Nitrogen deposition is negatively related to species richness and species composition of vascular plants and bryophytes in Swiss mountain grassland

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ABSTRACT

Nitrogen (N) deposition is a major threat to biodiversity of many habitats in the lowlands. In mountain habitats, however, the effect of N deposition on biodiversity is not well understood. Here, data from the biodiversity monitoring of Switzerland were used to investigate whether high N deposition is negatively related to species richness and community uniqueness of vascular plants and bryophytes in mountain grassland. The total species diversity, as well as the diversity of three subsets of species (i.e. oligotrophic species, eutrophic species and targeted grassland species according to conservation objectives of the Swiss authorities) were analyzed. Overall, the empirical data from the present study indicate that the currently expert-based range of the critical load of N deposition below which harmful effects on sensitive ecosystems should not occur (upper bound is currently at 20 kg N ha^{-1} yr^{-1}) is set too large for mountain hay meadows. Negative relations between N deposition and species richness and community uniqueness in mountain grassland were found already at 10–15 kg N ha^{-1} yr^{-1}. The results suggest that the negative effect of N deposition on plant diversity is mainly due to a decrease of oligotrophic plant species and to a lesser extent to an increase in eutrophic plant species. While for bryophytes, the decrease of community uniqueness is related to changes in both oligotrophic and eutrophic species. Furthermore, because plant species richness of target species for conservation was negatively related to N deposition, airborne N deposition is likely to defeat conservation efforts in mountain grassland.

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1. Introduction

Species-rich semi-natural grasslands are threatened biodiversity hotspots in Europe. Remaining semi-natural grassland is especially frequent in the Alps and other mountainous regions (Homburger and Hofer, 2012). Unfortunately, management regimes of accessible mountainous areas are intensified, while poorly accessible mountainous areas are being abandoned (Tasser and Tappeiner, 2002; Rudmann-Maurer et al., 2008). This change in traditional management regimes is considered as a major driver that endangers grassland biodiversity in mountainous regions of Europe (Niedrist et al., 2009; Homburger and Hofer, 2012). Yet, a further threat to the diversity of mountain grassland has rarely been considered: airborne nitrogen (N) deposition caused by human activities. N deposition can be high in comparably remote areas

of mountainous regions (Williams and Tonnessen, 2000; Weathers et al., 2006). It is thus likely that N deposition will negatively impact the biodiversity and ecosystem function of mountain grassland as it has been demonstrated for lowland grassland (Clark and Tilman, 2008; Maskell et al., 2010). Furthermore, due to a shorter vegetation period and the generally thinner and nutrient-poorer soils of mountain grassland, the effects of N deposition on mountain grassland diversity might be even stronger than the effects on the diversity in lowland grassland (Bowman et al., 2012).

Under the Convention on Long-range Transboundary Air Pollution effect-oriented thresholds for N deposition have been developed, below which harmful effects on sensitive ecosystems including significant losses of biotic diversity do not occur according to current knowledge (Achermann and Bobbink, 2003; Bobbink and Hettelingh, 2011). These thresholds are called critical loads, and the critical load concept has helped Parties to the Convention to make progress towards reducing N deposition on ecosystems (Hettelingh et al., 2001; Bobbink et al., 2010). However, studies on effects of N deposition on mesic mountain grassland are lacking, and this lack of information especially in mountain hay meadows

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has been identified as a major gap in our knowledge towards the development of empirical critical loads of nitrogen for natural and semi-natural ecosystems (Bobbink and Hettelingh, 2011).

Semi-natural grassland such as mountain hay meadows has high priority in conservation planning (Jacquemyn et al., 2003). Yet, studies with N addition are not available for mountain hay meadows and, therefore, the critical load range, which is currently set to 10–20 kg ha^{-1} yr^{-1}, is based on expert judgement (Bobbink and Hettelingh, 2011). This is in contrast to most other sensitive habitats for which the critical loads have been defined and revised based on empirical studies on observed changes in the structure and functioning of ecosystems (Bobbink and Hettelingh, 2011). Hence, there is a need for empirical studies that investigate the effect of N deposition on the biodiversity in mountain grasslands to establish empirical critical loads of N deposition and, thus, to help authorities to make progress towards reducing N deposition in mountain grasslands.

