Recovery of mountain plant communities in response to reductions in Nitrogen emissions is hidden by other drivers of global change

Tobias Roth[1, 2], Lukas Kohli[2], Beat Rihm[3], and Reto Meier[4]

[1]**Zoological Institute, University of Basel, Basel, Switzerland**
[2]**Hintermann Weber AG, Austrasse 2a, 4153 Reinach, Switzerland**
[3]**Meteotest,Fabrikstrasse 14, 3012 Bern, Switzerland**
[4]**Federal Office for the Environment (FOEN), Air Pollution Control and Chemicals Division, 3003 Bern, Switzerland**

Corresponding author:
Tobias Roth[1,2]

Email address: t.roth@unibas.ch

ABSTRACT

Nitrogen (N) deposition is a major threat to biodiversity of many habitats. The recent introduction of cleaner technologies in Switzerland has let to reductions in the emissions of nitrogen oxides, with affiliated decrease in Nitrogen deposition. We infered different drivers of community change (i.e. Nitrogen deposition, climate warming, land-use change) in Swiss mountain hay meadows. The data were obtained from the Swiss biodiversity monitoring.

INTRODUCTION

Nitrogen deposition is one of the major threats to biodiversity (Sala 2000, Bobbink 2010, Menier et al. 2016). Especially, there is strong evidence for the reduction in diversity of species-rich grasslands in Europe (Stevens et al. 2006, Maskell et al. 2010, Duprè et al. 2010).

Fertilizing experiments show that plant biodiversity in mountain grasslands is negatively affected by nitrogen addition, too (Humbert et al. 2016).

Since the late 1980s measures to reduce atmospheric pollution have successfully reduced emissions of nitrogen oxides, with affiliated decrease in Nitrogen deposition in many parts of Europe (Tørseth et al., 2012, Maas and Grennfelt, 2016) [Tørseth et al.,: Atmos. Chem. Phys., 12, 5447–5481, 2012]. However, it is an open question whether and how fast the reduction in N deposition rates will lead to the recovery of extant plant communities.

Quantifying the potential recovery of biodiversity in response to reducing air pollution requires an alternative to the space-for-time approach, ideally monitoring long-term community dynamics on permanent plots (Duprã, C. et al. Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. Glob. Change Biol. 16, 344–357, (2010).

One useful approach to understanding biodiversity change is through estimates of biodiversity turnover reflecting both immigration and extinction, often in a closed range of values (Hillebrand et al-2018.pdf).

Observation data of vascular plants from field recordings shows negative correlations of Nitrogen deposition with species richness and species composition in mountain hay meadows (Roth et al. 2013).

In Switzerland, grassland accounts for 70 per cent of the agricultural land. With extensive cultivation, permanent grassland has a very high biodiversity. This applies in particular to the meadows of the Swiss mountain region (Schlup et al. 2013). In the alpine region, meadows with a high plant diversity are of great importance agronomically (Leiber et al. 2005), for the image of the products and for the conservation of biodiversity (Hohl, 2006).

The meta-analysis of Humbert et al. (2016) showed management and abiotic factors to interact with nitrogen addition to drive plant community changes: The overall effects of N addition on plant species richness and diversity (Shannon index) were more pronounced in managed experimental sites with warmer summers. Management regimes of accessible mountainous areas are intensified, while poorly accessible mountainous areas are being abandoned (Tasser and Tappeiner, 2002; Graf et al., 2014, Strebel and Bühler, 2015). 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).

On European mountain summits, plants shifted upwards in the last decades (Rumpf et al. 2018). The authors conclude that ≪These results suggest that recent climate warming interacted with airborne nitrogen deposition in driving the observed dynamics. As changes increased more for species from lower elevations and eutrophic plant species showed the strongest increase in abundance, these findings might be relevant for mountain hay meadows, too.

MATERIALS & METHODS

Monitoring data and community measures

We analysed the presence/absence of vascular plants sampled within the scope of Switzerland's Biodiversity Monitoring (BDM) programme that was launched in 2001 to monitor Switzerland's biodiversity and to comply with the Convention on Biological Diversity of Rio de Janeiro (Weber, Hintermann, and Zangger 2004). The sampling sites were circles with a size of 10 m^2 and data collection was carried out by qualified botanists who visited each sampling site twice within the same season. During each visit all the vascular plant species detected on the plot were recorded. After the sampling of the plant data the botanists also assigned a habitat type to each sampling site according to the classification system developed for Switzerland (Delarze and Gonseth 2008).

