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RESEARCH PAPER

Decreasing nitrogen deposition rates: Good news for oligotrophic grassland species?

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Abstract

Several studies have found that increased nitrogen (N) deposition leads to a decline in species richness in semi-natural grasslands, mainly due to the loss of species typical of nutrient-poor soils. However, after reaching a peak around 1990, N deposition has decreased in Europe over the last 30 years. In this study, we investigated the changes in species number and composition of semi-natural grasslands during this period of declining N deposition. To this end, we compared the data from the first survey (2001-2005) of 147 grassland sites in Switzerland with those from the third survey (2011-2015). We further analysed the vegetation development of a specific hay meadow from 1992 to 2013. In this grassland, total vegetation cover and the cover of graminoid species decreased, while the cover of oligotrophic species increased. At the 147 grassland sites, total species number decreased at sites with still high levels of N deposition and it tended to increase at sites with low N deposition, i. e. below the critical load for N deposition. The number of oligotrophic grassland species increased at sites with a large decrease in N deposition and strong inclination. Thus, the results of this study indicate that the reduction of N emissions had a measurable positive effect on species diversity in these semi-natural grasslands. Most of the grasslands surveyed appear to be quite resilient against N deposition, i. e. they do not shift to an alternative low diversity state dominated by a few competitive species, and recovery of the species composition as a result of the decrease in N deposition seems possible, especially on steep slopes. Furthermore, the study underlines the importance of regular management of semi-natural, unfertilised, low-productivity grassland to maintain the diversity of oligotrophic grassland species.

Keywords: Biodiversity; Critical load; Deposition model; Eutrophication; Hay making; Humped-back model; Inclination; Semi-natural grasslands; Species conservation; Species richness

Introduction

Nitrogen (N) input is a major threat to biodiversity and the functioning of natural and semi-natural ecosystems (Sala et al., 2000; Bobbink et al., 2010; Steffen et al., 2015). In addition to the direct application of fertilisers on cultivated areas, natural and semi-natural ecosystems are unintentionally fertilised by the deposition of atmospheric reactive N compounds. The main emissions of N result from combustion of fossil fuels (NO_x) and from agricultural activities (NH_x) such as storage and handling of manure

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(Galloway, 1995; Fagerli & Aas, 2008; Bobbink et al., 2010). Since these N compounds are dispersed over long distances in the atmosphere, even most remote areas such as high alpine glaciers (e. g. Wagenbach et al., 1988) as well as typically unfertilised ecosystems such as forests (e. g. Becker Scarpitta et al., 2017) are affected by N deposition.

Increased N deposition will have the largest impact on vegetation and biodiversity in those ecosystems that are most N-limited (Sala et al., 2000; Bobbink et al., 2010). These include managed, semi-natural, temperate grasslands on nutrient-poor soils which are often very rich in plant species (Wilson et al., 2012). These grassland types contain many vulnerable and endangered habitat specialists and are of high conservation value (Bornand et al., 2016; Diekmann et al., 2019).

Using the space-for-time approach or temporal comparisons, several studies found significant negative relationships between N deposition and vascular plant species richness for acid grasslands in the United Kingdom (Stevens et al., 2004; Maskell et al., 2010) and across the Atlantic biogeographic region of Europe (Duprè et al., 2010; Stevens et al., 2010a; Berendse et al., 2021) or for unfertilised hay meadows in Switzerland (Roth et al., 2013). However, in calcareous grasslands no significant relationships between N deposition and species richness were found neither in Great Britain (Maskell et al., 2010; van den Berg et al., 2011) nor in Germany (Diekmann et al., 2014). For grazed subalpine grasslands in the Pyrenees, Boutin et al. (2017) observed a significant positive relationship of species richness with cumulative N deposition.

Although N may be partially immobilised (Phoenix et al., 2003), N deposition has the potential to increase plant-available N content in the soil (Duprè et al., 2010; Phoenix et al., 2012; Rowe et al., 2012), promoting thereby the growth of N-limited species and biomass production (Hautier et al., 2009; Bassin et al., 2012) as well as the occurrence of more nitrophilous plant species (Bennie et al., 2006; Duprè et al., 2010; Boutin et al., 2017). Especially, cover and species number of graminoid species increased with N deposition (Bobbink et al., 2010; Duprè et al., 2010; Maskell et al., 2010; Stevens et al., 2011). Within the taller and denser grassland stands, ground-level light becomes the limiting factor, leading to the competitive exclusion of light-demanding, slowly developing plant species (Hautier et al., 2009; Borer et al., 2014). Consistent with this mechanism, the number of species typical of oligotrophic grasslands decreased with N deposition in many studies (Stevens et al., 2004; Duprè et al., 2010; Roth et al., 2013; Boutin et al., 2017). However, especially in acid grasslands, soil acidification due to N deposition rather than eutrophication may be responsible for the decrease in species richness (Maskell et al., 2010; Stevens et al., 2010b; Berendse et al., 2021).

Nitrogen deposition has an effect not only on vegetation but also indirectly on animal life conditions. In nutrient-rich, species poor grasslands, the abundance of insects is smaller than in nutrient-poor, but species rich grasslands (Britschgi et al., 2006). Furthermore, bird species that feed on ground insects are dependent on patchy, low vegetation for food uptake, as may occur in nutrient-poor grasslands (Schaub et al., 2010).

Global emissions of NO_x began to increase in the late 1800s, while those of NH_x did not grow significantly until 1950 (Galloway, 1995; Schöpp et al., 2003). Both N compounds reached peak emissions around 1990 (Galloway, 1995; Schöpp et al., 2003; Fagerli & Aas, 2008), whereupon emissions in Europe began to decline (Schöpp et al., 2003; Fagerli & Aas, 2008). From 1990 to 2015 total N deposition in Switzerland was reduced by 28% (Rihm & Künzle, 2019) due to technical enhancements (NO_x) and the reduction of livestock (NH_x) (Schweizerischer Bundesrat, 2018).

In this study, we investigated the temporal changes in species number and composition of semi-natural grasslands in Switzerland. Given the decreasing N deposition, we expected that the number of oligotrophic grassland species as well as the total number of species would not decrease due to N deposition and we tested the null hypothesis that temporal changes in species number are independent of N deposition. Like Roth et al. (2013), we used grassland data of the Swiss Biodiversity Monitoring program (BDM, 2021) and analysed the records of the first three surveys conducted between 2001 and 2015.