Here, the effect of N deposition on species richness and species composition in mountain grassland was investigated using observational data of vascular plants and bryophytes from field survey conducted over entire Switzerland. Species richness of vascular plants in grassland is significantly higher at the subalpine level than in lowlands (Wohlgemuth et al., 2008), and therefore, mountain grassland is of general importance for biodiversity. While only few studies have investigated effects of N deposition on bryophyte species richness in Switzerland (Bergamini and Pauli, 2001), several studies have investigated plant species richness-nutrient availability relationships in Swiss grassland. These studies suggest that species richness is less affected in mountain regions due to the lower direct fertilizer input by farmers compared with lowlands (Kampmann et al., 2008; Rudmann-Maurer et al., 2008). However, whether species richness is also less affected by airborne N deposition in mountain regions compared to lowlands remains to be tested. In this study, the data on vascular plants and bryophytes from the Biodiversity Monitoring of Switzerland were used to test (i) whether N deposition is negatively related to species richness and community uniqueness in mountain grassland, (ii) whether N deposition is negatively related to species richness and community uniqueness of target species for the agricultural sector for which the Swiss agriculture has a particular responsibility to safeguard and promote (BAFU and BLW, 2008), and (iii) whether empirical data supports the current expert-based setting of the critical load for mountain hay meadows.

2. Materials and methods

About 70% of Switzerland is mountainous (60% Alps and 10% Jura Mountains); the altitudinal range is from 193 to 4634 m.a.s.l. Data stem from the Biodiversity Monitoring of Switzerland (BDM; www.biodiversitymonitoring.ch) that was launched in 2001 to monitor Switzerland's biodiversity and to comply with the Convention on Biological Diversity of Rio de Janeiro. In the BDM scheme, vascular plants and bryophytes are two of three species groups investigated in a systematic sample of about 1400 circular 10 m^2 plots laid out as a regular grid over entire Switzerland. Fieldwork for plants and bryophytes was highly standardized and was carried out by qualified botanists. For the plant surveys, the botanists visited each plot twice per season except for the plots at high altitudes with a short vegetation period that were inspected only once. During each visit all the plant species detected on the plot were recorded (for details see Plattner et al., 2004; Bühler and Roth, 2011). At a first plot visit all bryophytes up to 1.5 m were collected from the soil, dead wood, rocks, living trees and scrubs and sent to specialists for identification. The botanists also classified every plot according to its type of habitat following Delarze and Gonseth (1999). Plots

classified as nutrient-rich meadows or pastures situated above the colline level (Schreiber et al., 1997) were selected to mirror the 'mountain hay meadows' category of the EUNIS habitat classification system (i.e. code E2.3; Davies et al., 2004). Unfortunately, the managing practices of farmers applied on the surveyed plot were unknown and, therefore, it was difficult to exclude enriched grassland plots (EUNIS code 2.6 and 4.5) from mountain hay meadow plots. As suggested by Bühler and Roth (2011) only plots were analyzed with more than 35 species at the census from 2001 to 2005 (i.e. above average species richness of grassland plots). By doing so we are confident that most of the enriched grassland plots were excluded. These a priori selection rules resulted in a sample of 122 plots that were surveyed once between 2006 and 2010 and that were predominantly situated on the northern slope of the Alps at the montane (32%) and the subalpine level (20%) or in the Jura mountains at the montane level (10%). The remaining plots were situated on the central plateau, the central Alps and the southern Alps.

2.1. Modelling N deposition

Atmospheric N deposition was estimated using a pragmatic approach described in Rihm and Kurz (2001) that combines monitoring data, spatial interpolation methods, emission inventories, statistical dispersion models and inferential deposition models. The following parameters were included into the model: wet deposition of nitrate (NO$_3$$^{-}$) and ammonium (NH$_4$$^{+}$), gaseous ammonia (NH$_3$), nitrogen dioxide (NO$_2$) and nitric acid (HNO$_3$) and dry deposition of particulate NH$_4$$^{+}$ and NO$_3$$^{-}$ (secondary aerosols). Wet deposition was obtained by multiplying mean annual concentrations of soluble N compounds in precipitation with precipitation rate. In northern Switzerland, monitoring data on atmospheric deposition of soluble N compounds imply that there is no clear altitudinal pattern in rainwater concentrations at low altitudes, but a clear decrease of concentrations at higher altitudes (Thimonier et al., 2005). Therefore, we assumed a constant concentration of 0.74 mg N l^{-1} below 1000 m altitude and a linear decrease of 70% between 1000 and 3000 m altitude. In southern Switzerland, the regression model developed by Barbieri and Pozzi (2001) was used instead. Mean annual precipitation derived from a map interpolating 300 meteorological stations (FOWG, 2000).