We matched the habitat types of the Swiss classification system with the categories from the EUNIS system (level-3 classification; Davies, Moss, and Hill 2004) and selected all sampling sites in mountain hay meadows (EUNIS E2.3) For more details on the field methods see Plattner, Birrer, and Weber (2004), Roth et al. (2013) and Roth et al. (2017). We analysed the data from 2003 to 2017. During that study period each sampling site was surveyed once per five-year period: the first period lasted from 2003 to 2007, the second from 2008 to 2012 and the third from 2013 to 2017. These selection criteria resulted in sample of 129 sites.

For each survey (a survey consists of the two visits per season) we calculated the following community measures: (1) The number of recorded species (species richness), the community mean of indicator values of recorded species for temperature (2), humidity (3), nutrients (4) and light (5). The indicator values were obtained from the recalibrated indicator values for the Swiss Flora (Landolt et al. 2010). Additionally to these five community measures that describe the state of plant communities for each site at a given time point, we also estimated the temporal turnover (i.e. species exchange ratio sensu Hillebrand et al. (2018)) as the proportion of species that differ between two time points to describe the community change between two time points.

Environmental gradients

We expected different global change patterns to simultaneously cause temporal change in mountain hay communities. To better disentangle the importance of these mechanisms we ordered the sites along four main environmental gradients. First we expected communities to response to climate warming and the response might be different depending along the temperature gradient (Roth, Plattner, and Amrhein 2014). To describe the temperature gradient we used the mean annual temperature per site from the WordClim database (Fick and Hijmans 2017). Another key drivers for plants that is likely to be affected by climate change is precipitation (Beier et al. 2012). We used the annual precipitation per site from the WordClim database (Fick and Hijmans 2017).Further, we estimated atmospheric N deposition for each site 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. For details on the estimation of N deposition see Rihm and Kurz (2001) and Roth et al. (2017). Finally we used inclination as proxy for land-use intensity because we expected that steeper sites are likely to be less intensively managed (Strebel and Bühler 2015).

Statistical analyses

To estimate the linear trend over time for each of the five community measures we applied linear mixed models (LMM) with normal distribution except for species-richness with Poisson distribution and the logarithm as link function. We specified site specific trends with the assumption that the between-site differences in intercepts and slopes can be described with normal distributions (i.e. a random intercept random slope model, **???**). Model parameters were estimated in a Bayesian framework using the R-Package *rstanarm* (Stan Development Team 2016, Muth, Oravecz, and Gabry (2018)).

To infer whether species turnover was changing along the gradient, we used a Binomial-LMM with the proportion of species that differed between two surveys as dependent variable and the site gradients and period (first/second vs. second/third surveys) as predictors and site-ID as random effect. Model parameters were estimated in a Bayesian framework using the R-Package *rstanarm* (Stan Development Team 2016, Muth, Oravecz, and Gabry (2018)).

Table 1. Average measures of community structure for the three sampling periods (period 1: 2003-2007; period 2: 2008-2012; period: 2013-2017). The temporal trends are given as change per 10 years and were estimated from linear mixed models with normal distribution (except for species richness with Poisson distribution and a log-link function). The measure of precision for the temporal trend is given as the 5% and 95% quantiles of the marginal posterior distribution of the linear trend. The column 'Prob. for trend' gives the probability that the linear trend is > 0.

Measures	Period 1	Period 2	Period 3	Trend	5%	95%	Prob. for trend
Species-richness	45.72	46.02	45.74	0.00	-0.03	0.03	0.53
Temperature value	3.11	3.13	3.13	0.01	0.00	0.03	0.97
Huminity value	2.99	2.98	2.99	0.01	-0.01	0.02	0.80
Nutrients value	3.20	3.20	3.20	0.00	-0.02	0.01	0.33
Light value	3.56	3.55	3.55	-0.01	-0.02	0.00	0.07

To infer whether species that colonized or disappeared from a site had particular indicator values that differed from the other species at that site, we produced for each site a list with all species that were recorded during the three surveys (total community). We then calculated the community mean (CM) of the indicator value for all species that colonized the site during the three surveys (i.e. not recorded during first survey and recorded during second or not recorded during second and recorded during third). We then randomly selected the same number of species from the total community and also calculated the community mean of the value for these species (random-CM). We repeated the random selection of species 1000 times. Then we calculated the differences of the CM minus the average of the random-CMs to obtain a standardized measure (standardized-CM) of how different the disappearing species were from random expectation. A standardized-CM < 0 would suggest that the indicator value of colonizing species were lower than the average species that were occurring at this site. We applied this method for both colonizing and disappearing species and for the indicator values for temperature, humidity, nutrients and light (see Appendix A). We then inferred whether the standardized-CM is changing along the corresponding gradient using linear models. Model parameters were estimated in a Bayesian framework using the R-Package *rstanarm* (Stan Development Team 2016, Muth, Oravecz, and Gabry (2018)).

