parametern betreffend Biodiversität und Struktur zwischen 1986 und 2018. Sternchen (*** $p < 0{,}001$; ** $p < 0{,}01$; * $p < 0{,}05$; n.s. $p > 0{,}05$) geben das Signifikanz-Niveau von Unterschieden der Variablen zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

plant richness increased by on average 4.1 species per plot, while bryophytes declined by on average 3.3 species per plot. However, there was a gradual shift to more nutrient-demanding, mesophilous species. Floristic changes were much greater in the plots that originally contained wet heaths. In 1986, 15% of all species were character species of wet heaths, with a share of cover of 34% per plot. In 2018, these shares amounted to only 3% typical species, with a mean share of cover of 4%. Here, total species numbers rose from $\text{mean}_{1986} = 24.6$ to $\text{mean}_{2018} = 36.6$ species per plot, with vascular plant numbers increasing on average by 12.8 species and bryophytes decreasing by 0.7 species per plot. Species turnover was significantly higher in the wet heaths, with a mean gain of 0.62 and a mean loss of 0.45, meaning that 62% of the species in the relevés of 2018 were not present in 1986, and 45% of species in the relevés of 1986 were lost in 2018. For the *Nardus* grasslands, these numbers amounted to a gain of 0.38 and a loss of 0.37.

Between 1986 and 2018, evenness increased slightly in *Nardus* grasslands but not in wet heaths, while the fallow index decreased slightly (Fig. 2). The graminoids:forbs ratio showed no significant change across all plots. The number and cover of dwarf shrubs in wet heaths was significantly reduced from on average 2.8 species with a cover sum of 21% in 1986, to 1.6 species with a cover sum of 13% in 2018.

3.3 Species groups according to habitat preference

The number of *Nardetalia* character species (NardG) was unchanged in *Nardus* grasslands (Fig. 3), though their cover sums decreased significantly (Supplement E4). More species of agricultural grasslands (AgriG), nutrient-poor grasslands (PoorG) and small sedge fens (SSF) appeared in the relevés in 2018 compared to 1986, but cover sums only increased significantly for the SSF-group. The species composition of wet heaths in the study area

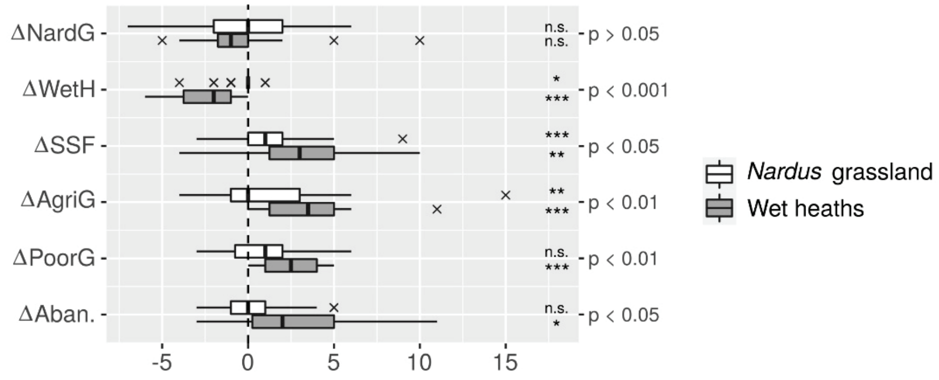

Fig. 3. Changes (Δ) in species numbers of several species groups: NardG = character species of *Nardus* grasslands; WetH = character species of wet heaths; SSF = character species of small sedge fens; AgriG = species of agricultural grasslands; PoorG = other species of nutrient-poor grasslands; Aban = fallow indicators. Significance symbols (*** $p < 0.001$; ** $p < 0.01$; * $p<0.05$; n.s. $p > 0.05$) indicate differences in species numbers between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abb. 3. Veränderung in der Frequenz von Arten der jeweiligen Artengruppen: NardG = Charakterarten der Borstgrasrasen; WetH = Charakterarten der Feuchtheiden; SSF = Charakterarten der Kleinseggenriede; AgriG = Arten des Wirtschaftsgrünlands; PoorG = andere Arten mageren Grünlands; Aban = Brachezeiger. Sternchen (*** $p < 0{,}001$; ** $p < 0{,}01$; * $p < 0{,}05$; n.s. $p > 0{,}05$) geben das Signifikanz-Niveau von Unterschieden der Artenzahlen zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

changed more drastically. The number and cover sums of wet heath character species (WetH) decreased in every relevé. The groups SSF, AgriG, PoorG and Aban increased significantly in numbers, and the groups SSF as well as AgriG also in cover.

3.4 Individual species

Comparisons of the prevalence of individual species showed that in *Nardus* grasslands, 10 species had significantly increased in either frequency or cover, or both (Supplement E5). Two small sedge species (*Carex pilulifera* and *C. echinata*) and the two hemiparasites *Pedicularis sylvatica* and *Rhinanthus minor* showed the strongest increases. *Rhytidiadelphus squarrosus* increased most in cover. Not reflected in the list of significantly increasing species are a number of agricultural grassland species ($n = 11$) that have only recently appeared in the sites, but are still very rare (e.g. *Cerastium holosteoides*, *Trifolium pratense*, *Vicia cracca).* Eleven species significantly decreased, more than half of which were mosses. Of the decreasing species, 55% belong to the *Nardetalia* character species group (NardG). The frequency of *Arnica montana* decreased from 74% to 52% of all plots, while its mean cover values declined by 80%. *Nardus stricta* showed the strongest decline in cover, but no change in frequency. The cover of *Molinia caerulea* decreased by on average 35%, however, this was not significant.

In the 14 wet heath sites, only two species (*Rhytidiadelphus squarrosus* and *Agrostis canina*) showed significant increases, while *Erica tetralix* decreased significantly in cover (Supplement E6).

Mean indicator values for temperature, soil moisture, soil reaction, and nutrients did not differ significantly between increasing and decreasing species of both initial syntaxa. The number of vascular plant species included in the Red List of Germany (METZING et al. 2018) increased from 29 to 32 over all plots, with more than half of the endangered species in 2018 being characteristic species of *Nardus* grasslands and wet heaths.

3.5 Multivariate analysis

The DCA containing all monitored plots from 1986 and 2018 supports the result that in the study period, wet heaths have changed more drastically than *Nardus* grasslands (Fig. 4). While the contours outlining all *Nardus* grassland plots in 1986 and 2018 show a considerable overlap, the contours surrounding the wet heath plots in 1986 and 2018 only overlap slightly. The first axis of the DCA represents a nutrient/pH-gradient, with typical species of agricultural grasslands increasingly occurring in the negative part of the axis, together with higher mR- and mN-values, pH, and total species numbers. The second axis describes a soil moisture gradient, being closely positively correlated with mF indicator values and character species of small sedge fens, and negatively correlated with typical species of *Nardus* grasslands. Both contours have shifted towards more moist and nutrient-rich conditions. In addition, floristically, plots of wet heath and *Nardus* grassland have become more similar: In 1986, contours outlining the separate syntaxa did not overlap, while they share about a third of their area in 2018.

3.6 Influence of site conditions on vegetation change

The results of the linear regression models showed which environmental variables had a significant effect on the changes in vegetation composition. Site and syntaxon were also included in the models, to account for local conditions and for initial differences between *Nardus* grasslands and wet heaths (see Supplement E7–9 for detailed model coefficients). For most dependent variables, the largest part of explained variance was accounted for by the differences between syntaxa or between sites. Increases of pH positively influenced cover-weighted changes in mN (Table 1), and were related to a higher presence/absence-based Sørensen-dissimilarity, increasing numbers of total vascular species, agricultural grasslands species, and small sedge sward species, but not their respective cover sums (Table 2). The rise in pH had a negative effect on the cover sums of *Nardetalia* character species which were, additionally, positively influenced by the fallow-index in 1986. A higher fallow index in 1986 also led to a higher qualitative Sørensen-dissimilarity, while numbers of bryophytes were reduced more strongly.

Variable selection in RDA revealed changes in pH, mF, and site as important variables influencing presence/absence-based vegetation change, with a total of 29% explained variance (Supplement E10). Individually, changes in pH explained only 3% of the total variance in the dataset of species differences, while 22% could be attributed to differences between the nine sampling sites. For differences in species cover values, changes in pH had no significant effect in the RDA. Changes in mF, the fallow-index$_{1986}$, syntaxon, and site together explained 42% of total variance, with the majority (22%) again accounted for by differences between sites. The syntaxon explained 5% of the total variance. No interaction terms between syntaxon and other variables were significant.

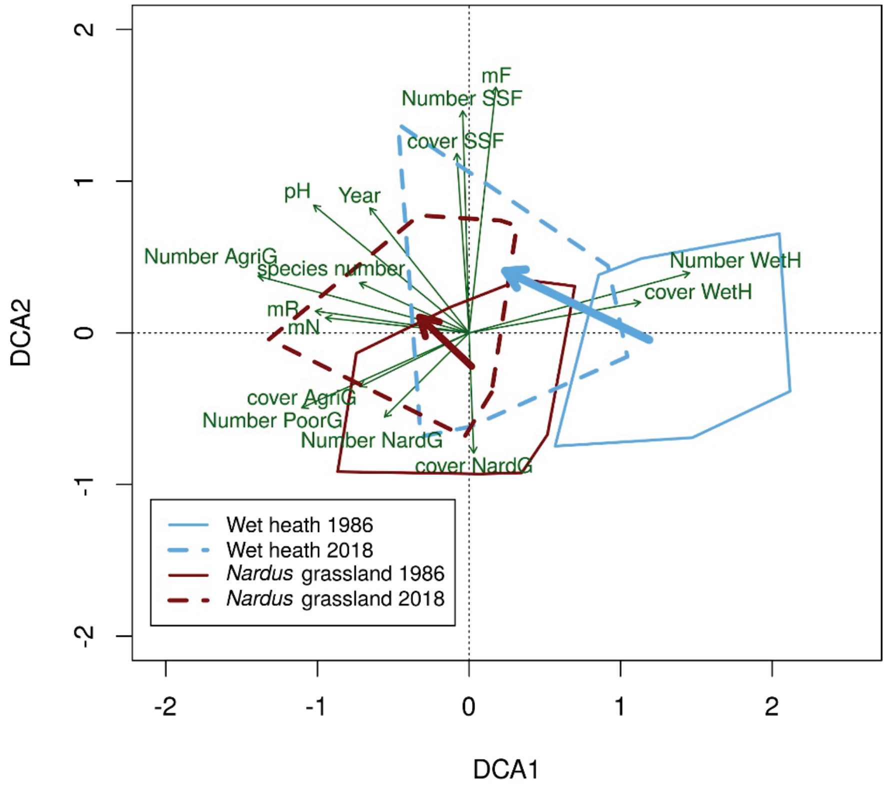

Fig. 4. DCA of all plots in 1986 and 2018, based on species presence/absence data. Red contours outline *Nardus* grasslands and blue contours wet heaths, with continuous outlines being the 1986 plots and dotted outlines the 2018 plots. Environmental variables included are significantly correlated to one of the DCA axes ($p < 0.05$) and with $R^2 \geq 0.15$. mF, mR, mN: Presence/absence-based Ellenberg indicator values for soil moisture, soil reaction, and nutrients; Species numbers (Number) and cover sums (cover) of following species groups: NardG = *Nardetalia* character species, WetH = wet heath character species, SSF = species of small sedge fens, AgriG = agricultural grassland species, and PoorG = species of other poor grasslands; Axis length is 3.45 for axis 1 and 2.31 for axis 2. A representation with species and single plots can be found in the Supplement E11.