Dry deposition of gases and aerosols was calculated on the basis of monitored and modelled air concentrations. For NH$_3$ and NO$_2$ the air concentrations were calculated applying an emission–dispersion approach. Emissions and concentrations of NH$_3$ were mapped on a grid of 100 by 100 m. Agriculture was the main source of NH$_3$ accounting for 94% of total ammonia emissions (Kupper et al., 2010). The sources were modelled based on the 2007 census of the Swiss agricultural enterprises, including their location, the number of animals and the farm class, which is a combination of region, altitude and production specialization, i.e. cattle, crops, mixed or other farms. For each farm, the livestock numbers were multiplied with emission factors that were stratified into 24 livestock categories, 36 farm classes and four emission stages (housing, hardstandings, grazing, manure storage and manure application; Kupper et al., 2010). It was assumed that the emissions from housing, hardstandings and manure storage were located near the farm buildings (point source). The emissions from grazing and manure application (area sources) were distributed over the agricultural areas within the municipality. Emissions from mineral fertilizers, waste water treatment, household, industries and natural sources were spatially allocated in a top-down approach to the relevant categories of the land-use statistics (SFSO, 1997; Kupper et al., 2010). The ammonia emissions from transport were mapped on the basis of a traffic model (SAEFL, 2004). The spatial pattern of the ammonia concentrations

in the air was calculated applying a dispersion model that was verified by measurements with passive samplers (Thoni et al., 2004; Rihm et al., 2009). For calculating the NH_3 deposition on hay meadows, a deposition velocity of $12\,mm\,s^{-1}$ was used, which is a typical value for agricultural land (Cape et al., 2009). Emissions and concentrations of NO_2 were mapped on a grid of 200 by 200 m. The NO_2 map for 2007 was derived from the existing models for 2005 and 2010 by linear interpolation (SAEFL, 2004). For the deposition velocity of NO_2 a value of $1.5\,mm\,s^{-1}$ was used. The concentration field for HNO_3 was derived from maps of air humidity, temperature, ozone concentrations and NO_2 concentrations applying an empirical relationship developed by ICP materials. The annual mean concentrations were between 0.2 and $1.0\,\mu g\,m^{-3}$. For the deposition velocity, a value of $15\,mm\,s^{-1}$ was used. The concentration of particulate NO_3^- and NH_4^+ was derived from modelled PM10 maps (SAEFL, 2003). The spatial pattern was determined by selecting only the model layers containing secondary aerosols assuming that primary particles hardly contain any nitrogen. According to chemical analysis of the PM10 on the Swiss Plateau, the mean concentration was approximately $2.0\,\mu g\,m^{-3}$ for ammonium and $2.8\,\mu g\,m^{-3}$ for nitrate (SAEFL, 2003). Deposition velocities used for aerosols were in a range of $1–2\,mm\,s^{-1}$ depending on altitude.

2.2. Statistical analysis

For each plot the species richness (i.e. the number of recorded plants or bryophyte species) and a measure of the uniqueness of the species composition recorded on each plot was calculated. The measure of uniqueness of species composition was calculated using the concept of species dissimilarity (i.e. the "differentiation diversity" for dissimilarity between samples, sensu Jurasinski et al., 2009). Each of the $i = 1, \ldots, 122$ surveyed plots was paired with every other plot, and for each pair of plots the dissimilarity of the species between the two plots was calculated using the Simpson dissimilarity index (Simpson, 1968; Koleff et al., 2003). The mean of the Simpson indices of plot i paired with every other plot was taken as a measure of the uniqueness of species composition of plot i, which was called "community uniqueness" throughout the text. A value close to one would indicate a plot with a high proportion of unique species (i.e. a high proportion of rare species); a value close to zero would indicate a high proportion of common species.