We used logistic-LMM to infer whether the colonization probability or local survival probability was changing along the Nitrogen deposition gradient and whether this changing depended on the species indicator value for nutrients. To analyse the colonization probability we selected all species that were not observed during the first survey, and asked if they were observed (then Occ = 1) or not observed (then Occ = 0) during the second survey. The same was also done for all species that were not observed during the second survey. The variable 'occ' was then used as dependent variable in the logistic-LMM. As predictor variables the model contained the Nitrogen deposition of the site, the indicator value for nutrients of the species and the interaction of these two variables. Additionally species-ID and site-ID were included as random effects. The same logistic_LMM was also used to infer local survival probability. In that case, however, we selected all species that were recorded during the first or second survey and the variable 'occ' then indicated whether or not the species was also observed during the next survey. Model parameters were estimated using an approximate Bayesian approach using the R-Package *arm* (Gelman and Su 2018).

To estimate the effect of Nitrogen deposition on total species richness at a given time point, we described the plant species richness at the sites using a generalized linear model with Poisson distribution and the logarithm as link function. As predictors we used the four environmental gradients as described above. Model parameters were estimated using an approximate Bayesian approach using the R-Package *arm* (Gelman and Su 2018).

RESULTS

Temporal change in community structures

The five measures of plant community structure suggested that plant communities in mountain hay meadows were rather stable between 2003 and 2017 and did not show a clear increase or decrease over time (Table 1): for each of the three 5-year survey periods the averages of species-richness and the average indicator values for temperature, humidity, nutrients and light did not vary much among the three sampling periods and the estimated trends were rather small. Except for average indicator value for temperature, the 90% credible-interval of the temporal trend contained zero. The results from the linear mixed models suggest that a linear temporal change was most likely for the community mean of the indicator value for temperature (probability of increase: 0.97), followed by the

Table 2. Change of species turnover along the four gradients. The slopes along the gradients (estimate) are given as the change per 10 years of the logit-probability of species that differed between two surveys. Estimates and the 5% and 95% quantiles of the marginal posterior distribution obtained from a Binomial-GLMM.

Gradient	Estimate	5%	95%
Annual mean temperature	0.04	-0.02	0.10
Annual mean precipitation	-0.03	-0.12	0.07
Nitrogen deposition	-0.14	-0.30	0.02
Inclination	-0.03	-0.10	0.03

Table 3. Difference in the average indicator value of species that (a) disappeared from site or (b) newly colonized a site compared to the same number of species that were randomly selected from all species recorded at a site. Shown are the results from linear model with the difference between disappeard/colonized species and random species as dependend variable and the sitemeasure (gradient) as predictor variable.

		Difference from random			Change along gradient		
Ellenberg value	Gradient	Estimate	5%	90%	Estimate	5%	90%
(a) Plants that disappeard from a site							
Temperature	Annual mean temperature	-0.012	-0.033	0.010	0.007	-0.002	0.017
Humidity	Annual mean precipitation	-0.006	-0.041	0.031	0.011	-0.010	0.032
Nutrients	Nitrogen deposition	-0.025	-0.061	0.011	0.014	-0.027	0.056
Light	Inclination	-0.023	-0.050	0.005	-0.003	-0.026	0.020
(b) Plants that newly colonized a site							
Temperature	Annual mean temperature	0.017	0.001	0.033	-0.001	-0.008	0.006
Humidity	Annual mean precipitation	0.020	-0.012	0.051	-0.003	-0.021	0.016
Nutrients	Nitrogen deposition	-0.076	-0.108	-0.044	0.061	0.022	0.098
Light	Inclination	-0.041	-0.065	-0.018	0.011	-0.009	0.030

community mean of the indicator value for light (probability of decrease: 0.93) and it was least likely for the species richness (probability of increase: 0.53). The chance that the community mean of the nutrient value decreased between 2003 and 2017 was 0.67.