Abb. 4. DCA aller Aufnahmen in 1986 und 2018, basierend auf Präsenz/Absenz-Daten. Rote Umrisse umfassen alle Aufnahmen von Borstgrasasen und blaue Umrisse umfassen alle Aufnahmen von Feuchtheiden. Dabei stellen durchgängige Linien die Aufnahmen von 1986 dar und gestrichelte Linien die Aufnahmen von 2018. Dargestellte Umweltvariablen sind signifikant mit einer der beiden DCA-Achsen korreliert ($p < 0{,}05$), mit $R^2 \geq 0{,}15$. mF, mR, mN: Präsenz/Absenz-basierte Ellenberg-Zahlen für Bodenfeuchte, Bodenreaktion und Nährstoffe; Artenzahl (Number) und Deckungssummen (cover) der Artengruppen: NardG = Charakterarten der Borstgrasrasen, WetH = Charakterarten der Feuchtheiden, SSF = Charakterarten der Kleinseggenriede, AgriG = Arten des Wirtschaftsgrünlands, PoorG = Arten anderer nährstoffarmer Wiesen. Achsenlänge ist 3,45 für Achse 1 und 2,31 für Achse 2. Eine Darstellung mit Arten und einzelnen Plots findet sich im Anhang E11.

Table 1. Coefficients (arrow pointing up: positive, arrow pointing down: negative) of multiple linear models for differences in presence/absence-based (p/a) and cover weighted Ellenberg indicator values for soil acidity (mR) and nutrients (mN) between 1986 and 2018. pH 1986, Fallow index 1986, mF 1986: pH, fallow index, and mF as measured in 1986. ΔpH, ΔmF: Changes of pH and mF between 1986 and 2018. Wet heath: syntaxon as compared to reference category *Nardus* grasslands. Site: all 8 sites as compared to reference category site 1.

Tabelle 1. Koeffizienten (Pfeil nach oben: positiv, Pfeil nach unten: negativ) der multiplen linearen Modelle für Differenzen von Präsenz/Absenz-basierten (p/a) und Deckungsgrad-gewichteten (cover) Ellenberg-Zeigerwerten für Bodenreaktion (mR) und Nährstoffe (mN) zwischen 1986 und 2018. pH 1986, Fallow index 1986, mF 1986: pH, Bracheindex und mF von 1986. ΔpH, ΔmF: Differenz der pH-Werte und mF zwischen 1986 und 2018. Wet heath: Syntaxon Feuchtheide im Verhältnis zur Bezugskategorie Borstgrasrasen. Site: Alle 8 Gebiete im Verhältnis zur Bezugskategorie Gebiet 1.

	R^2	pH 1986	ΔpH	Fallow index 1986	mF 1986	ΔmF	WH: mF 1986	WH: ΔmF	WH: pH 1986	Wet heath	Site
ΔmR p/a	0.38***									↑***	
ΔmR cover	0.24***	↑			↑*				↑**	↓**	
ΔmN p/a	0.44***				↓	↓	↑*	↓*		↓	↓↑***
ΔmN cover	0.08***		↑*								

4. Discussion

Our results indicate an overall trend of pH recovery, but different levels of vegetation response between *Nardus* grasslands and wet heaths.

4.1 Soil reaction recovery

The results confirm the expected rise in pH values, as previously reported by Kirk et al. (2010), McGovern et al. (2011), Mitchell et al. (2018) (all UK) and Peppler-Lisbach et al. (2020) from central Germany. It is commonly thought that this is the effect of strongly reduced SO_2 emissions since the 1990s. Tipping et al. (2021) assume that pH recovery largely contributed to recent increases in plant species richness in the UK. This process apparently completely overrides the simultaneous further acidification through ammonium deposition.

Fifty years after the peak of SO_2 emissions (McGovern et al. 2011, Mitchell et al. 2018), this is an exciting opportunity to observe the rates of recovery from acidification, which are not yet well known (Kirk et al. 2010). In acid soils as surveyed in this study, silicate mineral weathering is the main acid-buffering process. It is considered to be a slowly operating buffering system (Kirk et al. 2010, Scheffer & Schachtschabel 2010). A pH increase of 0.75 on average, equivalent to an 82 % reduction in H^+-concentrations over 32 years, is therefore unexpectedly strong. However, weathering rates increase logarithmically with declining pH values (Scheffer & Schachtschabel 2010). This may offer an explanation as to why soils with initially lower pH values show larger increases in pH. Our findings confirm the results of a *Nardus* grassland resurvey study in continental Germany, which also found stronger pH increases in initially more acid soils (Peppler-Lisbach et al. 2020).

Table 2. Coefficients (arrow pointing up: positive, arrow pointing down: negative) of multiple linear models for differences in species numbers of all species (total), vascular species, and bryophytes, qualitative Sørensen dissimilarity, and differences of species group, species numbers (p/a), and cover sums (cover) between 1986 and 2018. NardG = *Nardetalia* character species, AgriG = agricultural grassland species, SSF = species of small sedge fens, PoorG = other species of nutrient-poor grasslands. pH 1986, Fallow index 1986: pH and fallow index as measured in 1986. ΔpH = Change of pH between 1986 and 2018. Wet heath = syntaxon as compared to reference category *Nardus* grasslands. Site = all 8 sites as compared to reference category site 1. Models without significant results are not listed in the table: Sørensen quantitative, ΔNardG p/a, ΔAgriG cover, ΔSSF cover, ΔPoorG cover.

Tabelle 2. Koeffizienten (Pfeil nach oben: positiv, Pfeil nach unten: negativ) der multiplen linearen Modelle für Differenzen von Artenzahlen (species numbers) aller Arten (total), der Gefäßpflanzen (vascular) und der Moosarten (bryophytes), der qualitativen Sørensen-Unähnlichkeit, sowie der Differenzen von Artenzahlen (p/a) und Deckungssummen (cover) der soziologischen Kennartengruppen. NardG = Charakterarten der Borstgrasrasen, AgriG =Arten des Wirtschaftsgrünlands, SSF = Charakterarten der Kleinseggenriede; PoorG = andere Arten mageren Grünlands. pH 1986, Fallow index 1986 = pH und Bracheindex von 1986. ΔpH = Differenz der pH-Werte zwischen 1986 und 2018. Wet heath = Syntaxon Feuchtheide im Verhältnis zur Bezugskategorie Borstgrasrasen. Site = Alle 8 Gebiete im Verhältnis zur Bezugskategorie Gebiet 1. Modelle ohne signifikante Ergebnisse sind nicht in der Tabelle aufgeführt: Sørensen quantitative, ΔNardG p/a, ΔAgriG cover, ΔSSF cover, ΔPoorG cover.

	R^2	pH 1986	ΔpH	Fallow index 1986	WH: pH 1986	Wet heath	Site
Species Numbers							
Δspecies numbers total	0.28***					↑***	
Δspecies numbers vascular	0.27***		↑*			↑***	
Δspecies numbers bryophytes	0.19***			↓*		↑***	
Sørensen qualitative	0.41***	↑*	↑*	↑**		↑***	
Species groups							
ΔNardG cover	0.47***		↓*	↑**		↓*	↑↓***
ΔAgriG p/a	0.13**		↑*			↑*	
ΔSSF p/a	0.15**		↑*			↑*	
ΔPoorG p/a	0.19**	↓*			↑*	↓*	

4.2 Changes in soil moisture and temperature

The observed increase in soil moisture as reflected in the mF values can be explained by clogged ditches in the context of nature conservation projects in the area (BioStation 2018). Precipitation changes, in contrast, cannot be taken as an explanation for increased soil moisture, as yearly precipitation has slightly decreased since the initial survey (DWD CDC 2018).

The observed significant rise in mT values might be a first manifestation of rising temperatures due to anthropogenic climate change. Indeed, mean annual temperatures in the survey period 1986–2018 were 1 °C higher than in the preceding 40 years (DWD CDC 2018). However, a more likely explanation is that the increase in mean mT values is influenced both by the reduction of cold-indicating species, which are nearly exclusively mosses, and by an increase in species with higher mT values that are mainly species of agricultural grasslands. When only vascular species are included in the calculation of mT, the increase remains significant although less pronounced (mean change of mT, vascular plants: 0.08). The increase or decrease of these species groups is likely determined by factors other than climate change, e.g. nutrient levels or poor detectability of mosses due to very dry weather.

4.3 Vegetation changes

4.3.1 Changes in *Nardus* grasslands

Although the sampled *Nardus* grasslands are exposed to general regional and global drivers like climate change, pH recovery, and nitrogen deposition in the range of critical loads, the vegetation response of these *Nardus* grasslands was not very pronounced. The observed changes were rather quantitative than qualitative – mR and mN values only increased significantly when weighted with cover values of species. In contrast to findings by DUPRÉ et al. (2010) and PEPPLER-LISBACH et al. (2020), *Nardetalia* character species only decreased in cover, not in numbers. The rise in vascular plant species richness can be explained by the decline in Al-toxicity following pH recovery (DE GRAAF et al. 2009). Conditions have become suitable for a larger species pool, now also including acid-sensitive species that are mainly present in agricultural grasslands. However, these newly appearing species have not gained any dominance.

Evenness has slightly increased. There are no signs of competitive species like graminoids or tall herbs outcompeting small forbs (as in DUPRÉ et al. 2010, MASKELL et al. 2010, MCGOVERN et al. 2011). On the contrary, low-competitive plants like the hemiparasitic *Rhinanthus minor* and *Pedicularis sylvatica* have profited, along with several small sedge species. *Molinia caerulea* and *Nardus stricta*, as fallow indicators, were pushed back. All these findings can be attributed to the resumption of regular management after the fallow phase preceding the initial survey. The annual mowing reduced the advantage of competitive species, and therefore led to a more homogeneous vegetation structure (Fig. 5). Increased N-availability may be a reason for the decline of moss species (LEE & CAPORN 1998, CARROLL et al. 2003). At the same time, the summer of 2018 was exceptionally hot and dry, probably causing a temporary decline and poor detectability of bryophyte species.

