

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

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ABSTRACT

Nitrogen (N) deposition is a major threat to biodiversity of many habitats. The recent introduction of cleaner technologies in Switzerland has led to reductions in the emissions of nitrogen oxides, with affiliated decrease in Nitrogen deposition. We inferred 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 (N) deposition is a major threat to biodiversity. The recent introduction of cleaner technologies has led to reductions in the emissions of nitrogen oxides, with affiliated decrease in N-deposition in many parts of Europe. 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.

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).

Here we inferred mountain hay meadows in Switzerland. Explain why mountain hay meadows are important. Also explain other threats to mountain hay meadows (climate change, land-use change).

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 m² 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). For more details on the field methods see Plattner, Birrer, and Weber (2004), Roth et al. (2013) and Roth et al. (2017).

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). 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 within the same season) we calculated the following community measures: (1) The number of recorded species (species richness), (2) the community mean of the Ellenberg temperature values of recorded species (community temperature index), (3) the community mean of the Ellenberg humidity values of recorded species (community humidity index), (4) the community mean of the

Ellenberg nutrients values of recorded species (community nutrients index) and (5) the community mean of the Ellenberg light values of recorded species (community light index). The Ellenberg 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 heath 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 annual mean 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 mean 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 used. We expect that well-accessible sites become more intensively managed, whereas management intensity will rather decrease at remote sites (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 alpha-diversity 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)).

To infer whether species that colonized or disappeared from a site had particular Ellenberg 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 Ellenberg 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 Ellenberg 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 Ellenberg 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 Ellenberg 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 Ellenberg 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 Ellenberg value for Nutrients of the species and the interaction of these two variables. Additionally we 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

Table 1. Average measures of community structure for the three sampling periods (period 1: 2003-2007; period 2: 2008-2012; period 3: 2013-2017). The temporal trends are given as change per 10 years and were estimated from linear mixed models with normal distribution (except for alpha-diversity 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
Alpha-diversity	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
Humidity 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

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

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 N 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 that we 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 alpha-diversity and the average Ellenberg 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 Ellenberg 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 Ellenberg value for temperature (probability of increase: 0.97), followed by the community mean of the Ellenberg light value (probability of decrease: 0.93) and it was least likely for the alpha-diversity (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

Table 3. Difference in the average Ellenberg 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 disappeared/colonized species and random species as dependent variable and the sitemeasure (gradient) as predictor variable.

Ellenberg value	Gradient	Difference from random			Change along gradient		
		Estimate	5%	90%	Estimate	5%	90%
<i>(a) Plants that disappeared from a site</i>							
Temperature	Annual mean temperature	-0.012	-0.034	0.009	0.007	-0.002	0.016
Humidity	Annual mean precipitation	-0.006	-0.042	0.029	0.011	-0.010	0.032
Nutrients	Nitrogen deposition	-0.025	-0.059	0.010	0.013	-0.031	0.058
Light	Inclination	-0.023	-0.050	0.002	-0.003	-0.026	0.021
<i>(b) Plants that newly colonized a site</i>							
Temperature	Annual mean temperature	0.017	0.000	0.034	-0.001	-0.008	0.006
Humidity	Annual mean precipitation	0.019	-0.013	0.051	-0.002	-0.020	0.016
Nutrients	Nitrogen deposition	-0.076	-0.108	-0.045	0.060	0.023	0.098
Light	Inclination	-0.041	-0.063	-0.018	0.010	-0.010	0.029

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 Ellenberg 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 Ellenberg values of newly colonizing species differed more from random colonization than the Ellenberg values of disappearing species (Table 3). For colonizing species, we found the largest differences from random colonization in the Ellenberg value for nutrients: at sites with nitrogen deposition of $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ the newly colonizing species had in average a lower Ellenberg 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 N 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).

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 Ellenberg value for nutrients between colonizing species and random species. Nevertheless, the variation in Ellenberg 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 Ellenberg 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 where we present detailed results for the comparison between colonizing or disappearing species with randomly selected species.

Potential effects of reduction in Nitrogen emissions

In Fig. 1 we compare the colonization and local survival probability of oligotrophic (Ellenberg value of nutrients = 2) and eutrophic (Ellenberg value of nutrients = 4) species along the Nitrogen deposition gradient. Local survival probability was the same for oligotrophic and eutrophic species at a deposition rate of $11.66 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; colonization probability was the same for oligotrophic and eutrophic species at a deposition rate of $12.09 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. In only 0.36% of the sites the deposition rate was below $12.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ where the replacement of eutrophic with oligotrophic species is likely.