Bennie et al. (2006) and Diekmann et al. (2019) concluded that grasslands on steep slopes and dry grasslands are most resistant to changes in species composition induced by N deposition. Slope gradient is one of the major factors affecting runoff (Bronstert, 2016), and substantial export of N and especially of highly mobile nitrate through runoff can occur even on rather gently sloping grasslands (15-20°; Heathwaite et al., 1998; Parkinson et al., 2000), reducing thereby the amount of plant-available N in the soil (Phoenix et al., 2003). In dry soils, N uptake by plants may be limited due to reduced nutrient transport by mass flow and diffusion and insufficient contact of root tips and root hairs with soil particles (Lösch, 2003). Accordingly, we expected that there would be no decrease in oligotrophic grassland species on steep areas and at sites with potentially dry soils.

In the Swiss Biodiversity Monitoring program, species presence but not the abundance or cover of species within a survey site is recorded. Consequently, the biodiversity monitoring data are not suitable to provide insight into the causes of species behaviour, e. g. loss of oligotrophic species due to exclusion by competitive grasses. To understand the mechanisms of species loss or species survival, we include here as a case study the analysis of the development of the species composition in terms of cover and species numbers in a specific hay meadow (Bremgarten) near the city of Berne (Switzerland) from 1992 to 2013. Since the modelled N deposition at this site was reduced by 24% from 1990 to

2010 (this study), we expected quantitative vegetation changes, i. e. a decrease of the cover of eutrophic species as well as an increase of the cover of oligotrophic species, and we tested the null hypothesis that species cover in this specific hay meadow does not show statistically significant differences over time.

Materials and methods

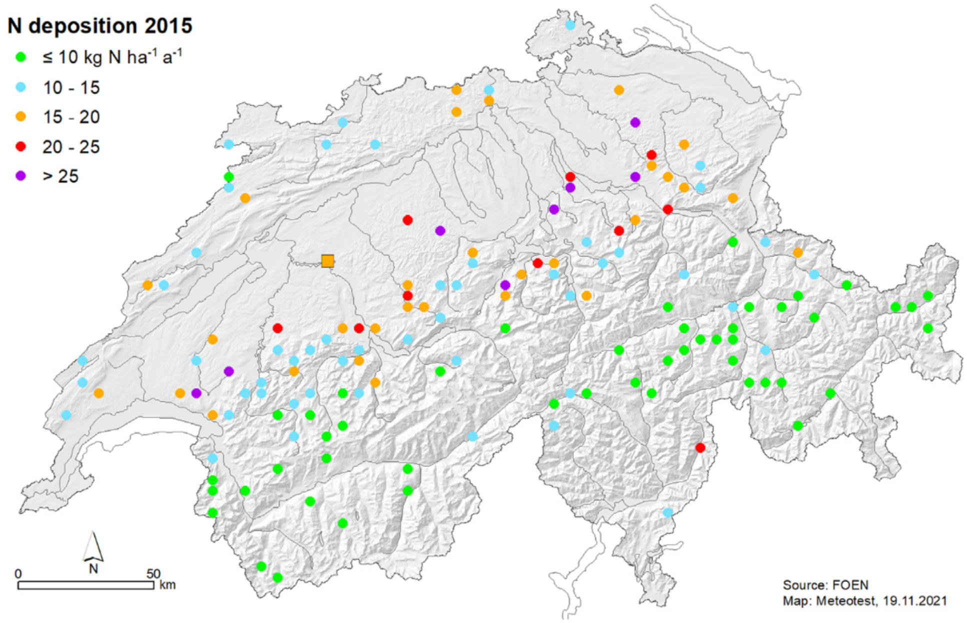
Swiss biodiversity monitoring

The Swiss Biodiversity Monitoring program was launched in 2001 to survey the long-term development of species diversity (BDM, 2021). We used data of the sub-program "species diversity in habitats" that aims to monitor species diversity development of four selected taxonomic groups, among them vascular plants, in major habitat types (α-diversity) and in various altitudinal zones. For this purpose, about 1400 sampling sites have been established in Switzerland in a regular grid. The exact position of each site was fixed with a magnet buried in its centre. For the plant surveys, qualified botanists visited each site twice a year except for high elevation sites that were inspected only once per year due to the short growing season. All species of vascular plants present in a circular area of 10 m^2 around the site centre were recorded (species presence data). One fifth of the sites were recorded for the first time in 2001, the second fifth in 2002 and so on. The second survey was conducted five years later, i. e. 2006-2010, and the third record after another five years (2011-2015).

Selection of biodiversity monitoring sites

Our aim was to exclusively analyse managed but unfertilised grasslands. To this end, the sites had to meet the following criteria: (1) At each survey, the botanists recorded habitat and land use type for every site. We only used sites that were classified as permanent grasslands (meadows and pastures) at each survey date. (2) A minimum of 50% of all species at a site had to be typical grassland species (see paragraph "Definition of species categories") to exclude transitional habitats such as grazed fens or fringe communities. (3) In order to eliminate fertilised grasslands, we only analysed sites that contained at least 35 species (10 m^2) at the first survey since fertilised grasslands typically have lower species richness (Bühler & Roth, 2011; Roth et al., 2013). However, some sites with fewer species were also included due to their high proportion of species typical of non-fertilised grasslands, e. g. a site with 29 species was included because it contained 10 oligotrophic grassland species. The resulting data set contained 147 sites that were sampled three times between 2001 and 2015. They were quite regularly distributed over Switzerland (Fig. 1): 96 sites were located in the Alps (65%), 16 in the Jura mountains (11%) and 35 sites in the Swiss midlands (24%).

Six sites were classified as most valuable areas of dry grassland following the mapping project of dry grasslands in Switzerland (Eggenberg et al., 2001). The other 141 sites represented average, "normal" grasslands that were difficult to unambiguously assign to a habitat type. About 20% of the sites corresponded relatively closely to mesic meadows and pastures of lower and high altitudes (order *Arrhenatheretalia elatioris*) containing no or only one to three species



Source: FOEN
Map: Meteotest, 19.11.2021

Fig. 1. Modelled total N deposition in 2015 at the biodiversity monitoring sites under study (circles) and at the Bremgarten study site (quadrat). Data provided by the Federal Office for the Environment (FOEN).

typical of oligotrophic habitats. The largest part of the sites (41%), however, represented transitions between mesic grasslands as described above on the one side and subatlantic semi-dry calcareous grasslands (order *Brometalia erecti*) on the other. At higher altitudes, these habitat types often revealed transitions either to alpine mat grass swards (alliance *Nardion strictae*; above 1000 m a. s. l.; 22% of the sites) or to calciphilous alpine grasslands (order *Seslerietalia caeruleae*; above 1300 m a. s. l.; 12%).

Slope and aspect of each site were extracted from a digital terrain model with a resolution of 25 m (DHM25 by Swisstopo, 2021). The irradiance at a site, as a proxy of potential soil drought, was calculated based on latitude, slope, and aspect according to Campbell and Norman (1998).