The lack of strong eutrophication signs in *Nardus* grasslands were possibly caused by a removal of excess nitrogen by mowing or a limitation of other nutrients, especially phosphorous (P) or potassium (K). Mowing has been found to quickly decrease K levels (MLÁDKOVÁ et al. 2015), while VERHOEVEN et al. (1993) reported a complete withdrawal of deposited nutrients by yearly mowing of grassland on fen soils in the Netherlands. Other studies estimate nitrogen removal by mowing to amount to 25–50 kg N ha^{-1} a^{-1} for Eifel grasslands (SCHUMACHER et al. 2013), 41 kg N ha^{-1} a^{-1} in continental mountainous grasslands (MLÁDKOVÁ et al. 2015) or 24–63 kg N ha^{-1} a^{-1} in coastal prairie grasslands (MARON & JEFFERIES 2001). All these values exceed the current N input by atmospheric deposition (approx. 11–12 kg N ha^{-1} a^{-1}, UBA 2020). SCHUMACHER et al. 2013 hypothesised this to be a major cause for continuously high alpha diversity in managed semi-natural grasslands of the Eifel mountains. Additionally, the low measured ortho-phosphate concentrations suggest a phosphorus limitation. Phosphorus concentrations in 1986 and 2018 cannot be compared directly, due to differing soil-water extraction methods. The reported decrease is nevertheless plausible, also due to the fact that the centrifuged equilibrium soil solution used in 2018 would rather have contained more dissolved ions than the soil water used in 1986. As shown in fertilising experiments, phosphorus limitation can inhibit the uptake of additional nitrogen (PHOENIX et al. 2003), as well as reduce eutrophication effects, including loss of species

(CHYTRÝ et al. 2009). To further investigate the nature of nutrient limitation, the plant tissue N:P ratio could be used (KOERSELMAN & MEULEMAN 1996). This type of analysis was beyond the scope of the present study.

Another important factor affecting the change in vegetation composition is the availability of source populations of species that might be able to invade the present swards (ZOBEL et al. 2000, FOSTER 2001). The meadows studied are mostly surrounded by coniferous forest and thus isolated, not only from each other, but also from other types of grassland. A lack of propagule availability might also explain why more nutrient-demanding species are slow to colonise the swards, as opposed e.g. to the Rhön mountains, where *Nardus* swards are mostly embedded in agricultural grassland areas.

In summary, the mechanism most likely affecting vegetation response is the management regime, which requires annual mowing in summer, counteracting eutrophication and the dominance of single species. However, the current type of management might not be optimal for all typical *Nardus* grassland species. Especially *Arnica montana,* as a flagship-species of montane meadows, displays significant losses in frequency and cover, most likely due to a lack of open soil structures for generative reproduction (Fig. 6) (KAHMEN & POSCHLOD 1998, RICHTER 2014). Moreover, the extremely dry season of 2018 might have contributed to the decreased frequency and cover of *Arnica,* which is known to be very drought sensitive (STANIK et al. 2020).

4.3.2 Changes in wet heaths

Although overall conditions, such as pH recovery, atmospheric depositions, and climate change, affect the sites of wet heaths in the same way as the *Nardus* grasslands, evidences of eutrophication in vegetation change were much more pronounced in the wet heath sites. This is reflected by significant increases in mR and mN indicator values. The former wet heaths have transformed into wet variants of *Nardus* grasslands, small sedge-dominated swards or wet meadows with signs of eutrophication (e.g. presence of *Angelica sylvestris* and *Galium mollugo* agg.) (Fig. 7). This agrees well with findings by BRITTON et al. (2017) from Scottish wet heaths.

The conditions of wet heaths were more acidic and nutrient-poor in 1986 than those of the *Nardus* grasslands, even after a 30-year fallow period preceding the initial survey. The historical land-use practices that facilitated the formation of heaths, in this case the so-called "Schiffelwirtschaft" (LUDWIG 1987, BFN 2017) consisted of a shorter arable phase, prepared by sod-cutting and burning to use the ash for fertilisation, and a longer fallow phase, with grazing and litter harvesting (BECKER 1970). Therefore, the heaths established on very poor, undeveloped soils. Additionally, the dominant dwarf shrub species, especially *Erica tetralix* and to a lesser extent *Calluna vulgaris*, may have further acidified the soil by their use of ammonium as a nitrogen source (BERENDSE 1998). They serve as net accumulators of humus, as their litter has a high lignin content and decomposes only slowly (LEUSCHNER & ELLENBERG 2017). Thus, after a fallow period of more than 30 years, a considerable humus layer had developed until 1986 (LUDWIG 1987, Tab. 12). The start of annual mowing since the late 1980s disadvantaged and pushed back the dwarf shrubs as they are less able to compensate for annual biomass losses than the more regenerative grasses (LEUSCHNER & ELLENBERG 2017). Once humus accumulation halted, decomposition could begin, leading to elevated nutrient availability (BERENDSE et al. 1987). Increased pH values and higher temperatures may have additionally enhanced the rate of humus decomposition

Fig. 5. a) *Nardus* grassland (*Juncenion squarrosi* and *Galium saxatile-Nardus* community) in the "Mäusenest" area in the nature reserve "Baasemer Heide" near Berk (Photo: G. Ludwig, July 1986). **b)** Same view of "Mäusenest" in the nature reserve "Baasemer Heide" in 2018. *Nardus* grassland (*Juncenion squarrosi*) with transitions to small sedge swards (*Caricetum nigrae* Br.-Bl. 1915) (Photo: L. Mazalla, 15.06.2018).

Abb. 5. a) Borstgrasrasen (*Juncenion squarrosi* und *Galium saxatile-Nardus*-Gesellschaft) im „Mäusenest" im NSG „Baasemer Heide" bei Berk (Foto: G., Ludwig, Juli 1986). **b)** Gleiche Ansicht des „Mäusenests" im NSG „Baasemer Heide" in 2018. Borstgrasrasen (*Juncenion squarrosi*) mit Übergängen zu Kleinseggenrieden (*Caricetum nigrae* Br.-Bl. 1915) (Foto: L. Mazalla, 15.06.2018).

Fig. 6. a) *Nardus* grassland (*Juncenion squarrosi*) with *Arnica* flowering aspect. “Westlich Ehrend” in the nature reserve “Baasemer Heide” near Baasem. In the 2000s, this population was considered the largest in the NRW-part of the Eifel (SCHUMACHER et al. 2007) (Photo: G. Ludwig, June 1987). **b)** Same view of “Westlich Ehrend” in the nature reserve “Basemer Heide” in 2018. *Nardus* grassland (*Juncenion squarrosi)* also at the end of the blossoming time of *Arnica* (Photo: L. Mazalla, 24.06.2018).

Abb. 6. a) *Arnica*-Aspekt des Borstgrasrasens (*Juncenion squarrosi*) „Westlich Ehrend“ im NSG „Baasemer Heide“ bei Baasem. In den 2000er Jahren wurde dieses Vorkommen als das größte im NRW-Teil der Eifel angesehen (SCHUMACHER et al. 2007) (Foto: G. Ludwig, Juni 1987). **b)** Gleiche Fläche in 2018 zum Ende der Blütezeit von *Arnica*, die aber kaum noch vorhanden war (Foto: L. Mazalla, 24.06.2018).

Fig. 7. a) Wet heath (*Ericion tetralicis*). Nature reserve "Rinner Heide" near Sötenich (Photo: G. Ludwig, July 1985). **b)** Same view of nature reserve "Rinner Heide" near Sötenich in 2018. Eutrophic wet heath (*Ericion tetralicis*) with nutrient indicators (e.g., *Galium mollugo* agg., *Angelica sylvestris*) (Photo: L. Mazalla, 20.06.2018).

Abb. 7. a) Feuchtheide (*Ericion tetralicis*). NSG „Rinner Heide" bei Sötenich (Foto: G. Ludwig, Juli 1985). **b)** Gleiche Ansicht des NSG „Rinner Heide" bei Sötenich in 2018. Eutrophierte Feuchtheide (*Ericion tetralicis*) mit Nährstoffzeigern (z. B. *Galium mollugo* agg., *Angelica sylvestris*) (Foto: L. Mazalla, 20.06.2018).

(LEUSCHNER & ELLENBERG 2017, PEPPLER-LISBACH & KÖNITZ 2017). The atmospheric inputs of nitrogen may have additionally given grasses a competitive advantage over dwarf shrub species (BERENDSE et al. 1987).

Another key species for nutrient cycling is *Molinia caerulea*, which is able to withhold nutrients from the community by internal nutrient cycling (BERENDSE et al. 1987). The observed reduction in cover values of *Molinia* due to regular and early mowing could have led to increased nutrient availability for other species.

Considering this background, the question arises, if annual mowing is a suitable management tool for preserving wet heath vegetation at all. More appropriate ways of managing and preserving the typical species composition of wet heaths are probably extensive grazing by sheep and occasional sod cutting.

4.4 Drivers of change

Differences between sites and initial syntaxon identity accounted for most of the explained variance in the data set. The differences between sites translated to local conditions such as changes in water regime, fragmentation, or the behaviour of single land-users. Differences between syntaxa represent the differing internal mechanisms that drive the responses of grasslands and heaths to annual mowing. Additionally, idiosyncrasies of single plots (e.g. plot-specific management history, disturbance events or pseudo-turnover) might have contributed to floristic turnover, but were not explicitly quantified. Obviously, changes in species composition were relatively poorly determined by the environmental factors investigated in this study, similar to findings reported by PEPPLER-LISBACH & KÖNITZ (2017). The influence of the drivers did not differ systematically in terms of strength or direction between wet heaths and *Nardus* grasslands. The increase in pH values between 1986 and 2018 did show the hypothesised influence on variables like total vascular species richness, number of agricultural grassland species, and cover of *Nardetalia* character species; its overall effect was, however, limited, as indicated by low proportions of explained variance in regression models and RDA. We conclude that even though pH recovery clearly drives some of the change, as previously reported by ROEM & BERENDSE (2000), DUPRÉ et al. (2010) and PEPPLER-LISBACH et al. (2020), it was not the main driver of overall vegetation change. It was not possible to directly test the influence of atmospheric deposition, due to the limited spatial extent of the study with relatively uniform deposition rates over all sites. The typical effects of elevated N deposition are, however, well described in the literature. As these are only moderately represented here, we assume that nitrogen deposition is also not the most crucial driver of vegetation change.