Since the aim was to estimate the effect of N deposition on species richness and community uniqueness by accounting for non-linear effects of confounding variables, generalized additive models were used (GAM; Zuur et al., 2009). To model species richness, we aimed to use GAM with Poisson distribution since the response variable was counts. However, overdispersion was detected in most of the GAM models on species richness, and therefore, the standard errors were corrected using a Quasipoisson-GAM where the variance is given by the dispersion parameter times the mean (Zuur et al., 2009). To model community uniqueness GAMs with normal distribution were used. The selection of the explanatory variables that were used additionally to N deposition in the GAMs was guided by previous work on the modelling of vascular plant diversity in Switzerland (Wohlgemuth et al., 2008). Additionally, to characterize the humidity and light conditions for each plot, the mean species indicator values was calculated of all recorded plant species using the recalibrated values for the Swiss Flora (Landolt et al., 2010). Variance inflation factors (VIF) were used to assess which explanatory variables are collinear and should not be used in the analyses (Zuur et al., 2009). Only variables with VIF values below 2 were used, which indicates that collinearity is not of concern (Zuur et al., 2009). A list with the explanatory variables that finally were considered in the GAMs additionally to N deposition is given in Table 1. Since the species composition of sites close to each other might be more similar than for sites far apart, the average distance from one plot to each other plot was included as an additional explanatory variably in the GAMs on community uniqueness to account for distance effects.

The following strategy was used for model selection and verification: First a full GAM model was fitted that included the linear and quadratic terms of N deposition and the linear and quadratic terms of the calcareous content of the soil 'CACO3', and the smoothers of the remaining explanatory variables from Table 1. Linear and quadratic effects instead of smoothers for N deposition were chosen because we were interested to quantify the relationship between N deposition and the depended variable (i.e. species richness or community uniqueness), while for 'CACO3' only integer values between one and six were possible and, therefore, a smoother seemed not sensible. For the remaining explanatory variables, low rank isotropic smoothers were used except for the variable 'exposition'. The variable exposition is cyclic (i.e. $0–360°$) and therefore a cyclic version of a P-spline was used (Eilers and Marx, 1996). Starting with the full model backward selection was performed to get the final model that included at least the linear term of N deposition and the significant smoothers of the confounding variables. Backward selection was based on approximate significance of smooth terms and all terms with $p > 0.05$ were removed. The last step was then to visually check homogeneity of variance and normality of error using plots of scaled Pearson residuals. Inference was then based on the minimal adequate model.

The relation of N deposition to species richness and community uniqueness was analyzed for all recorded species together, but also for three subsets of species: (1) species that are typically found on nutrient poor sites (i.e. oligotrophic species with N-values of one and two; Landolt et al., 2010), (2) species that are typically found on nutrient rich sites (i.e. eutrophic species with N-values of four and five; Landolt et al., 2010), and (3) target species for the agricultural sector (BAFU and BLW, 2008). All analyses were done with the software R (R Development Core Team, 2012) using the packages 'mgcv' (Wood, 2011), 'simba' (Jurasinski and Retzer, 2012) and 'AED' (Zuur et al., 2009).

For the figures the sample was divided into the following five classes: one class with N deposition below the critical load ($<10\,kg$ $N\,ha^{-1}\,yr^{-1}$, $n = 8$), two classes with N deposition within the range of the critical loads ($10–15\,kg\,N\,ha^{-1}\,yr^{-1}$, $n = 25$ and $15–20\,kg$ $N\,ha^{-1}\,yr^{-1}$, $n = 42$), and two classes with N deposition above the critical load ($20–25\,kg\,N\,ha^{-1}\,yr^{-1}$, $n = 32$ and $>25\,kg\,N\,ha^{-1}\,yr^{-1}$, $n = 15$).

3. Results

The total nitrogen deposition in Switzerland for the year 2007 amounted to $17.9\,kg\,N\,ha^{-1}\,yr^{-1}$ to which gaseous NH_3 contributed 34%, wet NH_4^+ 29%, wet NO_3^- 21%, gaseous NO_2 8%, dry NH_4^+ 4%, gaseous HNO_3 3% and dry NO_3^- 2%. The average ($\pm SD$) N deposition on the 122 plots was $18.3\,(\pm 5.8)\,kg\,N\,ha^{-1}\,yr^{-1}$. On these plots, the N deposition exceeded in 93% the minimum empirical critical load of $10\,kg$ $N\,ha^{-1}\,yr^{-1}$, and in 38% the maximum critical load of $20\,kg\,N\,ha^{-1}\,yr^{-1}$. The BDM surveys on the 122 plots resulted in 5808 records of 558 vascular plant species and in 1391 records of 173 bryophyte species; the average ($\pm SD$) species richness per plot was $47.6\,(\pm 11.0)$ plant species and $11.4\,(\pm 8.3)$ bryophyte species.