Definition of species categories

A total of 707 vascular plant species were identified at the 147 biodiversity monitoring sites on the three survey dates (Appendix A: Table 6). Based on phytosociological literature (Theurillat et al., 1995; Eggenberg et al., 2001; Ellenberg & Leuschner, 2010; Landolt, 2010; Delarze et al., 2015), we first separated species typical of grasslands (n = 340) from herbaceous species of other habitats (n = 307) and woody species (n = 60). Within the grassland species, we distinguished oligotrophic (n = 154), eutrophic (n = 47), and mesotrophic grassland species (n = 139). Oligotrophic grassland species were defined as those with an indicator value for nutrients of 1 or 2 (Landolt N value; Landolt, 2010), which are consistently listed in the phytosociological literature as characteristic of nutrient-poor grasslands. These species typically occur in habitats such as calcareous grasslands (class *Festuco-Brometea*), calcareous alpine and subalpine grasslands (class *Elyno-Seslerietea*), and acid alpine and subalpine grasslands (class *Juncetea trifidi*). Eutrophic grassland species have a Landolt indiciator value for nutrients of 4 and are consistently cited as characteristic of mesic meadows and pastures of lower and high altitudes (order *Molinio-Arrhenatheretea*) or of tall-herb communities (class *Mulgedio-Aconitetea*). The remaining grassland species were classified as mesotrophic species. These species have a Landolt indicator value for nutrients of 3 and/or are not clearly assigned to either nutrient-poor or nutrient-rich grassland in the phytosociological literature.

Scientific names of plant species follow Eggenberg et al. (2018).

Bremgarten: study site and data sampling

The case study was performed in the nature reserve “Hoger” at Bremgarten near Berne, Switzerland. The nature reserve consists mainly of a hay meadow on a SSE-facing slope with an inclination of 22-27° and an elevation between 530 and 570 m. It is located in a suburban region on the outskirts of the city of Berne, a highway is about 1 km away. The meadow is quite isolated from other semi-natural grasslands and borders a settlement to the west, a small wood to the eastern, and arable fields at the upper (northern) and lower (southern) edges. Species typical of nutrient-poor grasslands as well as species typical of nutrient-rich grasslands were represented in approximately equal proportions in the meadow. It corresponds quite closely to the habitat type of mesophile, baso-neutrophile, subatlanatic meadows (alliance *Mesobromion*; Theurillat et al., 1995). The meadow is mown once a year by local farmers and has not been fertilised since at least 1958 (Kammer, 1997). Since 2006 the grassland is additionally grazed by cattle in late summer (Fasching, 2007).

Within the area studied of about 0.48 ha, ten sets of nested plots were permanently fixed following a regular grid with 16 m distance between each 1 m^2-plot (Kammer, 1997). The 25 m^2-plots were laid out around the 1 m^2-plots so that the 1 m^2-plots were each in the southwest corner of the 25 m^2-plots. Four sets were located on the upper slope and three sets each in the middle and lower slope. For vegetation sampling, the 1 m^2-plots were divided with the help of an aluminium frame and rubber ribbon in 16 quadrats of 25 × 25 cm each. Within each quadrat, species cover relative to the size of the quadrat was estimated to the nearest 1%. In addition, the cover of mosses, litter and bare soil was also determined. For the analyses, species cover in relation to the total cover of all vascular plant species per plot was used to compensate for fluctuations in total vegetation cover from year to year. Species richness was measured as the number of rooted species present in the 25 m^2-plots. Data sampling was executed annually from 1992 to 2004 and from 2011 to 2013 at the end of May beginning of June. From 2002 to 2004 only six out of the ten plots were sampled due to lack of time. Over the whole study period, data sampling was always performed by the same person. In 2013, plants in ten areas of 0.89×0.89 m, that were located just beside the 1 m^2-plots, were clipped 1-2 cm above ground with the help of an electric lawn trimmer. The plant material was oven-dried at 100°C for 48 h and afterwards weighted to the nearest 0.1 g. Cutting occurred in mid-June, i. e. approximately two weeks before maximum standing crop and the regular mowing date.

For the analyses, we distinguished oligotrophic, eutrophic and mesotrophic species. Oligotrophic species were defined as those with a Landolt indicator value for nutrients of 2 (Landolt, 2010), while eutrophic species have a value of 4, and mesotrophic species a value of 3. Since graminoid species often increase with N deposition (Bobbink et al., 2010; Duprè et al., 2010; Maskell et al., 2010; Stevens et al., 2011) and contribute to the competitive exclusion of light-demanding, slowly developing plant species (Hautier et al., 2009; Borer et al., 2014), species of the Poaceae family as well as *Carex caryophyllea* and *Luzula campestris* were

pooled and analysed as an additional category. Moreover, each species which regularly occurred in the ten 1 m^2-plots during the entire study period was analysed separately.

Landolt indicator values

Average Landolt indicator values (Landolt, 2010) were calculated for each biodiversity monitoring site and each survey date based on all species identified and on grassland species only. The indices calculated are temperature (9-step scale), soil moisture (9-step scale), reaction of soil solution (5-step scale), and soil nutrients (5-step scale). The latter indicates the content of plant-available nutrients, especially nitrogen, but also phosphorus (Landolt, 2010). For Bremgarten, average Landolt indicator values for temperature, moisture, reaction, and nurtrients were calculated for each plot and each sample year based on presence/absence data.

Modelling of N deposition

Nitrogen deposition was estimated for the years 1990, 2000, 2005, 2010, and 2015 in 100 × 100 m grid cells across Switzerland, based on a practical approach that combined monitoring data, spatial interpolation methods, emission inventories, statistical dispersion models, and inferential deposition models (Rihm & Achermann, 2016; Rihm & Künzle, 2019). Seven relevant compounds of reactive nitrogen were included: gaseous NH_3, NO_2 and HNO_3, as well as wet and dry deposition of NH_4^+ and NO_3^-.

Statistical analyses

To assess the response of species number to N deposition over the last approximately twenty years, we used a linear mixed effects model with log-transformed species numbers per biodiversity monitoring site as response variable and the modelled N deposition, time, i. e. the survey period as a categorical variable with three levels (early = 2001-05, mid = 2006-10, late = 2011-15), and their interaction as fixed effects. Site ID as the unit of replication over time was included as random term. Significance was tested with type-I analysis of variance.

To assess the response of oligotrophic grassland species numbers to changes in N deposition over time, and whether this response is mediated by the slope of the sampling site, we conducted a linear regression model with the change in oligotrophic grassland species number from the first (2001-05) to the third survey (2011-15) as response variable, the change in N deposition from 2000 to 2010, the slope of the sampling site and their interaction as fixed effects and the initial level of N deposition in 2000 as a covariate. Significance of each fixed effect and covariate was tested with type-I analysis of variance. The same analysis was performed with irradiance at a site instead of slope.