In sum, we think that the initial community type (and the conditions that shaped it), together with the reintroduction of management after 1986, and other local factors, mainly determined the changes that occurred since then. Studies from forests also found that management legacies dictate floristic community responses to global drivers like deposition and climate change (PERRING et al. 2018).

4.5 Pseudo-turnover

Observer and location bias are sources of uncertainty in all resurvey studies (KAPFER et al. 2017). However, due to careful study design, we consider it very unlikely that the consistent directional trends uncovered in the present study should have been decisively influenced by pseudo-turnover. We are confident that the general patterns and trends reflect the true development of vegetation composition in these grasslands and heaths.

5. Conclusions

Since the original survey in 1986, we found the expected increase in soil pH, presumably due to the reduction of sulphur dioxide emissions. It is likely that the appearance of several acid-sensitive species can be attributed to the effects of increased pH, i.e. decreased aluminium or ammonium toxicity and increased nutrient supply due to increased remineralisation. The anticipated eutrophication was especially pronounced in the wet heath sites that had transformed into more mesotrophic vegetation types. In *Nardus* grasslands, however, species composition shifts towards eutrophication were relatively weak. This result was somewhat unexpected, especially compared to other studies from German *Nardus* grasslands, where even less pronounced increases in pH were linked to more distinct indications of eutrophication. We conclude that the regular management applied to the sites contributed essentially to this outcome by counteracting eutrophication in an effective way. In the surveyed *Nardus* grasslands, the relatively early date of mowing (from mid-July) enabled a successful removal of nutrients and resulted in a characteristic structure and species composition. However, some quantitative changes (increase in cover-weighted mR and mN, decrease in cover of character species) indicate a certain risk of eutrophication and loss of specialist species, and that continuing management will be crucial for a sustained conservation of *Nardus* grasslands. The same management, however, was not able to preserve wet heaths equivalently. By strongly disadvantaging the dominant dwarf shrubs, regular mowing altered the internal nutrient cycling of the heaths which led to increased eutrophication effects. Other management strategies, e.g. periodic top soil removal, possibly combined with extensive grazing, should be considered for maintaining the wet heath stands. In any case, we recommend further monitoring, preferably every five years, to calibrate management plans to secure the survival of these important remnants of historical land use.

Erweiterte deutsche Zusammenfassung

Einleitung – Halbnatürliche Offenlandvegetation ist in Europa ein Hotspot der Biodiversität (HABEL et al. 2013, DENGLER et al. 2014). Von der jüngeren Vergangenheit bis in die Gegenwart stellen Landnutzungsveränderungen, atmosphärische Depositionen, insbesondere von reaktivem Stickstoff und Schwefeldioxid, und neuerdings auch der Klimawandel eine Gefahr für die Artenvielfalt dieser Habitate dar (SALA et al. 2000, POSCHLOD et al. 2005). Die vorliegende Wiederholungsuntersuchung der Vegetation von Borstgrasrasen, Pflanzengesellschaft des Jahres 2020 (SCHWABE et al. 2019), und Feuchtheiden in der Eifel zwischen 1986 und 2018 hatte zum Ziel, die Entwicklung dieser Vegetationstypen unter dem Einfluss der genannten Stressoren zu untersuchen. Die Landnutzung der Untersuchungsflächen bestand im Untersuchungszeitraum aus einem Pflegemanagement durch den Vertragsnaturschutz; bis kurz vor der Erstaufnahme hatten die Flächen längere Zeit brach gelegen. Gemäß diesen Rahmenbedingungen erwarteten wir daher, dass (1) das Pflegemanagement mit einschüriger Mahd die Vegetationstypen zumindest erhalten konnte, (2) der pH-Wert des Bodens durch den Rückgang der Schwefeldioxid-Emissionen seit den 1980er Jahren wieder angestiegen ist, und (3) dieser pH-Anstieg in Kombination mit Stickstoff-Emissionen zu einer Eutrophierung der Standorte mit entsprechenden Veränderungen der Artenzusammensetzung geführt hat.

Methoden und Methoden – Die Studie basiert auf Aufnahmen von Gerhard Ludwig aus dem Jahre 1986 (LUDWIG 1987). Die untersuchten Borstgrasrasen und Feuchtheiden befinden sich in der Nord-Eifel, ca. 50 km südwestlich Bonn. Bis kurz vor der Erstaufnahme hatten die Flächen ca. 30 Jahre lang brach gelegen. Seitdem wurden sie im Rahmen von Vertragsnaturschutzprogrammen jährlich einmal ab Mitte Juli gemäht. Im Jahre 2018 wurden dann in neun Gebieten 50 Vegetationsaufnahmen von Borstgrasrasen und 14 von Feuchtheiden wiederholt und in allen Aufnahmeflächen der pH-Wert, in 22 Flächen auch der Phosphat-Gehalt des Bodens gemessen. Aus der Artenkombination der Aufnahmen wurden mittlere T-, F-, R- und N-Zeigerwerte nach Ellenberg berechnet. Ferner diente die Stetigkeit und Deckung der Arten von sechs syntaxonomisch-ökologischen Artengruppen als abhängige Variablen; diese Artengruppen beinhalteten die Charakterarten der (1) Borstgrasrasen, (2) Feuchtheiden, (3) Kleinseggenriede und des (4) Wirtschaftsgrünlands sowie (5) weitere Arten der Magerwiesen und (6) Brachezeiger. Weiterhin wurden die Veränderung der Artenzahl, Evenness, Artenzugewinne und -verluste, das Verhältnis von Gräsern i. w. S. zu Kräutern, die Deckung von Zwergsträuchern sowie ein Bracheindex der Vegetation untersucht. Signifikante Unterschiede in der Häufigkeit und Abundanz von einzelnen Arten wurden ebenfalls ermittelt. Um den Effekt der Faktoren pH_{1986}, Veränderung des pH, $\mathrm{Bracheindex}_{1986}$, Gebiet und Syntaxon auf die Vegetationsveränderungen zu untersuchen, wurden multiple lineare Modelle und eine RDA erstellt.

Ergebnisse – Die pH-Werte stiegen zwischen 1986 und 2018 im Mittel von 3,9 auf 4,6 an. Die Ellenberg-Zeigerwerte für Bodenreaktion und Nährstoffe stiegen lediglich in den Feuchtheiden signifikant an, während sie in den Borstgrasrasen stabil blieben (Abb. 1). Die mittlere Artenzahl pro Aufnahme blieb in den Borstgrasrasen unverändert, erhöhte sich dagegen in den Feuchtheiden signifikant. Die Evenness und das Verhältnis von Gräsern zu Kräutern veränderten sich nicht signifikant (Abb. 2). Alle 1986 vorhandenen Borstgrasrasen konnten, mit hohen Gesamt-Artenzahlen (Mittel von 34,3 Arten pro 20 m^2) und einem Anteil von 40 % *Nardetalia*-Charakterarten, auch 2018 noch als solche angesprochen werden. Die Deckungssumme der Charakterarten der Borstgrasrasen ging allerdings zurück, während die Anzahl der Arten des Wirtschaftsgrünlands und der Kleinseggenriede zunahmen (Abb. 3, Anhang E4). Wohl als Ergebnis der regelmäßigen Mahd profitierten konkurrenzschwache Arten (z. B. *Carex pilulifera*, *Pedicularis sylvatica*), während Arten, die bei Brache zur Dominanz gelangen können (insb. *Molinia caerulea*), zurückgedrängt wurden. In den Feuchtheiden waren die Veränderungen insgesamt deutlich stärker; die Bestände haben sich zu feuchten Varianten von Borstgrasrasen, von Kleinseggen dominierten Rasen oder Feuchtwiesen entwickelt. Die Charakterarten der Feuchtheiden (z. B. *Erica tetralix*, *Trichophorum cespitosum* subsp. *germanicum*) nahmen stark ab und traten nur noch mit einem Anteil von 3 % an der Gesamt-Artenzahl auf. Auch die multivariate Analyse zeigt, dass sich die Feuchtheiden im Untersuchungszeitraum deutlich stärker verändert haben als die Borstgrasrasen (Abb. 4). Zudem sind sich die Feuchtheiden und Borstgrasrasen floristisch ähnlicher geworden. Gleichzeitig haben sich die Aufnahmewerte in der DCA in Richtung feuchterer und nährstoffreicherer Bedingungen verschoben. Die linearen Regressionsmodelle und die RDA zeigen, dass die Vegetationsveränderung in einem signifikanten Kontext mit der Veränderung des pH-Wertes und des Bracheindex im Jahr 1986 stand (Tab. 1 und 2). Ein Großteil der Veränderungen hing laut Modellen jedoch vom Ausgangstyp der Bestände (Borstgrasrasen *vs*. Feuchtheiden) ab, d. h. die Vegetationstypen haben sich unterschiedlich entwickelt.

Diskussion – Der durchgängige Anstieg des pH-Werts kann auf den Rückgang der $\mathrm{SO_2}$-Emissionen seit den 1980er Jahren zurückgeführt werden (KIRK et al. 2010, PEPPLER-LISBACH et al. 2020). Er hatte zwar die erwarteten Effekte auf die floristischen Veränderungen, wie z. B. einen positiven Einfluss auf Nährstoffzeiger und einen negativen auf Kennarten der Borstgrasrasen, trug allerdings in einem relativ geringen Umfang zur Veränderung der Vegetation bei. Dabei konnten Eutrophierungserscheinungen vor allem in den Feuchtheiden beobachtet werden, wohingegen die Borstgrasrasen stabiler waren. Diese relativ schwachen Veränderungen der Borstgrasrasen sind sehr wahrscheinlich ein Erfolg der regelmäßigen und nicht zu spät stattfindenden Mahd und den damit einhergehenden Austrägen von Stickstoff oder anderen Nährstoffen (v.a. Phosphor und Kalium) (VERHOEVEN et al. 1993, MLÁDKOVÁ et al. 2015). Der Grund für die stärkeren Veränderungen in den Feuchtheiden liegt zum einen in der Reduktion der ursprünglich dominierenden Zwergsträucher aufgrund ihrer geringen Verträglichkeit gegenüber regelmäßiger Mahd (LEUSCHNER & ELLENBERG 2017). Zum anderen konnte als Folge die maßgeblich durch die Zwergsträucher aufgebaute Rohhumus-Auflage zunehmend zersetzt werden, was zu einer erhöhten Nährstoffverfügbarkeit führte (BERENDSE et al. 1987). Erhöhte pH-Werte (PEPPLER-LISBACH & KÖNITZ 2017) und Temperaturen (LEUSCHNER & ELLENBERG 2017) könnten die Geschwindigkeit des Humusabbaus zusätzlich gefördert haben. Zusammenfassend sind wir der Überzeugung, dass der Anstieg der pH-Werte und möglicherweise auch atmosphärische Stickstoff-Einträge nur eine Mitursache für die beobachteten Vegetationsveränderungen waren, während die wiedereingeführte und regelmäßig praktizierte Pflegemahd entscheidend war.