Analysing all recorded plant species together, the mean plant species richness in mountain grasslands was highest if N deposition was low and decreased with increasing N deposition (linear effect of N deposition: slope $= -0.02$, $t = 6.3$, $p < 0.001$). The mean species richness of vascular plants was also related to precipitation (approximate significance of smooth terms: $F = 3.1$, $p = 0.004$), humidity ($F = 12.2$, $p < 0.001$) and light ($F = 15.3$, $p < 0.001$). In contrast, the mean bryophyte species richness was not significantly related to N deposition (linear effect of N deposition: $|slope| < 0.001$, $t = 0.03$, $p = 0.971$). The mean species richness of bryophytes was related to altitude ($F = 15.6$, $p < 0.001$), light ($F = 15.1$, $p < 0.001$) and exposition ($F = 0.6$, $p = 0.019$). The community uniqueness of plants decreased with increasing N deposition (linear effect of N deposition: slope $= -0.003$, $t = 2.0$, $p = 0.043$). Additional variables that explained plant community uniqueness were altitude ($F = 14.4$, $p < 0.001$), humidity ($F = 6.2$, $p < 0.001$) and light ($F = 11.3$, $p < 0.001$). Also the community uniqueness of bryophyte species was negatively related to N deposition (linear effect of N deposition: slope $= -0.026$, $t = 2.3$, $p = 0.026$). Additional variables

Table 1

Explanatory variables considered as covariates in the general additive models ('VIF' = variance inflation factors for the full set of explanatory variables (Zuur et al., 2009)).

Description	VIF	Mean ± SD	Min	Max	Source
Elevation (m.a.s.l.)	1.4	1189 ± 420	424	2246	Wohlgemuth et al. (2008)
Inclination (°)	1.4	16 ± 8	0	41	Wohlgemuth et al. (2008)
Mean annual precipitation (mm)	1.4	1484 ± 294	681	2185	Wohlgemuth et al. (2008)
Calcareous content of soil (classes 1–6)	1.2	3.7 ± 1.4	1	6	BAFU and GRID-Europe (2010)
Indicator value of humidity (mean indicator value of recorded plants)	1.6	3.0 ± 0.2	2.5	3.8	Landolt et al. (2010)
Indicator value of light (mean indicator value of recorded plants)	1.6	3.5 ± 0.2	2.9	4.2	Landolt et al. (2010)
Exposition (0–360°)	1.0	205 ± 101	8	357	Wohlgemuth et al. (2008)
Average distance between plots (km)[a]	1.4	104.4 ± 216.9	79.1	182.1	–

[a] Average distance between plots was only used in the general additive model on community uniqueness.
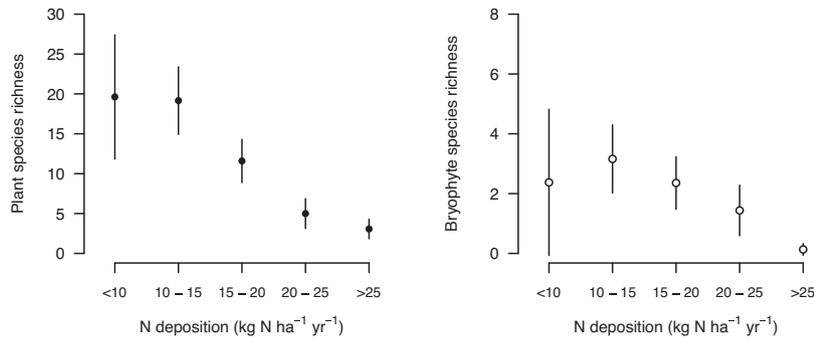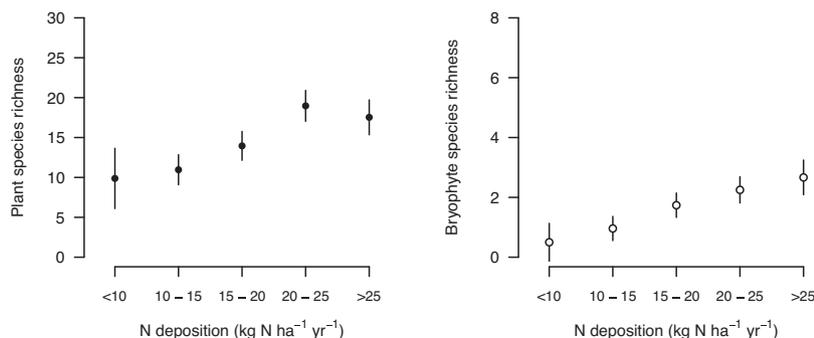