To test for significant changes in Landolt indicator values over the monitoring period, we ran linear mixed effects models with the indicator value of each site for the three survey periods as response variable and the three survey periods as fixed effects. Site ID was included as random term. Significance of the factor ‘time’ was assessed with type-I analysis of variance.

For the Bremgarten data, we used linear mixed effects models to assess the changes of species number, total vegetation cover, cover of bare soil and the cover of graminoids, oligotrophic and eutrophic species over time. The number of species was determined in 25 m^2-plots (n = 10), while 1 m^2-plots were used to record the cover variables (n = 10). The plot ID, where measurements were repeated, was included as random term. The differences of individual species cover over time was assessed with the same model structure but with generalised linear mixed models and a Poisson distribution of error terms. The changes in the Landolt indicator values over time at Bremgarten were assessed with time as a continuous fixed effect and plot ID as a random effect. Significance of the variable time was assessed with type-I analysis of variance.

All statistical analyses were conducted with R version 3.6.3 (R Core Team, 2020) and the library nlme (Pinheiro et al., 2020) for mixed effects models.

Results

Biodiversity monitoring sites

The mean modelled total N deposition to the sites under study decreased quite sharply from 18.8 ($s = \pm 7.2$) to 15.8 kg N ha^{-1} a^{-1} ($s = \pm 6.0$) between 1990 and 2000. Thereafter, it continued to decline, but less sharply to 14.1 kg N ha^{-1} a^{-1} ($s = \pm 5.8$) in 2010 and to 13.1 kg N ha^{-1} a^{-1} ($s = \pm 5.7$) in 2015. In 138 out of the 147 sites N deposition decreased from 2000 to 2010, while in 9 sites it increased. In 2015, high values of N deposition (above 15 kg N ha^{-1} a^{-1}) still occurred at sites in the midlands and on the northern edge of the Alps, whereas the lowest values (below 10 kg N ha^{-1} a^{-1}) were calculated for sites in the central Alps (Fig. 1).

Overall, species richness proved to be very stable over time and showed no significant change (Appendix A: Table 1). Mean total number of species per site was 46.6 in both the first (2001-05) and the third survey (2011-15). The mean number of grassland species and oligotrophic grassland species increased very slightly from 35.1 (2001-05) to 35.8 (2011-15) and from 8.3 (2001-05) to 8.6 species per site (2011-15), respectively, while the mean number of eutrophic grassland species remained constant (9.2 species per site).

Table 1. ANOVA table of the linear regression models testing the effects of the change in N deposition (Δ N dep.) from 2000 to 2010 and slope or irradiance (irrad.) at the biodiversity monitoring sites on changes in the number of oligotrophic grassland species from the first (2001-05) to the third survey (2011-15).

Change of N deposition and		Num. d. f.	Sum of squares	Mean squares	*F*-value	*P*-value
slope	N dep. 2000	1	0.0612	0.0612	0.3385	0.5616
	Δ N dep.	1	0.6407	0.6407	3.5466	*0.0617*
	slope	1	0.1771	0.1771	0.9802	0.3238
	Δ N dep. : slope	1	0.9373	0.9373	5.1885	0.0242
	residuals	142	25.6535	0.1807		
irradiance	N dep. 2000	1	0.0612	0.0612	0.3259	0.5690
	Δ N dep.	1	0.6407	0.6407	3.4143	*0.0667*
	irrad.	1	0.0149	0.0149	0.0796	0.7782
	Δ N dep. : irrad.	1	0.1057	0.1057	0.5634	0.4541
	residuals	142	26.6472	0.1877		

Species numbers were log-transformed. Level of N deposition at the start of the monitoring period (N dep. 2000) was included as a covariate. $n = 147$. F- and *P*-values are based on the decomposition of the total Sum of squares. Num. d. f.: numerator degrees of freedom.

N deposition had a significant effect on total species number as well as on the numbers of grassland, oligotrophic and eutrophic grassland species (Appendix A: Table 2). Total species number declined more with increasing N deposition in the two later (2006-10 and 2011-15) compared to the first survey (2001-05), resulting in lower species numbers in the two later compared to the first survey under N deposition above 15 kg N ha^{-1} a^{-1} (Fig. 2A). At sites with rather low N deposition (below 10 kg N ha^{-1} a^{-1}), a tendency towards higher species numbers compared to the first survey can be observed in the two later surveys. The number of grassland species shows the same pattern as total species number, but less pronounced (Fig. 2B, Appendix A: Table 2). The numbers of oligotrophic and eutrophic grassland species showed no significant change over time in relation to N deposition (Fig. 2C and D, Appendix A: Table 2). However, the decline in total species number as well as the numbers of grassland and oligotrophic grassland species at sites with high N deposition was more pronounced at the second (2006-10) than at the third survey date (2011-15; Fig. 2A-C).

The number of oligotrophic grassland species significantly increased at sites where steep slopes coincided with large decreases in N deposition (Table 1). Irradiance, as a proxy of potential soil drought, had no effect on the change of the number of oligotrophic grassland species (Table 1).

The average Landolt indicator value for soil moisture calculated on the basis of all species per biodiversity monitoring site increased very slightly but statistically significantly from 2.95 at the first (2001-05) to 2.97 at the second survey (2011-15). All the other average indicator values showed no significant changes over time (Appendix A: Table 3).

Bremgarten

In the hay meadow at Bremgarten, the modelled total N deposition was 27.2 kg N ha^{-1} a^{-1} in 1990 and 20.8 kg N ha^{-1} a^{-1} in 2010. Mean standing crop (dry-matter) in mid-June 2013 was 224.3 g m^{-2} ($s = \pm 33.9$).

The mean number of species in ten 25 m^2-plots remained constant over the 22-year period ($F_{(1,137)} = 2.66$, $P = 0.11$) and was 30.7 at the beginning (1992-94) and 30.9 at the end of the study period (2011-13), respectively. Total vegetation cover (Fig. 3) decreased from 83.2% in 1992-94 to 68.3% in 2011-13 ($F_{(1,137)} = 13.21$, $P < 0.001$). The cover of graminoid species (Poaceae, *Carex caryophyllea*, and *Luzula campestris*) also declined from 49.2% at the beginning to 36.2% at the end of the study period ($F_{(1,137)} = 13.20$, $P < 0.001$). This was predominantly due to the reduction in cover of eutrophic (e. g. *Arrhenatherum elatius, Trisetum flavescens*) and mesotrophic grasses such as *Festuca rubra* (Fig. 3) or *Holcus lanatus* (Table 2). However, cover of the oligotrophic grass species *Bromus erectus* showed a reverse trend and increased from 21.2% in 1992-94 to 26.5% in 2011-13 (Table 2).