Species turnover

This temporal stability as inferred from the community measures was, however, in contrast to a rather large observed temporal turnover of species. The average percentage $\pm$ SD of species that differed between the first and second survey at a site was 37.65 $\pm$ 10.43% and the percentage of species that differ between the second and third survey was 35.66 $\pm$ 10.36%. Thus, it seemed that the turnover from the first/second survey to the turnover of the second/third survey moderately decreased (90% Credible interval of the change in turnover estimated from the Binomial generalized linear mixed model: -0.14 - -0.03). Variation in species turnover was largest along the Nitrogen deposition gradient with highest species turnover at sites with low Nitrogen deposition (Table 2). The other three gradients were less important to explain the variation in species turnover among sites.

High species turnover at a site is the result of species that disappeared from the site and species that newly colonized the site. To better understand the factors that drive these changes we are particularly interested whether the species that disappeared or colonized the sites differed in indicator values compared to what would be expected if the same number of species randomly disappeared or colonized the sites (i.e. random disappearance and random colonization) and whether there is a change along the gradients. It seems that the indicator values of newly colonizing species differed more from random colonization than the indicator values of disappearing species (Table 3). For colonizing species, we found the largest differences from random colonization in the indicator value for nutrients: at sites with nitrogen deposition of 10 kg ha^{-1} yr^{-1} the newly colonizing species had in average a lower indicator value for nutrients than species under random disappearance (column “Difference from random” in Table 3), but this differences between colonizing species and random colonization decreased with increasing Nitrogen deposition (column “Change along gradient” in Table 3). Thus at high Nitrogen deposition colonizing species did not differ from random species (see Figure 3b in Appendix A).

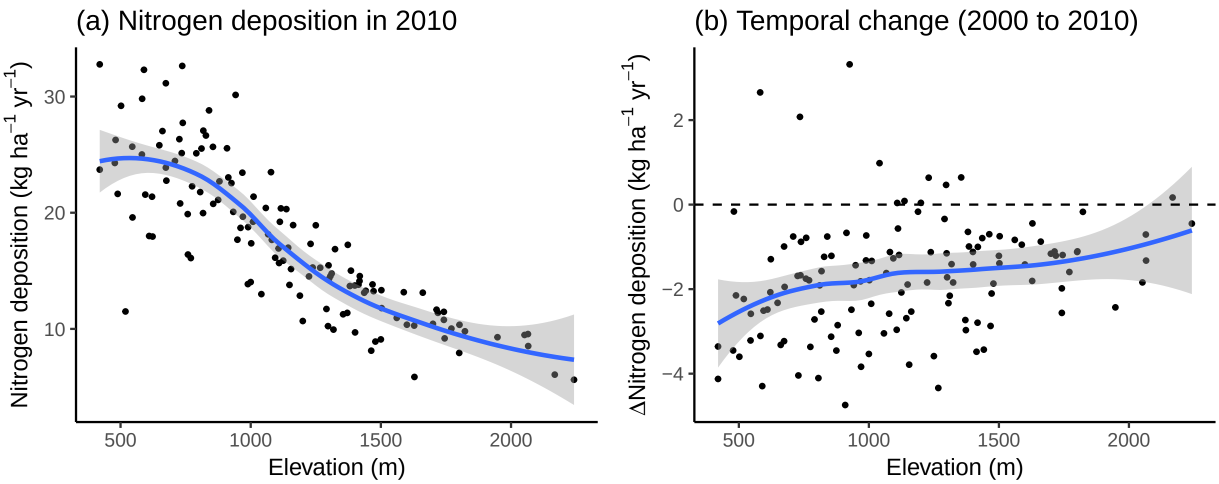

Figure 1. (a) The nitrogen deposition in 2010 and (b) the change in Nitrogen deposition between 2000 and 2010 along the elevational gradient of the study sites.

While colonizing species had higher temperature values compared to what we would expect under random colonization, the differences between colonizing species and random colonization was about four times smaller compared to the difference in indicator value for nutrients between colonizing species and random species. Nevertheless, the variation in indicator value for temperature seemed important to explain the total species turnover. This is because, disappearing species tend to have lower temperature value than random species as well as colonizing species tend to have higher temperature values than random species; both processes lead to an overall replacement of species with lower temperature value with species with higher temperature values. This was not the case for the indicator value for nutrients: species with lower nutrients values tended to be more likely to disappear from as well as to colonize sites compared to random species (Table 3). See also Appendix A were we present detailed results for the comparison between colonizing or disappearing species with randomly selected species.