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Author contributions

GL conducted the original survey in 1986 and helped with questions regarding methodology and plot locations. CPL and LM designed the study, LM conducted the vegetation resurvey and soil analyses. CPL and LM analysed the vegetation and environmental data and discussed the interpretation of results. LM wrote the first draft of the manuscript. All authors gave their final approval for publication.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Complete list of species with habitat preference group and taxonomic group assignment.

Anhang E1. Vollständige Artenliste mit Zuordnung zu taxonomischen Gruppen und Habitat-Präferenz Gruppen.

Supplement E2. Mean and standard deviations of pH values and presence/absence-based Ellenberg indicator values for soil reaction (mR) and nutrients (mN) for *Nardus* grasslands and wet heaths in 1986 and 2018.

Anhang E2. Mittelwerte und Standardabweichungen von pH-Werten und Präsenz/Absenz-basierten Ellenberg-Zahlen für Bodenreaktion (mR) und Nährstoffe (mN) in Borstgrasrasen und Feuchtheiden in 1986 und 2018.

Supplement E3. Changes of pH and cover-weighted Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR) and soil nutrients (mN).

Anhang E3. Veränderungen von pH-Wert und mit Deckungsgraden gewichteten Ellenberg-Zahlen für Temperatur (mT), Bodenfeuchte (mF), Bodenreaktion (mR) und Nährstoffe (mN).

Supplement E4. Changes in total cover and cover sums of character species groups.

Anhang E4. Veränderungen von Gesamtdeckung und Deckungssummen von Artengruppen.

Supplement E5. Changes of single species in *Nardus* grasslands in frequency and cover value between 1986 and 2018.

Anhang E5. Veränderungen einzelner Arten in Borstgrasrasen hinsichtlich Frequenz und Abundanz zwischen 1986 und 2018.

Supplement E6. Changes of single species in wet heaths in frequency and cover value between 1986 and 2018.

Anhang E6. Veränderungen einzelner Arten in Feuchtheiden hinsichtlich Frequenz und Abundanz zwischen 1986 und 2018.

Supplement E7. Coefficients for best multiple linear regression models for changes in Ellenberg indicator values for soil reaction (mR) and nutrients (mN), presence/absence-based (p/a) and abundance-weighted (cov) respectively.

Anhang E7. Koeffizienten der besten linearen Modelle für Veränderungen von Ellenberg-Zeigerwerten für Bodenreaktion (mR) und Nährstoffe (mN), sowohl Präsenz/Absenz-basiert (p/a) als auch mit Deckungsgrad gewichtet (cov).

Supplement E8. Coefficients for best multiple linear regression models for changes in species numbers and Sørensen indices, calculated with presence/absence data (qualitative) or cover values (quantitative) respectively.

Anhang E8. Koeffizienten der besten multiplen linearen Modelle für Veränderungen von Artenzahlen und Sørensen-Indizes, berechnet mit Präsenz/Absenz-Daten (qualitativ) und Deckungsgraden (quantitativ).

Supplement E9. Coefficients for best multiple linear regression models for changes in species group presence (p/a) and cover sums (cover) respectively.

Anhang E9. Koeffizienten der besten multiplen linearen Modelle für Veränderungen der Artengruppen Frequenz (p/a) und Deckungssummen (cover).

Supplement E10. Results of an RDA on species diffierences between 1986 and 2018, based on presence/absence (p/a) and square-root transformed cover values (cover) respectively.

Anhang E10. Ergebnisse einer RDA mit Differenzen aller Arten zwischen 1986 und 2018, basierend auf Präsenz/Absenz-Daten (p/a) bzw. Quadratwurzel-transformierten Deckungswerten (cover).

Supplement E11. DCA of all plots in 1986 and 2018 based on species presence/absence data, only species with at least 10 occurrences in the total data set are displayed.

Anhang E11. DCA aller Aufnahmen von 1986 und 2018, basierend auf Präsenz/Absenz-Daten. Nur Arten mit mindestens 10 Vorkommen im Gesamtdatensatz sind dargestellt.

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Supplement E1. Complete list of species with habitat preference group and taxonomic group assignment. Taxonomic groups: Dico = herbaceous dicotyledones, Gram = graminoids, Phan = bushes and trees, dw. shrub = dwarf shrubs, Mono = herbaceous monocotyledones, Moss = cryptogams. Habitat-preference groups: NardG = character species of *Nardus* grasslands from the class *Calluno-Ulicetea* Br.-Bl. et Tüxen 1943 ex Klika et Hadac 1944 (according to Peppler-Lisbach & Petersen 2001); WetH = character species of wet heaths from the class *Oxycocco-Sphagnetea* Br.-Bl. & Tx. Ex Westhoff et al. 1946 (group 1.8 in Ellenberg et al. 1992, classification of mosses according to Dierssen 1982); SSF: character species of small sedge fens (*Scheuchzerio-Caricetea nigrae* Tx. 1937, group 1.7 in Ellenberg et al. 1992, classification of mosses according to Dierssen 1982); AgriG = species of agricultural grasslands (*Molinio-Arrhenatheretea* Tx. 1937, group 5.4 in Ellenberg et al. 1992 with N > 3); PoorG = species of nutrient-poor grasslands (groups 5.2 - 5.4 in Ellenberg et al. 1992 with N <= 3); Aban: fallow indicators like trees, bushes and typical understorey species (groups 6 - 8 in Ellenberg et al. 1992). Red List Code (Metzing et al. 2018): V = early warning, 3 = endangered, 2 = highly endangered, / = not assessed, D = not enough data.

Anhang E1. Vollständige Artenliste mit Zuordnung zu taxonomischen Gruppen und Habitat-Präferenz Gruppen. Taxonomische Gruppen: Dico = krautige Dikotyle, Gram = Grasartige, Phan = Bäume und Sträucher, dw. shrub = Zwergsträucher, Mono = krautige Monokotyle, Moss = Kryptogamen. Gruppen der Habitatpräferenz: NardG = Charakterarten der Borstgrasrasen aus der Klasse *Calluno-Ulicetea* Br.-Bl. et Tüxen 1943 ex Klika et Hadac 1944 (nach Peppler-Lisbach & Petersen 2001); WetH = Charakterarten der Feuchtheiden aus der Klasse *Oxycocco-Sphagnetea* Br.-Bl. & Tx. Ex Westhoff et al. 1946 (Gruppe 1.8 in Ellenberg et al. 1992, Klassifikation der Moose nach Dierssen 1982); SSF = Charakterarten der Kleinseggenriede (*Scheuchzerio-Caricetea nigrae* Tx. 1937, Gruppe 1.7 in Ellenberg et al. 1992, Klassifikation der Moose nach Dierssen 1982); AgriG = Arten des Wirtschaftsgrünlands (*Molinio-Arrhenatheretea* Tx. 1937, Gruppe 5.4 in Ellenberg et al. 1992 mit N > 3); PoorG = weitere Arten des mageren Grünlandes (Gruppen 5.2-5.4 in Ellenberg et al. 1992 mit N <= 3); Aban = Brachezeiger wie Bäume, Büsche und typische Unterholz-Arten (Gruppen 6-8 in Ellenberg et al. 1992). Code der Roten Liste (Metzing et al. 2018): V = Vorwarnliste, 3 = gefährdet, 2 = stark gefährdet, / = nicht bewertet, D = nicht genug Daten.

	Red List BRD	taxon. group	habitat group
Achillea millefolium	.	Dico	AgriG
Achillea ptarmica	.	Dico	PoorG
Agrostis canina	.	Gram	SSF
Agrostis capillaris	.	Gram	AgriG
Anemone nemorosa	.	Dico	Indiff
Angelica sylvestris	.	Dico	AgriG
Anthoxanthum odoratum	.	Gram	Indiff
Anthyllis vulneraria	.	Dico	PoorG
Arnica montana	3	Dico	NardG
Arrhenatherum elatius	.	Gram	AgriG
Athyrium filix-femina	.	Moss	Indiff
Atrichum undulatum	.	Moss	Indiff
Aulacomnium palustre	V	Moss	Indiff
Barbilophozia kunzeana	2	Moss	Indiff
Betonica officinalis	V	Dico	AgriG
Betula pendula	.	Phan	Aban
Betula pubescens	.	Phan	Aban
Botrychium lunaria	3	Moss	NardG
Brachythecium rivulare	.	Moss	Indiff
Brachythecium rutabulum	.	Moss	Indiff
Briza media	.	Gram	PoorG
Bryum caespiticium	.	Moss	Indiff
Bryum pseudotriquetrum	.	Moss	SSF
Calluna vulgaris	.	dw. shrub	NardG
Calliergon stramineum	V	Moss	SSF
Calliergonella cuspidata	.	Moss	Indiff
Calypogeia arguta	.	Moss	Indiff
Calypogeia muelleriana	.	Moss	Indiff
Calypogeia fissa	.	Moss	Indiff
Caltha palustris	V	Dico	AgriG
Campylopus flexuosus	.	Moss	WetH
Campylopus fragilis	V	Moss	Indiff
Campylopus introflexus	/	Moss	Indiff
Campylopus pyriformis	.	Moss	Indiff
Campanula rotundifolia	.	Dico	PoorG
Cardamine pratensis	.	Dico	Indiff
Carex caryophyllea	V	Gram	PoorG
Carex demissa	V	Gram	SSF
Carex echinata	.	Gram	SSF
Carex flacca	.	Gram	Indiff
Carex montana	.	Gram	Indiff