The decrease of the graminoid species and total vegetation cover resulted in an increase of the proportion of bare soil (Fig. 3) from 5.6% at the beginning (1992-94) to 17.7% at the end of the study period (2011-13; $F_{(1,137)} = 97.87$, $P < 0.001$). The cover of oligotrophic herbaceous species such as *Hippocrepis comosa* (Fig. 3), *Pimpinella saxifraga, Sanguisorba minor*, and *Silene nutans* increased (Table 2) just like the cover of oligotrophic species in general (including oligotrophic graminoids) that increased from 56.1% in 1992-94 to 70.9% in 2011-13 ($F_{(1,137)} = 49.69$, $P < 0.001$). The cover of eutrophic species remained stable ($F_{(1,137)} = 0.14$, $P = 0.71$).

The average Landolt indicator value for soil moisture of the ten 1 m^2-plots decreased very slightly but statistically significantly from 2.60 at the beginning (1992-94) to 2.57 at the end of the study period (2011-13), while the indicator value for reaction similarly weakly but significantly increased from 3.18 to 3.21 over the same period (Appendix A: Table 5). The indicator values for temperature and nutrients showed no significant changes over time.

Table 2. Changes in cover of individual species over time (from 1992 to 2013) at the Bremgarten study site. Changes were quantified with generalised linear mixed effects models with time as a fixed effect and plot ID as a random term. Positive estimates indicate an increase in cover, negative estimates a decrease. For mesotrophic herbs, see Appendix A: Table 4.

Ecological group	X^2	Num. d. f.	*P*-value	Estimate
Oligotrophic species				
Anthoxanthum odoratum[G]	4.361	1	<0.001	-0.0232
Anthyllis vulneraria	0.269	1	0.558	0.0067
Bromus erectus[G]	0.645	1	<0.001	0.0033
Carex caryophyllea[G]	35.949	1	<0.001	0.0873
Centaurea scabiosa	3.641	1	0.644	0.0056
Daucus carota	1.565	1	0.678	-0.0051
Hippocrepis comosa	15.974	1	<0.001	0.0310
Luzula campestris[G]	78.442	1	<0.001	-0.0434
Orobanche alba	0.678	1	0.896	-0.0016
Pimpinella saxifraga	33.279	1	<0.001	0.0756
Ranunculus bulbosus	0.557	1	<0.001	-0.0076
Salvia pratensis	88.030	1	<0.001	-0.0835
Sanguisorba minor	4.978	1	<0.001	0.0318
Silene nutans	31.697	1	<0.001	0.1567
Silene vulgaris	13.807	1	<0.001	0.1020
Thymus pulegioides	0.613	1	<0.001	-0.0098
Eutrophic species				
Arenaria serpyllifolia	17.094	1	0.039	0.0232
Arrhenatherum elatius[G]	19.067	1	<0.001	-0.0383
Cerastium fontanum	2.299	1	<0.001	0.0273
Dactylis glomerata[G]	2.842	1	<0.001	0.0234
Erigeron annuus	3.641	1	0.100	0.0189
Galium album	4.402	1	<0.001	0.0094
Poa pratensis[G]	0.682	1	<0.001	0.0089
Rumex acetosa	3.503	1	<0.001	-0.0131
Trisetum flavescens[G]	11.430	1	<0.001	-0.0373
Mesotrophic grass species				
Festuca rubra[G]	75.517	1	<0.001	-0.0879
Helictotrichon pubescens[G]	17.681	1	<0.001	-0.0534
Holcus lanatus[G]	8.059	1	<0.001	-0.0496

P-values in bold show statistically significant results at $\alpha = 0.05$. Num. d. f.: numerator degrees of freedom.

[G] graminoid species.

Discussion

Biodiversity monitoring sites

The mean total number of species per site as well as the mean number of grassland, oligotrophic and eutrophic grassland species remained constant during the study period from 2001 to 2015. The relationship between N deposition and species number was negative, i. e. the pattern of species richness across the study sites reflects the pattern of N deposition. At sites with high N deposition, total species number and the number of oligotrophic grassland species are low, while the number of eutrophic grassland species is high. This pattern did not change over time. Total species number, however, decreased at sites where N deposition was still high in 2010 (above 15 kg N ha^{-1} a^{-1}; Northern Alps and midlands) and shows a tendency to increase at sites with rather low N deposition (below 10 kg N ha^{-1} a^{-1}; Central Alps). A similar development was shown by the number of grassland species. However, the low number of grassland species in the third survey (2011-15) at sites with still high N deposition was not due to a decrease in the number of oligotrophic grassland species, nor was it due to a decrease in the number of eutrophic grassland species. Consequently, the decline of the number of grassland species is attributed to a decrease of the number of mesotrophic grassland species. The lack of a decrease in the number of oligotrophic grassland species at sites with still high N deposition from the first (2001-05) to the third survey (2011-15) may be due to the previous disappearance of species sensitive to N deposition at these sites (Stevens et al., 2010a; Phoenix et al., 2012).

We further expected no decrease in the number of oligotrophic grassland species on steep slopes due to N leaching and/or on dry soils due to limited N uptake by plants. In fact, we found a significant increase in the number of oligotrophic grassland species at sites with large decreases in N deposition combined with steep slopes. For example, in a grassland situated on a slope with an inclination of 26° and with a decrease of modelled N deposition of 2.7 kg N ha^{-1} a^{-1}, the new occurrence of seven species typical of oligotrophic grasslands, such as *Carex montana, Linum catharticum*, or *Trifolium montanum*, was detected. However, there was no significant effect of irradiance on changes in the number of oligotrophic grassland species. Most likely, irradiance calculated based on latitude, slope, and aspect did not reflect soil water conditions at a specific site with sufficient accuracy.

The fact that the number of oligotrophic grassland species increased at sites with steep slopes in combination with a strong decrease in N deposition was not reflected in a decrease of the average Landolt indicator value for nutrients. In addition to N deposition, climate change may have influenced vegetation changes in the grassland areas studied. Since 1986, the average annual temperature in Switzerland has been up to 2°C above the 1961-90 mean every year (Meteoswiss, 2021). However, the average indicator value for temperature has not changed significantly over the study period, indicating that temperature increase is most likely not responsible for the increase in oligotrophic grassland species. Annual precipitation does not show a clear trend: periods with wet years alternate with periods with drier years. In the period from 1979 to 2002, there were predominantly years with annual precipitation above the 1961-90 mean (Meteoswiss, 2021). After 2002, there were about as many dry years as wet years. The weak but statistically significant increase in the average indicator value for moisture from the first (2001-05) to the third survey (2011-15) could be a delayed response of vegetation to the wet period before 2002. Indeed, new appearances of