Fig. 1. Effects of different loads of N deposition on oligotrophic plant (left panel) and bryophyte (right panel) species richness. The error bars give the 95% confidence intervals.

to explain bryophyte community uniqueness were altitude ($F = 4.0$, $p = 0.009$) and humidity ($F = 4.9$, $p = 0.003$).

Overall, 208 oligotrophic plant species and 53 oligotrophic bryophyte species were recorded. The species richness of oligotrophic plant species decreased with increasing N deposition (linear effect of N deposition: slope = −0.06, $t = 2.61$, $p = 0.010$, left panel of Fig. 1), whereas the bryophyte species richness peaked at 10–15 kg N ha^{-1} yr^{-1} and then decreased with increasing N deposition (linear effect of N deposition: slope = 0.389, $t = 2.89$, $p = 0.008$; quadratic effect of N deposition: slope = −0.01, $t = 2.63$, $p = 0.009$, right panel of Fig. 1). For eutrophic plant species the species richness seemed to increase with increasing N deposition (left panel of Fig. 2); apparently, however, this pattern was due to an altitudinal effect and plant species richness was not significantly affected by N deposition when accounting for altitude (linear effect of N deposition: slope = −0.001, $t = 0.16$, $p = 0.87$). The species richness of eutrophic bryophyte species increased from 10 to 15 kg N ha^{-1} yr^{-1} with increasing N deposition (linear effect of N deposition: slope = 0.24, $t = 2.80$, $p = 0.006$; quadratic effect of N deposition: slope = −0.004, $t = 2.05$, $p = 0.042$, right panel of Fig. 2).

The community uniqueness of oligotrophic plant species was negatively related to N deposition (linear effect of N deposition: slope = −0.01, $t = 2.88$, $p = 0.005$), while the community uniqueness of eutrophic plant species was not significantly related to N deposition (linear effect of N deposition: |slope| < 0.001, $t = 0.04$, $p = 0.965$). For bryophytes we did not find evidence that community uniqueness of oligotrophic species was related to N deposition (linear effect of N deposition: slope = −0.002, $t = 0.55$, $p = 0.582$), whereas for eutrophic bryophyte species there was clear indication that the community uniqueness is decreasing with increasing N deposition (linear effect of N deposition: slope = −0.087, $t = 3.99$, $p < 0.001$; quadratic effect of N deposition: slope = 0.002, $t = 3.54$, $p < 0.001$).

The species richness of target agricultural plant species peaked at N deposition of 10–15 kg ha^{-1} yr^{-1}, but decreased above that range with increasing N deposition (linear effect of N deposition: slope = 0.09, $t = 2.05$, $p = 0.043$, quadratic effect of N deposition: slope = −0.003, $t = 2.49$, $p = 0.014$, left panel of Fig. 3). Apparently, however, this only had a weak and non-significant effect on community uniqueness of target plant species (linear effect of N deposition: slope = −0.002, $t = 1.48$, $p = 0.141$). The species richness of target bryophyte species (e.g. Phascum cuspidatum, Fissidens adianthoides) tended to increase with increasing N deposition (linear effect of N deposition: slope = 0.04, $t = 1.85$, $p = 0.067$, right panel of Fig. 3) and the community uniqueness of target bryophyte species tended to decrease (linear effect of N deposition: slope = −0.002, $t = 1.48$, $p = 0.141$).