	Red List BRD	taxon. group	habitat group
Carex nigra	.	Gram	SSF
Carex ovalis	.	Gram	NardG
Carex pallescens	.	Gram	NardG
Carex panicea	V	Gram	SSF
Carex pulicaris	2	Gram	SSF
Carex remota	.	Gram	Aban
Carex pilulifera	.	Gram	NardG
Centaurea jacea agg.	.	Dico	PoorG
Centaurea nigra subsp. *nemoralis*	.	Dico	PoorG
Cephalozia bicuspidata	.	Moss	Indiff
Cerastium holosteoides	.	Dico	AgriG
Ceratodon purpureus	.	Moss	Indiff
Cetraria islandica	2	Moss	Indiff
Chamaespartium sagittale	V	Dico	NardG
Cirsium palustre	.	Dico	AgriG
Cladonia portentosa	3	Moss	Indiff
Cladonia arbuscula subsp. *mitis*	3	Moss	Indiff
Climacium dendroides	.	Moss	Indiff
Colchicum autumnale	.	Mono	AgriG
Crataegus monogyna	.	Phan	Aban
Cytisus scoparius	.	Phan	Aban
Dactylorhiza maculata agg.	V	Mono	Indiff
Dactylis glomerata	.	Gram	Indiff
Danthonia decumbens	V	Gram	NardG
Deschampsia cespitosa	.	Gram	Indiff
Deschampsia flexuosa	.	Gram	NardG
Dicranum bonjeanii	3	Moss	Indiff
Dicranum polysetum	V	Moss	Indiff
Dicranum scoparium	.	Moss	Indiff
Dicranoweisia cirrata	.	Moss	Indiff
Dicranella heteromalla	.	Moss	Indiff
Diplophyllum albicans	.	Moss	Indiff
Dryopteris carthusiana	.	Mono	Aban
Epilobium angustifolium	.	Dico	Aban
Epilobium montanum	.	Dico	Aban
Equisetum arvense	.	Moss	Indiff
Erica tetralix	V	dw. shrub	WetH
Eriophorum angustifolium	V	Gram	SSF
Euphrasia frigida	2	Dico	NardG
Eurhynchium praelongum	.	Moss	Indiff
Eurhynchium striatum	.	Moss	Indiff
Fagus sylvatica	.	Phan	Aban
Festuca rubra agg.	.	Gram	AgriG
Festuca filiformis	.	Gram	NardG
Frangula alnus	.	Phan	Aban
Galium mollugo agg.	.	Dico	Indiff
Galium palustre	.	Dico	Indiff
Galium saxatile	.	Dico	NardG
Galium verum	.	Dico	PoorG
Galium uliginosum	.	Dico	PoorG
Galeopsis tetrahit	.	Dico	Aban
Genista anglica	3	dw. shrub	NardG
Genista pilosa	V	dw. shrub	NardG
Gentiana pneumonanthe	2	Dico	PoorG
Gymnocolea inflata	V	Moss	Indiff
Hedera helix	.	Phan	Aban
Helictotrichon pratense	V	Gram	PoorG
Heracleum sphondylium	.	Dico	AgriG
Hieracium lachenalii	.	Dico	NardG
Hieracium laevigatum	.	Dico	PoorG
Hieracium laurinum	.	Dico	Aban
Hieracium sabaudum	.	Dico	Aban
Hieracium pilosella	.	Dico	PoorG
Hieracium umbellatum	.	Dico	Aban
Holcus lanatus	.	Gram	AgriG
Holcus mollis	.	Gram	Aban
Hylocomium splendens	.	Moss	Indiff
Hypericum maculatum	.	Dico	PoorG
Hypericum pulchrum	.	Dico	PoorG

	Red List BRD	taxon. group	habitat group
Hypericum perforatum	.	Dico	Aban
Hypnum jutlandicum	.	Moss	NardG
Hypochaeris radicata	.	Dico	PoorG
Juncus acutiflorus	.	Gram	PoorG
Juncus articulatus	.	Gram	SSF
Juncus bufonius	.	Gram	Indiff
Juncus bulbosus	.	Gram	Indiff
Juncus conglomeratus	.	Gram	PoorG
Juncus effusus	.	Gram	AgriG
Juncus conglomeratus × effusus	.	Gram	AgriG
Juncus squarrosus	V	Gram	NardG
Jungermannia gracillima	V	Moss	Indiff
Knautia arvensis	.	Dico	AgriG
Koeleria pyramidata	V	Gram	PoorG
Lathyrus linifolius	V	Dico	NardG
Lathyrus pratensis	.	Dico	AgriG
Leontodon autumnalis	.	Dico	AgriG
Leucanthemum ircutianum	.	Dico	AgriG
Leucobryum glaucum	.	Moss	Indiff
Linum catharticum	.	Dico	PoorG
Lonicera periclymenum	.	Phan	Aban
Lophocolea bidentata	.	Moss	Indiff
Lophocolea heterophylla	.	Moss	Indiff
Lophozia ventricosa	D	Moss	Indiff
Lophozia wenzelii	.	Moss	Indiff
Lotus corniculatus	.	Dico	PoorG
Lotus pedunculatus	.	Dico	AgriG
Luzula congesta	3	Gram	NardG
Luzula campestris	.	Gram	NardG
Luzula multiflora	.	Gram	NardG
Maianthemum bifolium	.	Mono	Aban
Melampyrum pratense	.	Dico	Aban
Mentha aquatica	.	Dico	Indiff
Meum athamanticum	V	Dico	PoorG
Mnium hornum	.	Moss	Indiff
Molinia caerulea	.	Gram	PoorG
Myosotis nemorosa	.	Dico	AgriG
Narcissus pseudonarcissus	3	Mono	NardG
Nardus stricta	V	Gram	NardG
Narthecium ossifragum	3	Mono	WetH
Odontoschisma sphagni	3	Moss	WetH
Pedicularis sylvatica	3	Dico	NardG
Phyteuma nigrum	V	Dico	AgriG
Picea abies	.	Phan	Aban
Pimpinella saxifraga	.	Dico	PoorG
Pinus sylvestris	.	Phan	Aban
Plantago lanceolata	.	Dico	AgriG
Platanthera bifolia	3	Mono	Indiff
Platanthera chlorantha	3	Mono	Indiff
Pleuridium acuminatum	.	Moss	Indiff
Pleurozium schreberi	.	Moss	NardG
Plagiomnium rostratum	.	Moss	Indiff
Plagiothecium laetum var. *curvifolium*	.	Moss	Indiff
Poa humilis	.	Gram	PoorG
Poa trivialis	.	Gram	AgriG
Poa pratensis	.	Gram	AgriG
Pohlia nutans	.	Moss	Indiff
Polytrichum commune var. *commune*	.	Moss	Indiff
Polytrichum commune var. *perigoniale*	V	Moss	Indiff
Polytrichum commune	.	Moss	Indiff
Polytrichum formosum	.	Moss	Indiff
Polygala serpyllifolia	3	Dico	NardG
Polygala vulgaris	V	Dico	NardG
Populus tremula	.	Phan	Aban
Potentilla erecta	.	Dico	NardG
Primula veris	V	Dico	PoorG
Prunus avium	.	Phan	Aban
Prunus padus	.	Phan	Aban
Prunella vulgaris	.	Dico	AgriG

	Red List BRD	taxon. group	habitat group
Pseudorchis albida	3	Mono	NardG
Pseudotaxiphyllum elegans	.	Moss	Indiff
Ptilidium ciliare	3	Moss	NardG
Quercus petraea	.	Phan	Aban
Quercus robur	.	Phan	Aban
Ranunculus acris	.	Dico	AgriG
Ranunculus flammula	.	Dico	SSF
Ranunculus nemorosus	V	Dico	Indiff
Ranunculus repens	.	Dico	AgriG
Rhizomnium punctatum	.	Moss	Indiff
Rhinanthus minor	.	Dico	AgriG
Rhytidiadelphus squarrosus	.	Moss	Indiff
Rubus fruticosus agg.	.	Phan	Aban
Rubus idaeus	.	Phan	Aban
Rumex acetosa	.	Dico	AgriG
Salix aurita	.	Phan	Aban
Salix caprea	.	Phan	Aban
Salix repens	.	Dico	PoorG
Salix × multinervis	.	Phan	Aban
Salix cinerea	.	Phan	Aban
Sanguisorba minor	.	Dico	AgriG
Sanguisorba officinalis	V	Moss	Indiff
Scapania paludicola	2	Moss	Indiff
Scapania nemorea	.	Moss	Indiff
Scapania undulata	.	Moss	Indiff
Scapania irrigua	V	Moss	Indiff
Scleropodium purum	.	Dico	PoorG
Scorzonera humilis	3	Dico	AgriG
Silene flos-cuculi	.	Dico	Indiff
Solidago virgaurea	.	Phan	Aban
Sorbus aucuparia	.	Phan	Aban
Sphagnum capillifolium	.	Moss	Indiff
Sphagnum compactum	3	Moss	WetH
Sphagnum denticulatum var. *inundatum*	3	Moss	SSF
Sphagnum denticulatum	.	Moss	SSF
Sphagnum fallax	.	Moss	SSF
Sphagnum magellanicum	3	Moss	WetH
Sphagnum molle	2	Moss	WetH
Sphagnum subsecundum	3	Moss	SSF
Sphagnum palustre	.	Moss	SSF
Sphagnum papillosum	3	Moss	WetH
Sphagnum quinquefarium	.	Moss	Indiff
Sphagnum rubellum var. *subtile*	3	Moss	WetH
Sphagnum tenellum	2	Moss	WetH
Stellaria alsine	.	Dico	Indiff
Stellaria graminea	.	Dico	Indiff
Succisa pratensis	V	Dico	PoorG
Taraxacum sect. *Alpina et Hamata et Ruderalia*	.	Dico	AgriG
Teucrium scorodonia	.	Dico	Aban
Thesium pyrenaicum	3	Dico	PoorG
Thuidium delicatulum	V	Moss	Indiff
Thuidium tamariscinum	.	Moss	Indiff
Thymus pulegioides	.	Dico	PoorG
Trichophorum cespitosum subsp. *germanicum*	2	Gram	WetH
Trientalis europaea	.	Dico	Aban
Trifolium medium	.	Dico	Indiff
Trifolium pratense	.	Dico	AgriG
Trifolium repens	.	Dico	AgriG
Vaccinium myrtillus	.	dw. shrub	NardG
Valeriana dioica	.	Dico	AgriG
Veronica chamaedrys	.	Dico	Indiff
Veronica officinalis	.	Dico	NardG
Viburnum opulus	.	Phan	Aban
Vicia cracca	.	Dico	AgriG
Viola canina	V	Dico	NardG
Viola palustris	.	Dico	SSF
Viola reichenbachiana	.	Dico	Aban

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Supplement E2. Mean and standard deviations of pH values and presence/absence-based Ellenberg indicator values for soil reaction (mR) and nutrients (mN) for *Nardus* grasslands and wet heaths in 1986 and 2018. Small letters indicate significant differences between the groups. Groups were tested for similarity with a pairwise Wilcoxon rank sum test corrected for multiple comparisons with the “Bonferroni”-method.