Potential effects of reduction in Nitrogen emmissions

Nitrogen deposition decreased with increasing elevation (1a). In 2010 only 19.38% of sites had a Nitrogen deposition rate of less than 10 kg N ha^{-1} yr^{-1}, which lied all above 1000m. Between 2000 and 2010 the Nitrogen deposition decreased in average around 2 kg N ha^{-1} yr^{-1} with slightly larger net decreases at lower elevation (1a).

In Fig. 2 we compare the colonization and local survival probability of oligotrophic (indicator value of nutrients = 2) and eutrophic (indicator value of nutrients = 4) species along the Nitrogen deposition gradient. Local survival probability was the same for oligotrophic and euthrophic species at a deposition rate of 11.95 kg N ha^{-1} yr^{-1}; colonization probability was the same for for oligotrophic and euthrophic species at a deposition rate of 12.33 kg N ha^{-1} yr^{-1}. In only 0.36% of the sites the deposition rate was below 12.5 kg N ha^{-1} yr^{-1} where the replacement of eutrophic with oligotrophic species is likely.

While we could not detect a consistent decrease in average indicator value for nutrients (Table 1), the higher colonization rate of species with low nutrient value at sites with low deposition rate seems to affect the spatial variation of species richness: sites with low Nitrogen deposition are likely to become more species rich over time likely resulting in steeper slope of the negative relationship between Nitrogen deposition and species richness. Indeed, if we apply at different time points a similar model as in Roth et al. (2013) to infer the effects of Nitrogen deposition on the spatial variation of species richness, the resulting effect size (i.e. the slope) becomes more negative over time (Fig. 3).

DISCUSSION

- *General points*: Although N deposition considerably declined between 2005 and 2015, we could not detect major shifts in plant community structure during the same time period. Although NOx emissions in Switzerland decreased by 46% between 1990 and 2010 and NH3 emissions by 14% (Maas and Grennfelt, 2016), nitrogen deposition on our plots decreased by only 2.7 kg ha^{-1} yr^{-1} on average between 2000 and 2015 (Meteotest, 2018). This is only about one tenth of the decrease in England in the same period, where Nitrogen deposition

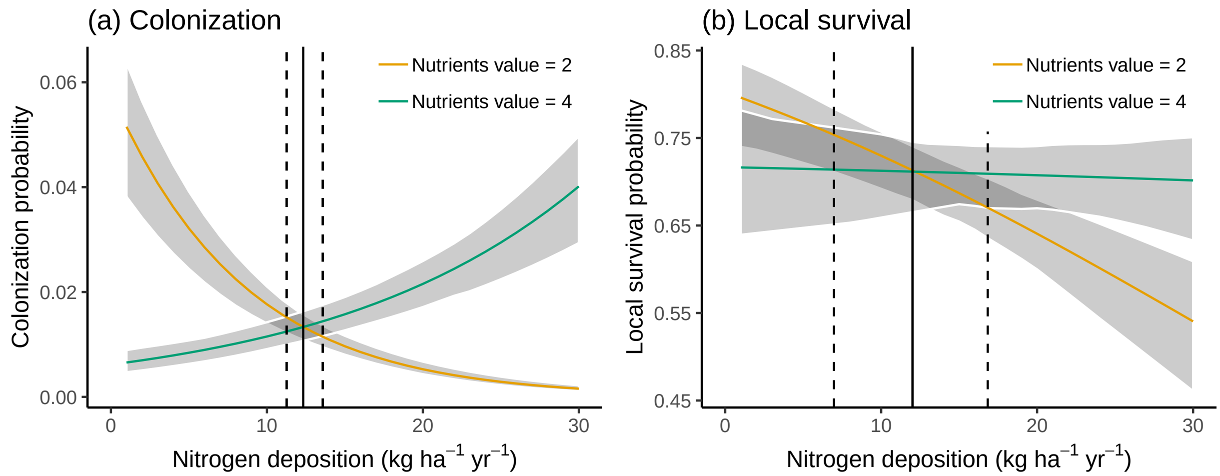

Figure 2. Colonization (a) and local survival (b) of oligotrophic (Ellenberg N = 2; red line) and eutrophic (Ellengerg N = 4) species along the N deposition gradient. Given are means and 95%-Credible Intervals from logistic linear mixed models. The vertical lines indicat the deposition rate with equal colonization or survival probabilities for oligotrophic and eutrophic species with the solid line indicating the median and the dashed lines the 5% and 95% quantiels of the margional posterior distribution.