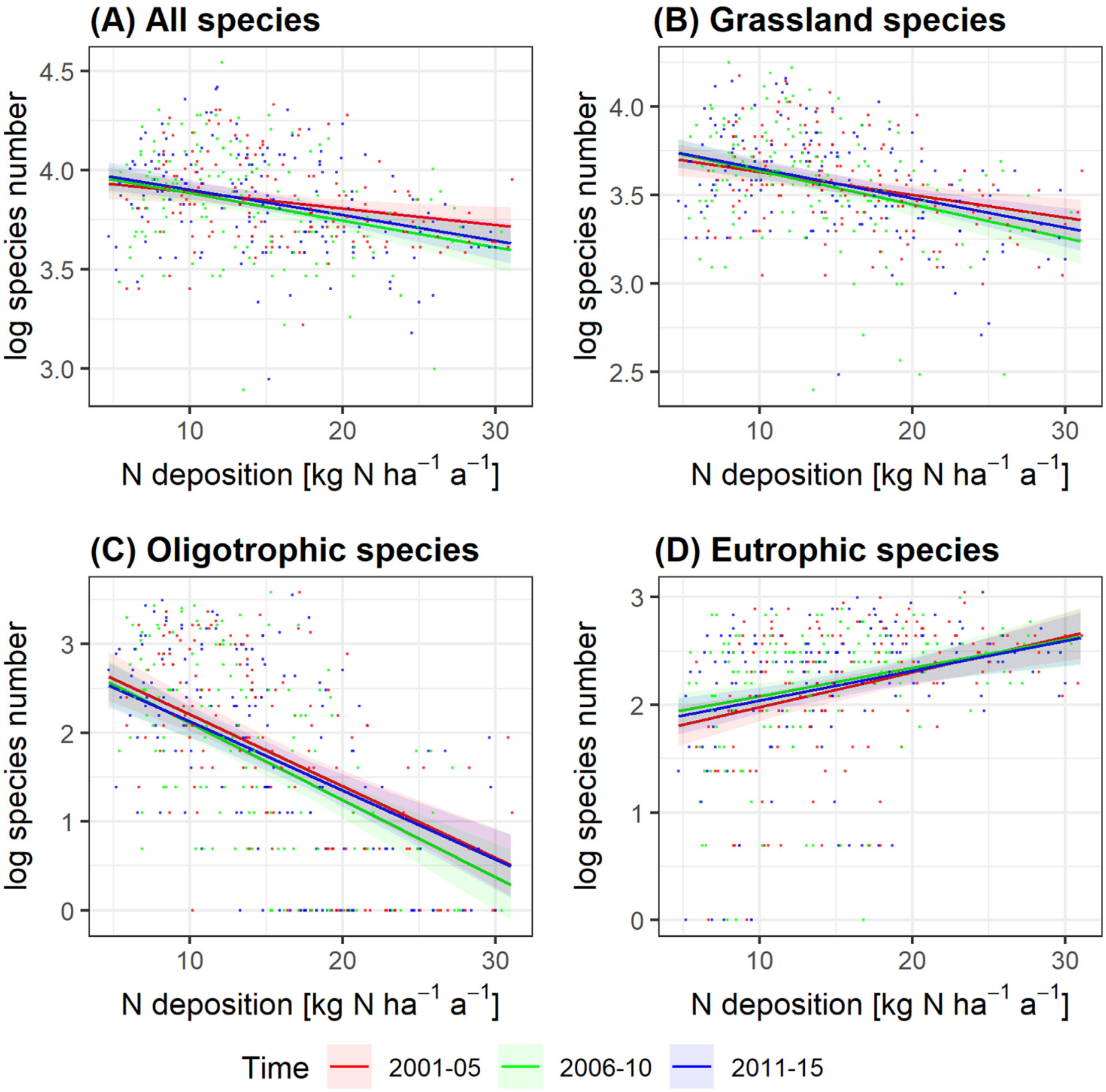


Fig. 2. Response of total species number (A), number of grassland (B), oligotrophic (C) and eutrophic grassland species (D) per biodiversity monitoring site to N deposition in 2000, 2005, and 2010. Time points are first (2001-05), second (2006-10) and third survey (2011-15). Coloured dots: values of the biodiversity monitoring sites in the respective sampling periods; solid lines: model predicted means; shading: 95% confidence intervals. $n = 441$.

fen species such as *Carex echinata* or *C. panicea* could be detected at some sites at the second (2006-10) and the third survey (2011-15). The increased water availability may also have promoted N uptake and thus growth of nitrophilous species. As a result, mesotrophic and oligotrophic species may have been outcompeted, which could explain the temporary drop in species numbers at sites with high N deposition at the second survey (Fig. 2A-C). However, even the statistically significant change in the moisture value is extremely small and should therefore not be overestimated (Diekmann, 2003).

The average Landolt indicator value for reaction did not change significantly during the study period, indicating that decreasing N deposition did not lead to an increase in the pH of the soil solution, which would be reflected in the vegetation.

Bremgarten

The hay meadow at Bremgarten is a nature reserve and has not been fertilised at least since 1958 (Kammer, 1997).