Anhang E2. Mittelwerte und Standardabweichungen von pH-Werten und Präsenz/Absenz-basierten Ellenberg-Zahlen für Bodenreaktion (mR) und Nährstoffe (mN) in Borstgrasrasen und Feuchtheiden in 1986 und 2018. Hochgestellte Buchstaben geben die Signifikanz von Unterschieden zwischen den Gruppen an. Tests auf signifikante Unterschiede wurden mit einem paarweisen Wilcoxon-Vorzeichen-Rang-Test durchgeführt und mit der „Bonferroni”-Methode für multiple Vergleiche korrigiert.

	Nardus grassland		Wet heaths	
	1986	2018	1986	2018
pH	3.94 (0.20)^{a}	4.67 (0.23)^{b}	3.62 (0.33)^{c}	4.44 (0.37)^{d}
mR	3.10 (0.30)^{a}	3.40 (0.25)^{a}	2.36 (0.18)^{b}	3.14 (0.49)^{a}
mN	2.49 (0.19)^{a}	2.55 (0.20)^{a}	2.29 (0.35)^{b}	2.56 (0.37)^{ab}

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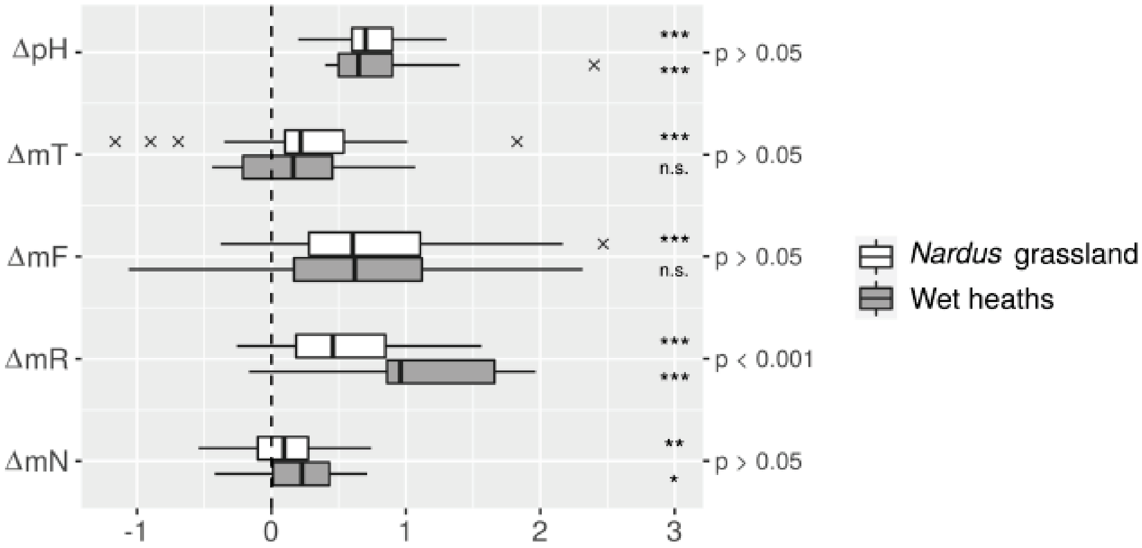
Supplement E3. Changes of pH and cover-weighted Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR) and soil nutrients (mN). Significance symbols (*** p<0.001 ** p<0.01 * p<0.05 n.s. p>0.05) indicate differences in indicator values between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Anhang E3. Veränderungen von pH-Wert und mit Deckungsgraden gewichteten Ellenberg-Zahlen für Temperatur (mT), Bodenfeuchte (mF), Bodenreaktion (mR) und Nährstoffe (mN). Sternchen (*** p<0,001 ** p<0,01 * p<0,05 n.s. p>0,05) geben das Signifikanz-Niveau von Unterschieden der Zeigerwerte zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.



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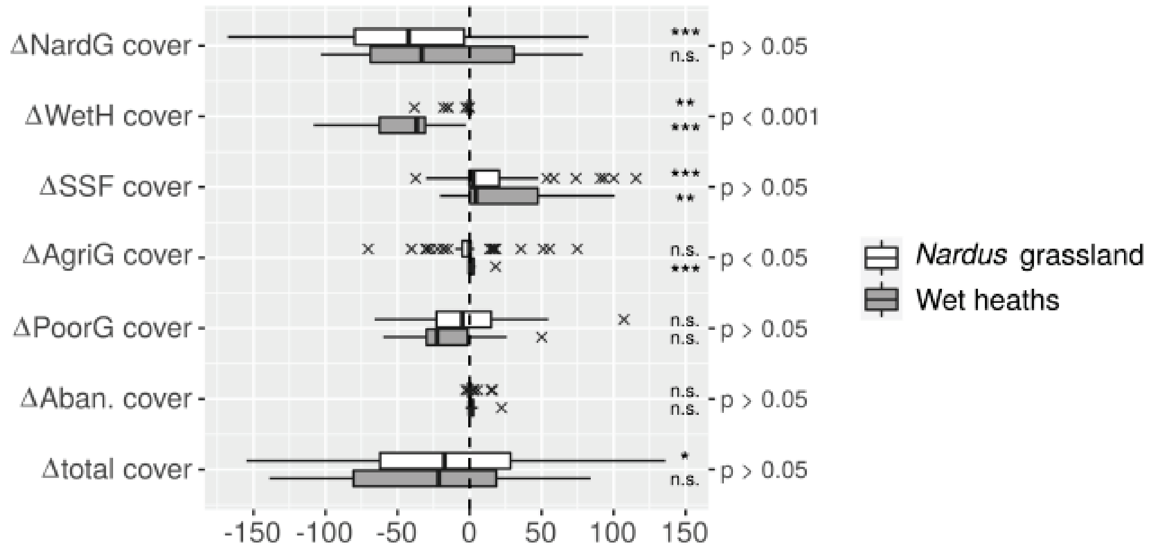
Supplement E4. Changes in total cover and cover sums of character species groups. NardG = character species of *Nardus* grasslands; WetH = character species of wet heaths; SSF = character species of small sedge fens; AgriG = species of agricultural grasslands; PoorG = other species of nutrient-poor grasslands; Aban = fallow indicators. Significance symbols (*** $p<0.001$ ** $p<0.01$ * $p<0.05$ n.s. $p>0.05$) indicate differences in species group cover between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Anhang E4. Veränderungen von Gesamtdeckung und Deckungssummen von Artengruppen. NardG = Charakterarten der Borstgrasrasen; WetH = Charakterarten der Feuchtheiden; SSF = Charakterarten der Kleinseggenriede; AgriG = Arten des Wirtschaftsgrünlands; PoorG = andere Arten mageren Grünlands; Aban = Brachezeiger. Sternchen (*** $p<0{,}001$ ** $p<0{,}01$ * $p<0{,}05$ n.s. $p>0{,}05$) geben das Signifikanz-Niveau von Unterschieden der Deckungssummen der Artengruppen zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.



Supplement E5. Changes of single species in *Nardus* grasslands in frequency and cover value between 1986 and 2018. Habitat and taxonomic group abbreviations: see Table S8. T, F, R, N: Ellenberg indicator values for temperature, soil moisture, soil reaction and nutrients. *p*-value: Wilcoxon signed rank test of differences, adjusted for false detection rate (“fdr”). Levels of significance: *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$.

Anhang E5. Veränderungen einzelner Arten in Borstgrasrasen hinsichtlich Frequenz und Abundanz zwischen 1986 und 2018. Abkürzungen der taxonomischen und Habitat-Gruppen: siehe Tab. S8. T, F, R, N: Ellenberg-Zahlen für Temperatur, Bodenfeuchte, Bodenreaktion und Nährstoffe. *p*-Werte: Wilcoxon-Vorzeichen-Rang-Tests, korrigiert für die Falscherkennungsrate („fdr“). Signifikanz-Niveaus: *** $p < 0{,}001$ ** $p < 0{,}01$ * $p < 0{,}05$.

	freq 1986	freq 2018	Δfreq	Δcover	habitat group	taxon. Group	T	F	R	N
Increase Frequency & Cover										
Carex pilulifera	17	47	30**	5.19***	SSF	Gram	.	5	3	3
Pedicularis sylvatica	20	45	25***	1.42*	NardG	Dico	5	8	1	2
Carex echinata	0	22	22***	2.57***	SSF	Gram	.	8	3	2
Rhinanthus minor	1	20	19***	0.08***	AgriG	Dico	5	4	.	3
Quercus robur	0	13	13*	0.02*	Aban	Phan	6	.	.	.
Increase Frequency										
Plantago lanceolata	3	17	14*	0.4	AgriG	Dico	.	.	.	.
Increase Cover										
Rhytidiadelphus squarrosus	39	48	9	15.34*	Indiff	Moss	3	6	5	.
Danthonia decumbens	39	48	9	11.49***	NardG	Gram	.	.	3	2
Hylocomium splendens	27	42	15	5.38*	Indiff	Moss	.	.	.	.
Juncus acutiflorus	1	14	13	0.99*	PoorG	Gram	6	8	5	3
							Ø 5.0	6.5	3.3	2
Decrease Frequency & Cover										
Lophocolea bidentata	30	0	-30***	-0.45***	WetH	Moss	3	6	5	.
Pleurozium schreber	50	27	-23***	-18.24***	Indiff	Moss	3	4	2	.
Luzula multiflora	32	13	-19*	-0.21*	NardG	Gram	.	5	5	3
Dicranum scoparium	27	9	-18**	-0.53***	NardG	Moss	.	4	4	.
Hypnum jutlandicum	48	27	-11***	-5.12**	Indiff	Moss	3	2	2	.
Decrease Frequency										
Aulacomnium palustre	39	22	-17**	-1.94	Indiff	Moss	2	7	3	.
Decrease Cover										
Nardus stricta	47	48	1	-20.25***	NardG	Gram	.	.	2	2
Festuca filiformis	50	48	-2	-6.23***	NardG	Gram	6	4	3	2
Arnica montana	37	26	-11	-4.43**	NardG	Dico	4	5	3	2
Polytrichum commune var. perigionale	33	22	-11	-3.56**	Indiff	Moss	.	.	.	.
Polygala serpyllifolia	43	44	1	-0.48***	NardG	Dico	4	6	2	2
							Ø 3.6 P = 0.11	4.8 P = 0.09	3.1 P = 0.65	2.2 P = 0.55

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Supplement E6. Changes of single species in wet heaths in frequency and cover value between 1986 and 2018. Habitat and taxonomic group abbreviations: see Table S8. T, F, R, N: Ellenberg indicator values for temperature, soil moisture, soil reaction and nutrients. p-value: Wilcoxon signed rank test of differences, adjusted for false detection rate ("fdr"). Levels of significance: *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$.