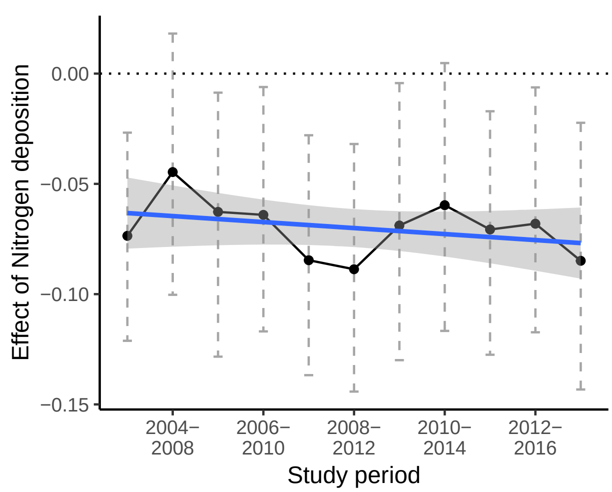

Figure 3. Effect size of Nitrogen deposition on total species richness estimated from applying the Poisson-GLM with species richness as dependend variable and Nitrogen deposition plus other site covariates as predictors using only the surveys from one five-year interval. Note that within every five-year interval all plots were sampled once.

decreased by 24kg ha^{-1} yr^{-1} from 1996 to 2011 (Storkey et al. 2015). In 2015, average N deposition was 14.8 kg ha^{-1} yr^{-1}, about 85% of 2000 deposition, and due to the rather short period of time and the small decrease in nitrogen deposition, it is not surprising that species richness has not reacted significantly.

- *Replacement of oligotrophic with eutrophic species is faster than the oposite direction*: Eutrophic species have rather high local survival across the entire deposition gradient, while oligotrophic species have much reduced local survival at high N deposition. This suggests that it takes more time to replace eutrophic by oligotrophic species than replacing oligotrophic by eutrophic species. Climatic effects may be more likely to be reversed than effects due to fertilization.

- *Methodological point*: The rather large spatial turnover might be partly explained by species that remained undetected in one of the surveys. From the randomly selected quality control of the BDM 17 mountain hay meadows were investigated from 2003 to 2017. Species richness was surveyed in the same year by two independent botanists. The species match is (mean $\pm$ SD) 85 $\pm$ 5.2 per cent, suggesting that at least a portion of the turn over is due to agent effects. However, our results suggest that turnover is caused at least partly by species with specific indicator values. This deviation from what we would expect under random species turnover is unlikely to be explained by species that remained undetected.

- *Empirical critical loads*: Our data on colonization and local survival (i.e. temporal variation) confirm the empirical critical loads that we inferred from analysing spatial co-variation of N deposition and species richness.

- *Space for time substitution*: Often observational studies infer the change of plant diversity along a gradient of N deposi- tion. Thus, they infer how the spatial variation in species richness is related to N deposition and assume that this spatial variation in species richness arose because over time some areas lost more species than others because they chronically experienced higher N deposition. Alt- hough there is evidence supporting the use of such a 'space for time substitution' for detecting the effects of N deposition on plant diversity (Stevens et al. 2010), they can not replace stud- ies that relate temporal patterns in species with N deposition (De Schrijver et al. 2011). While recovery of acidified surface waters has been well investigated (De Vries et al. 2015), there are only a limited number of studies inferring temporal trends of plant species diversity relat- ed to varying amounts of N-deposition. Storkey et al. (2015) demonstrated a positive response of biodiversity to reducing N addition from either atmospheric pollution or fertilizers in the Park Grass Experiment: ≪The proportion of legumes, species richness and diversity increased across the experiment between 1991 and 2012 as N-deposition declined≫. For forest floor vegetation in permanent plots across Europe the exceedance of critical loads of N over a peri- od from 9 to 42 years had negative effects on the cover of oligotrophic plant species, i.e spe- cies that prefer nutrient-poor soils, although species richness remained constant (Dirnböck et al. 2014). Another example of recovery in eutrophicated habitats gives the recovery of species richness in previously fertilized plots (Clark and Tilman 2008). In this study, the recorded recovery in species richness within one or two decade was likely due to the species rich vege- tation surrounding the experimental plots, from where immigration was easily feasible.

CONCLUSIONS

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