4. Discussion

In the present study negative relationships of N deposition with plant species richness and with community uniqueness of plants and bryophytes were found. These results are in line with recent studies in other habitats highlighting the decline of species richness due to N deposition (De Schrijver et al., 2011; Payne et al., 2011; Phoenix et al., 2012). Furthermore, a negative relationship between the number of oligotrophic plant species and N deposition was found. As oligotrophic species are generally rare, the species composition became more similar with increasing N deposition because the rare and thus more unique species disappeared at higher level
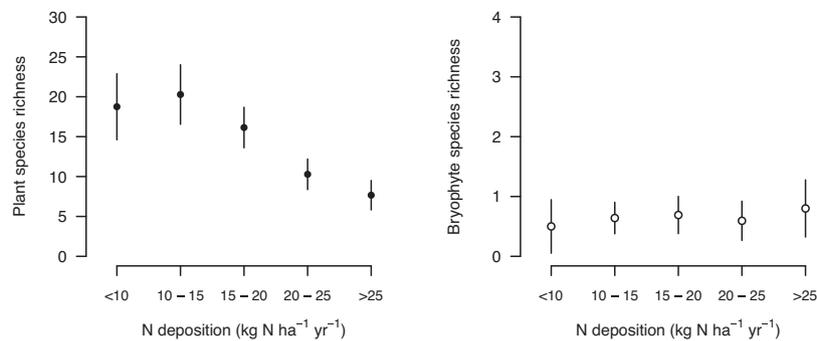

Fig. 2. Effects of different loads of N deposition on eutrophic plant (left panel) and bryophyte (right panel) species richness. The error bars give the 95% confidence intervals.

Fig. 3. Effects of different loads of N deposition on target species for the agricultural sector (BAFU and BLW, 2008). Given are mean vascular plant (left panel) and bryophyte (right panel) species richness. The error bars give the 95% confidence intervals.

of N deposition. In contrast, the group of eutrophic plant species consisted of few but common species, and neither species richness nor community uniqueness of eutrophic species was significantly related to N deposition in this study. Although no direct analyses of the temporal trends in species diversity were conducted, these results suggest that high N deposition could be an important driver of floristic homogenization in mountain hay meadows through the decrease of generally rare oligotrophic plant species, while for bryophytes, the decrease of community uniqueness is related to changes in both oligotrophic and eutrophic species.

Over the last decade, populations of common plant species that include eutrophic species were observed to increase and this spread of common species resulted in floristic homogenization of grassland in Switzerland according to Bühler and Roth (2011) who analyzed the change in community uniqueness over time, whereas the present study compared the current state of community uniqueness over sites with different N deposition. Since it usually takes a much longer time period to demonstrate a decline of uncommon specialists caused by the spread of common generalists (Naaf and Wulf, 2010), the differences in the relevant time period between the two studies might explain why Bühler and Roth (2011) reported the increase of common species as the main cause of currently on-going floristic homogenization, while in the present study the decrease of rare oligotrophic species was the main cause of floristic homogenization.

The Convention on Long-range Transboundary Air Pollution in 2010 (Bobbink and Hettelingh, 2011) based the range of the critical load of nitrogen for mountain hay meadows at 10–20 kg N ha^{-1} yr^{-1} using expert judgement only whereas the present study on plants and bryophytes demonstrated that it should be set at about 10–15 kg only.

In other habitats, the role of N deposition as a driver of biodiversity loss has mainly been surveyed in field studies with experimental addition of N (Bobbink and Hettelingh, 2011; Phoenix et al., 2012). Such experiments are important for determining the impacts of N deposition on ecosystems and for a more mechanistic understanding of the link between N deposition and change in biodiversity. However, studies with experimental addition of N are labour intensive, expensive, and usually of limited spatial scale. They probably overestimate the consequences of elevated N deposition (Pearce and Van der Wal, 2008). Thus, the assessment of the threat of N deposition on biodiversity should be complemented by the analysis of observational data covering large spatial scales.

The negative relationship of species richness of target plant species for the agricultural sector with N deposition suggests that airborne N deposition may defeat conservation efforts in mountain hay meadows. Enhanced N deposition can similarly reduce species richness, species richness of targeted species and community uniqueness and, thereby, mountain hay meadows are not only

at risk to loose species due to enhanced N deposition, but they may also lose their site-specific aspects.

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