Anhang E6. Veränderungen einzelner Arten in Feuchtheiden hinsichtlich Frequenz und Abundanz zwischen 1986 und 2018. Abkürzungen der taxonomischen Gruppen und Habitat-Gruppen: siehe Tab. S8. T, F, R, N: Ellenberg-Zahlen für Temperatur, Bodenfeuchte, Bodenreaktion und Nährstoffe. P-Werte: Wilcoxon-Vorzeichen-Rang-Tests, korrigiert für die Falscherkennungsrate („fdr"). Signifikanz-Niveaus: *** $p < 0{,}001$ ** $p < 0{,}01$ * $p < 0{,}05$.

	freq 1986	freq 2018	Δfreq	Δcover	habitat group	taxon. Group	T	F	R	N
Increase Frequency and Cover										
Rhytidiadelphus squarrosus	0	13	13***	15.21**	Indiff.	Moss	3	6	5	.
Increase Cover										
Agrostis canina	2	11	9	3.83*	SSF	Gram	5	9	3	2
Decrease Cover										
Erica tetralix	12	6	6	-13.50*	Indiff	dw.shrub	5	8	1	2

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Supplement E7. Coefficients for best multiple linear regression models for changes in Ellenberg indicator values for soil reaction (mR) and nutrients (mN), presence/absence-based (p/a) and abundance-weighted (cov) respectively. pH 1986, Fallow index 1986, mF 1986: pH, fallow-index and Ellenberg indicator value for soil moisture as measured in 1986. ΔpH, ΔmF: changes in pH and Ellenberg indicator value for soil moisture between 1986 and 2018. WH: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. WH:mF1986, WH: ΔmF, WH:pH1986: interaction terms with wet heath. *p*-values were calculated with a type III test (t-test). Share: share of explained variance calculated with hierarchical partitioning.

Anhang E7. Koeffizienten der besten linearen Modelle für Veränderungen von Ellenberg-Zeigerwerten für Bodenreaktion (mR) und Nährstoffe (mN), sowohl Präsenz/Absenz-basiert (p/a) als auch mit Deckungsgrad gewichtet (cov). pH 1986, Fallow index 1986, mF 1986: pH, Brache-Index und Ellenberg-Zahlen für Bodenfeuchte in 1986. ΔpH, ΔmF: Veränderungen des pH-Werts und der Ellenberg-Zahl für Bodenfeuchte zwischen 1986 und 2018. WH: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. WH:mF1986, WH: ΔmF, WH:pH1986: Interaktionsterme der jeweiligen Variablen mit dem Faktor „Feuchtheide“. *p*-Werte wurden mit einem Typ-III Test (t-test) berechnet. Share: Anteil erklärter Varianz, berechnet mit hierarchischer Partitionierung.

	p	R^2	pH 1986	p/ share	ΔpH	p/ share	Fallow index 1986	WH	p/ share	Site	p/ share	mF 1986	p/ share	ΔmF	p/ share	WH:mF 1986	p/ share	WH:ΔmF	p/ share	WH:pH 1986	p/ share
ΔmR p/a	<0.001	0.38	.	.	.	.	.	0.67	<0.001 100%	.	.	.	.	.	.	.	.	.	.	.	.
ΔmR cov	<0.001	0.24	-0.32	0.353/ 3%	.	.	.	-6.29	0.006/ 40%	.	.	-0.27	0.033/ 10%	.	.	.	.	.	.	1.85	0.003/ 47%
ΔmN p/a	<0.001	0.44	.	.	.	.	.	-2.22	0.070/ 6%	9 coeff.	<0.001/ 80%	-0.03	0.773/ 1%	-0.03	0.697/1%	0.42	0.043/ 7%	-0.37	0.038/ 6%	.	.
ΔmN cov	<0.001	0.08	.	.	0.25	0.017/ 100%	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Supplement E8. Coefficients for best multiple linear regression models for changes in species numbers and Sørensen indices, calculated with presence/absence data (qualitative) or cover values (quantitative) respectively. pH 1986, Fallow index 1986: pH, fallow index as measured in 1986. ΔpH: changes in pH between 1986 and 2018. WH: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. p-values were calculated with a type III test (t-test). Share: share of explained variance calculated with hierarchical partitioning.

Anhang E8. Koeffizienten der besten multiplen linearen Modelle für Veränderungen von Artenzahlen und Sørensen-Indizes, berechnet mit Präsenz/Absenz-Daten (qualitativ) und Deckungsgraden (quantitativ). pH 1986, Fallow index 1986: pH und Bracheindex in 1986. ΔpH: Veränderungen des pH-Werts zwischen 1986 und 2018. WH: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. p-Werte wurden mit einem Typ-III Test (t-test) berechnet. Share: Anteil erklärter Varianz, berechnet mit hierarchischer Partitionierung.

	p	R^2	pH 1986	p/ share	ΔpH	p/ share	Fallow index 1986	p/ share	WH	p/ share	Site	p/ share
Δspecies number total	<0.001	0.28	.	.	.	.	.	.	11.31	<0.001/ 100%	.	.
Δspecies number vascular	<0.001	0.27	.	.	5.13	0.041/ 23%	.	.	8.19	<0.001/ 77%	.	.
Δspecies number bryophytes	<0.001	0.19	.	.	.	.	-1.7	0.021/ 26%	18.83	<0.001/ 74%	.	.
Sørensen quantitative	n.s.	.	.	.	.	.	.	.	.	.	.	.
Sørensen qualitative	<0.001	0.41	0.17	0.020/ 8%	0.11	0.034/ 7%	0.01	0.002/ 24%	0.2	<0.001/ 62%	.	.

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Supplement E9. Coefficients for best multiple linear regression models for changes in species group presence (p/a) and cover sums (cover) respectively. Species groups: NardG = character species of *Nardus* grasslands; SSF = character species of small sedge fens; AgriG = species of agricultural grasslands; PoorG = other species of nutrient-poor grasslands. pH 1986, Fallow index 1986: pH and fallow index as measured in 1986. ΔpH: changes in pH between 2018 and 1986. WH: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. p-values were calculated with a type III test (t-test). Share: share of explained variance calculated with hierarchical partitioning.

Anhang E9. Koeffizienten der besten multiplen linearen Modelle für Veränderungen der Artengruppen Frequenz (p/a) und Deckungssummen (cover). Artengruppen: NardG = Charakterarten der Borstgrasrasen; SSF = Charakterarten der Kleinseggenriede; AgriG = Arten des Wirtschaftsgrünlands; PoorG = andere Arten mageren Grünlands. pH 1986, Fallow index 1986: pH und Bracheindex in 1986. ΔpH: Veränderungen des pH-Werts zwischen 1986 und 2018. WH: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. p-Werte wurden mit einem Typ-III Test (t-test) berechnet. Share: Anteil erklärter Varianz, berechnet mit hierarchischer Partitionierung.

	p	R^2	pH 1986	p/ share	ΔpH	p/ share	Fallow index 1986	p/ share	WH	p/ share	Site	p/ share	WH: pH 1986	p/ share
ΔNardG p/a	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.
ΔNardG cover	<0.001	0.47	.	.	-46.04	0.015/ 5%	7.76	0.007/ 14%	-67.64	0.033/ 7%	9 coeff.	<0.001/ 75%	.	.
ΔAgriG p/a	0.006	0.13	.	.	2.58	0.030/ 51%	.	.	1.97	0.035/ 49%	.	.	.	.
ΔAgriG cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.
ΔSSF p/a	0.003	0.15	.	.	16.55	0.014/ 55%	.	.	11.74	0.027/ 45%	.	.	.	.
ΔSSF cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.
ΔPoorG p/a	0.001	0.19	-3.54	0.018/ 23%	.	.	.	.	-20.24	0.018/ 36%	.	.	5.81	0.011/ 41%
ΔPoorG cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.

Supplement E10. Results of an RDA on species diffierences between 1986 and 2018, based on presence/absence (p/a) and square-root transformed cover values (cover) respectively. Predictor variables were automatically selected via permutation testing. ΔpH: changes in pH between 2018 and 1986. Wet heath: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. Share: share of explained variance calculated by ANOVA.

Anhang E10. Ergebnisse einer RDA mit Differenzen aller Arten zwischen 1986 und 2018, basierend auf Präsenz/Absenz-Daten (p/a) bzw. Quadratwurzel-transformierten Deckungswerten (cover). Prädiktorvariablen wurden automatisch durch Permutationstests ausgewählt. ΔpH: Änderungen des pH-Werts zwischen 2018 und 1986. Wet heath: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. Share: Anteil der erklärten Varianz, berechnet durch eine ANOVA.

	p	proportion constrained	ΔpH		ΔmF		fallow index 1986		wet heath		site	
			p	share	p	share	p	share	p	share	p	share
species differences p/a	0.001	29 %	0.001	3 %	0.001	5 %	.	.	.	.	0.001	22 %
species differences cover	0.001	42 %	.	.	0.001	8 %	0.001	7 %	0.001	5 %	0.001	22 %

Supplement E11. DCA of all plots in 1986 and 2018 based on species presence/absence data, only species with at least 10 occurrences in the total data set are displayed. Environmental variables included are significantly correlated to one of the two first DCA axis ($p < 0.05$) with $R^2 \geq 0.15$. mF, mR and mN: presence/absence based Ellenberg indicator values for soil moisture, soil reaction and soil nutrients; Species numbers (Number) and cover sums (cover) of the following species groups: NardG = character species of *Nardus* grasslands, WetH = wet heath character species, SSF = species of small sedge fens, AgriG = agricultural grassland species, and PoorG = species of other poor grasslands; Axis length is 3.45 for axis 1 and 2.31 for axis 2.

Anhang E11. DCA aller Aufnahmen von 1986 und 2018, basierend auf Präsenz/Absenz-Daten. Nur Arten mit mindestens 10 Vorkommen im Gesamtdatensatz sind dargestellt. Dargestellte Umweltvariablen sind signifikant mit einer der beiden DCA-Achsen korreliert ($p < 0{,}05$), mit $R^2 \geq 0{,}15$. mF, mR und mN: Präsenz/Absenz-basierte Ellenberg-Zahlen für Bodenfeuchte, Bodenreaktion und Nährstoffe; Artenzahl (Number) und Deckungssummen (cover) der Artengruppen: NardG = Charakterarten der Borstgrasrasen, WetH = Charakterarten der Feuchtheiden, SSF = Charakterarten der Kleinseggenriede, AgriG = Arten des Wirtschaftsgrünlands, PoorG = Arten anderer nährstoffarmer Wiesen. Achsenlänge ist 3,45 für Achse 1 und 2,31 für Achse 2.