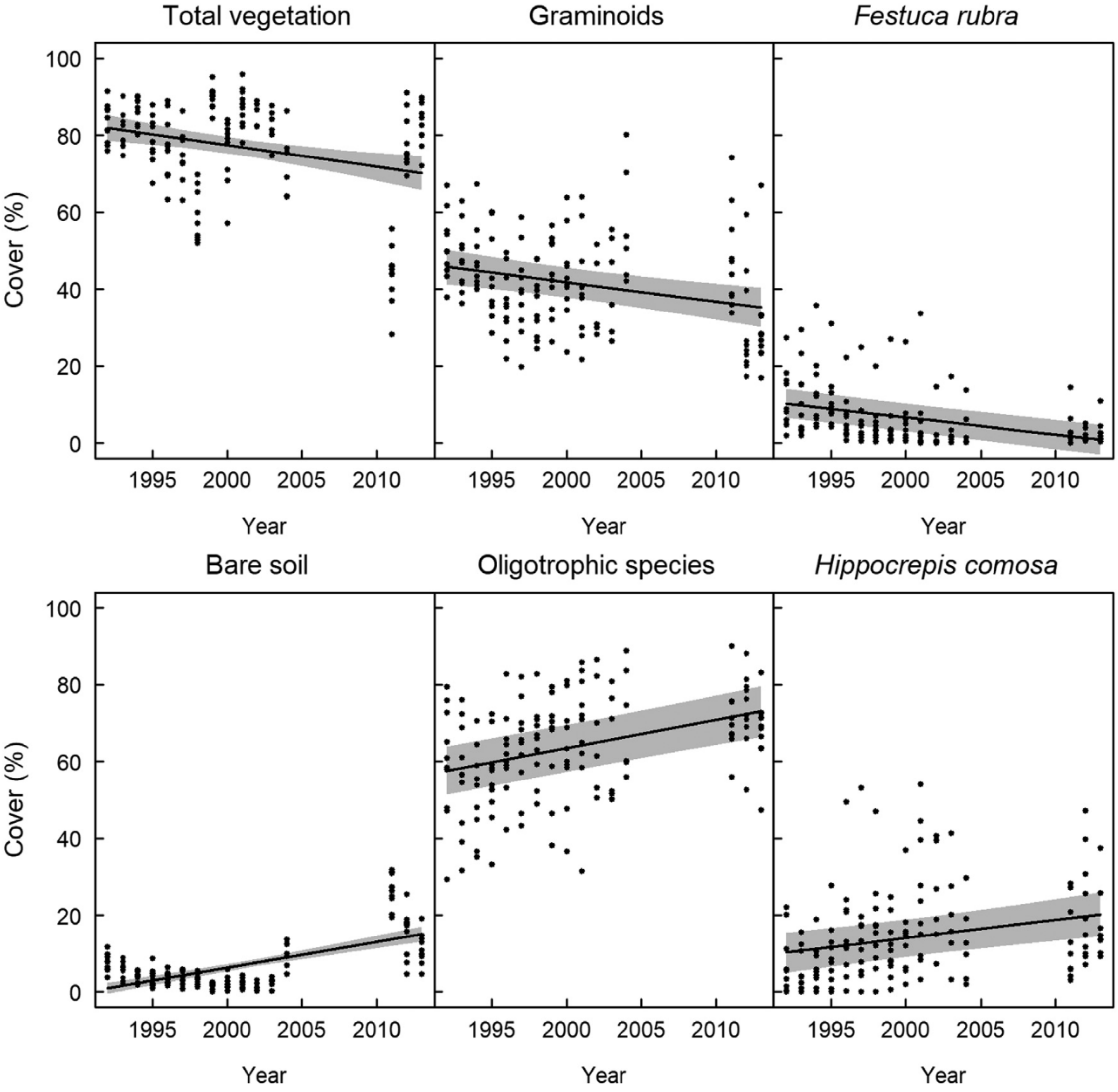


Fig. 3. Development of total vegetation cover, cover of all graminoids (Poaceae, *Carex caryophyllea*, and *Luzula campestris*), bare soil, oligotrophic species (including oligotrophic graminoids) as well as *Festuca rubra* and *Hippocrepis comosa* in the hay meadow at Bremgarten from 1992 to 2013. Note that the reference for total vegetation cover and bare soil is the sample quadrat (1 m^2 = 100%), while the cover values for the other variables refer to total vegetation cover (= 100%). Black dots: values of the sampling plots (1 m^2); solid line: mean of 10 (6 from 2002 to 04) sampling plots; shading: 95% confidence intervals.

Our investigations started in 1992 which more or less coincides with the peak of N deposition (Galloway, 1995; Schöpp et al., 2003; Fagerli & Aas, 2008). From 1990 to 2010, N deposition at Bremgarten decreased from 27.2 to 20.8 kg N ha^{-1} a^{-1}. At the same time, the relative cover of graminoid species (excluding the dominant *Bromus erectus*) decreased from 28.0 (1992-94) to 9.7% (2011-13), whereas the cover of oligotrophic species (including *B. erectus*) increased from 56.1 (1992-94) to 70.9% (2011-13). In 1992, the Bremgarten hay meadow may have been in its most eutrophic state. Subsequently, the decline in N deposition may have limited the development of nitrophilous species, particularly N-demanding grasses, and created space for the development of oligotrophic, light-demanding species whose foliage is concentrated near the soil surface. The leaching of N due to the steepness of the slope (22-27°) may have accelerated this process.

As with the biodiversity monitoring sites, the average Landolt indicator values in Bremgarten changed very little during the study period, so that the ecological interpretation should be treated with caution. Both the increased temperature and the decrease in N deposition are not reflected in significant changes in the indicator values for temperature or nutrients, respectively. The small but statistically significant decrease in the indicator value for moisture can be attributed to several dry spring periods between 2003 and 2013 (Meteoswiss, 2021). In particular, the spring periods of 2003, 2004, and 2011 were exceptionally dry and resulted in comparatively high proportions of bare soil in 2004 and 2011 (Fig. 3). The small and statistically significant increase

in the indicator value for reaction could be due to the decrease in N deposition. Besides the decrease in N deposition, the increase in cover of oligotrophic species may have been favoured by an increase in soil pH and drought events in spring. Kammer (2002) showed for the hay meadow at Bremgarten that pronounced drought periods can lead to permanent quantitative changes in species composition.

A similar development as in the Bremgarten study area may have occurred at those biodiversity monitoring sites with a sharp decrease in N deposition and steep slopes, where the number of oligotrophic species increased from the first (2001-05) to the third survey (2011-15). This finding may be judged as a sign of recovery from atmospheric N deposition, i. e. a significant change in a response variable in the opposite direction to change induced by N deposition (Stevens, 2016). However, whether the stopping of species loss and recovery of oligotrophic species are sustainable remains to be confirmed.

Decrease in N deposition

The concept of critical load for N deposition and biodiversity protection defines the maximum N deposition that an ecosystem is able to sustain in the long term (Bobbink et al., 2010), i. e. without a decrease in species richness. It ranges from 15 to 25 kg N ha^{-1} a^{-1} for subatlantic semi-dry calcareous grasslands and from 10 to 30 kg N ha^{-1} a^{-1} for hay meadows (Bobbink et al., 2010). In Rihm and Achermann (2016), an empirical critical load of 12 kg N ha^{-1} a^{-1} is assigned to dry grasslands. For subalpine and alpine grasslands, Bobbink et al. (2010) specify a critical load for N deposition of 5 to 10 kg N ha^{-1} a^{-1} and Rihm and Achermann (2016) assign 7 kg N ha^{-1} a^{-1} to this vegetation type. As Fig. 2A shows, the critical load for the grasslands studied here appears to be between 10 and 15 kg N ha^{-1} a^{-1} and is consistent with the values reported above. At sites where N deposition was above the critical load, species numbers decreased with increasing N deposition, and even more so in the two later (2006-10 and 2011-15) than in the first survey (2001-05). A tendency towards higher species numbers compared to the first survey can be observed in the two later surveys at sites with N deposition below the critical load. In 2010, the average N deposition rate across all study sites was 14.1 kg N ha^{-1} a^{-1}, which is in the range of the critical load for N deposition for semi-dry calcareous grasslands and hay meadows. Therefore, it can be expected that a further decrease of N deposition would favour the recovery of these types of grasslands.

N leaching

Slope had a positive effect on the increase in the number of oligotrophic grassland species at sites with a sharp decrease in N deposition suggesting that the leaching of mobile N compounds restricted the accumulation of plant-available N on steep slopes. Leaching can contribute to the export of mobile N compounds originating from wet deposition, which accounted for the largest part of total N deposition (i. e. 58% in 2010) at the study sites (data not shown). Furthermore, soils on steep slopes are generally free-draining and therefore have higher susceptibility to soil drought than soils on flat terrain. Soil drought may have contributed to the increase in the number of oligotrophic grassland species by limiting N uptake by plants. However, our approach using irradiance as proxy for potential soil drought was not able to detect such an effect. Bennie et al. (2006) found that the magnitude of vegetation change (measured as changes in Ellenberg values) in British chalk grasslands during the second half of the 20th century was strongly associated with slope and aspect. In particular, steep and south-facing slopes showed little change and maintained a stress-tolerant and light-demanding flora (Bennie et al., 2006). Diekmann et al. (2014, 2019) also concluded that dry grasslands that are often confined to steep and south-exposed slopes are most resistant to vegetation change and species loss due to water and phosphorous limitation.

Hay making

Beside of the decrease in N deposition and N leaching on steep slopes, N export through hay making, low biomass (standing crop), and the specific environment of the sites may have further contributed to the observed recovery.

Hay making and grazing are other forms of nutrient export of managed grasslands. Nitrogen concentration in archived herbage samples from the first hay cut of a non-fertilised grassland was 1.5 -.0% of dry matter (Storkey et al., 2015). Körner (1989) measured N concentrations of 1.4-3.1% of dry matter in leaves of low altitude grassland species in the Austrian Alps. Assuming an N concentration of 2%, standing crop in the unfertilised hay meadow at Bremgarten of 224 g m^{-1} contains 4.48 g N m^{-1} and its removal by hay making corresponds to an N export of 44.8 kg N ha^{-1}. This means that N export by hay making was twice as high as N input by N deposition, which was 20.8 kg ha^{-1} a^{-1} in 2010. Generally, N export through hay production of 20-100 kg ha^{-1} for unfertilised, oligotrophic grasslands with a standing crop of 100-500 g m^{-2} a^{-1} (Ellenberg & Leuschner, 2010) exceeds N input by N deposition, which currently is rarely greater than 40 kg N ha^{-1} a^{-1} in Switzerland (Rihm & Künzle, 2019). However, microbial N mineralisation prevents N depletion and may result in high N availability even when N export through haying and lack of N input (by N deposition and/or fertilisation) occur together (van Dobben et al., 2017).

The importance of N export by hay making for the recovery of species richness after N input is supported by the studies of Isbell et al. (2013) and Storkey et al. (2015). Isbell et al. (2013) observed little, if any, recovery two

decades after cessation of nitrogen fertilisation in a grassland that was never hayed. In the study of Storkey et al. (2015), however, species richness in regularly hayed grasslands increased within 20 years after the peak of N deposition to about 80% of its original level. Berendse et al. (2021) also found rapid recovery of plant species diversity in hay meadows as a result of N deposition decline, but without restoration of the original plant species composition. As long as the grasslands are managed by hay making or grazing, they seem to be quite resilient, i. e. the probability that they shift to an alternative low diversity state dominated by competitive grass species, as brought forward by Isbell et al. (2013), appears to be small.

In grazed grasslands, N export is less effective since a part remains in the system in form of dung. Nevertheless, longstanding extensive grazing is considered to counteract the negative effects of N deposition and to be responsible for maintaining species richness in subalpine grasslands (Boutin et al., 2017).

Low standing crop

Standing crop of 224 g m^{-2} measured for the hay meadow at Bremgarten is in the lower range of values typically between 100 and 500 g m^{-2} a^{-1} for unfertilised, oligotrophic grasslands (Ellenberg & Leuschner, 2010). These values fall within the rising leg of Grime's humped-back model of biomass and species richness (Grime, 2001) suggesting that a further increase in biomass means an increase rather than a decrease in species richness, because the site may also be colonised by species less tolerant of nutrient-poor conditions (Diekmann et al., 2014, 2019). The general validity of the humped-back curve for grasslands was supported by several studies such as van Dobben et al. (2017) or Berendse et al. (2021). An analysis of alkali and loess grasslands in eastern Hungary (Kelemen et al., 2013) showed that maximum species richness falls in the range of 600-750 g m^{-2}, as in Grime's original model. Except for the mesic meadows, standing crop of most biodiversity monitoring sites was probably less than 500 g m^{-2}. This means, according to the humped-back model, an increase of biomass due to N deposition will not necessarily lead to the displacement of non-competitive species and to the decrease in species numbers in these grassland types.

Environment

Most of the study sites (76%) are located in the Alps and in the Jura mountains. In these regions, semi-natural, oligotrophic grasslands are more frequent, particularly on steep hillslopes, than in the densely populated and intensively used Swiss midlands. Thus, the immigration of oligotrophic species on steep sloping grasslands was probably favoured by other oligotrophic grasslands in the vicinity, which acted as source habitats (Dias, 1996; Pulliam, 2000). In the hay meadow at Bremgarten, we did not observe any immigration of oligotrophic species despite the improvement in growing conditions for these species. This is likely because this meadow is isolated from other oligotrophic grasslands that harbour potential source populations of oligotrophic species not found in Bremgarten.

Conclusions

The null hypothesis that the temporal changes in species number are independent of N deposition could be partially rejected. Between 10 and 25 years after the peak of N deposition, total species number decreased at sites with still high levels of N deposition. At sites with low N deposition, i. e. below the critical load for N deposition, total species number tended to increase and at sites with a large decrease in N deposition and strong inclination, the number of oligotrophic grassland species increased. Thus, the results of this study indicate that the reduction of N emissions had a measurable positive effect on species diversity in these semi-natural grasslands. Most of the grasslands surveyed appear to be quite resilient against N deposition, i. e. they do not shift to an alternative low diversity state dominated by a few competitive species, and recovery of the species composition as a result of the decrease in N deposition seems possible, especially on steep slopes. Accordingly, our findings confirm the statements of Bennie et al. (2006) and Diekmann et al. (2019) that grasslands on steep slopes are least susceptible to species loss and more resistant to invasion by competitive species than grassland on flatter terrain.

Our study highlights the relevance of interconnected, unfertilised, but regularly managed low productivity grasslands (occurring on steep slopes) for biological conservation. Beside their resilience against N input and their ability to recover after reduction of N input, they may act as source habitats for oligotrophic grassland species. In order to maintain the diversity of oligotrophic grassland species, policy should aim to (1) further reduce N emissions and (2) support regular management, primarily in form of hay making, of semi-natural low productivity grasslands, especially when located on steep slopes. The last point is of particular importance, as grasslands on steep slopes (and in peripheral locations) are especially affected by abandonment (Bornand et al., 2016).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.06.001.

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