While we could not detect a consistent decrease in average Ellenberg 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

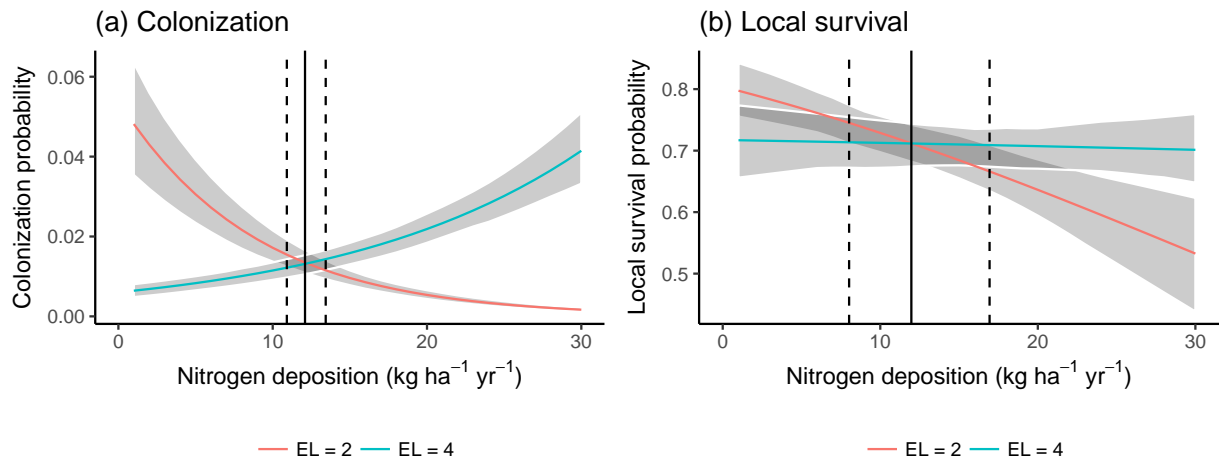


Figure 1. Colonization (a) and local survival (b) of oligotrophic (Ellenberg N = 2; red line) and eutrophic (Ellenberg N = 4) species along the N deposition gradient. Given are means and 95%-Credible Intervals from logistic linear mixed models. The vertical lines indicate the deposition rate with equal colonization or survival probabilities for oligotrophic and eutrophic species with the solid line indicating the median and the dashed lines the 5% and 95% quantiles of the marginal posterior distribution.

likely resulting in steeper slope of the negative relationship between N 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 N deposition on the spatial variation of species richness, the resulting effect size (i.e. the slope) becomes more negative over time (Fig. 2).

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.
- *Replacement of oligotrophic with eutrophic species is faster than the opposite 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. However, our results suggest that turnover is caused at least partly by species with specific Ellenberg values. These 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 deposition. 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. Although 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 studies 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 related 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

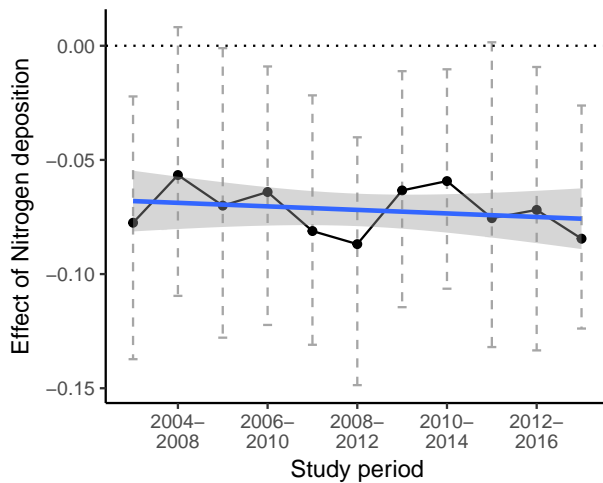


Figure 2. Effect size of Nitrogen deposition on total species richness estimated from applying the Poisson-GLM with species richness as dependent variable and Nitrogen deposition plus other site covariates as predictors using only the surveys from one five-year interval. Note that within every five-year interval all plots were sampled once.

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 period from 9 to 42 years had negative effects on the cover of oligotrophic plant species, i.e. species 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 vegetation surrounding the experimental plots, from where immigration was easily feasible.

CONCLUSIONS

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REFERENCES

- Beier, Claus, Carl Beierkuhnlein, Thomas Wohlgemuth, Josep Penuelas, Bridget Emmett, Christian Körner, Hans Boeck, et al. 2012. "Precipitation Manipulation Experiments—challenges and Recommendations for the Future." *Ecology Letters* 15 (8): 899–911.
- Davies, CE, D Moss, and MO Hill. 2004. "EUNIS Habitat Classification, Revised 2004. Report to European Environment Agency, European Topic Centre on Nature Protection and Biodiversity."
- Delarze, Raymond, and Yves Gonseth. 2008. *Lebensräume Der Schweiz: Ökologie - Gefährdung - Kennarten*. Ott. <https://books.google.ch/books?id=8kFrAAAACAAJ>.
- Fick, Stephen E, and Robert J Hijmans. 2017. "WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37 (12): 4302–15.
- Gelman, Andrew, and Yu-Sung Su. 2018. *Arm: Data Analysis Using Regression and Multilevel/Hierarchical Models*. <https://CRAN.R-project.org/package=arm>.
- Hillebrand, Helmut, Bernd Blasius, Elizabeth T. Borer, Jonathan M. Chase, John A. Downing, Britas Klemens Eriksson, Christopher T. Filstrup, et al. 2018. "Biodiversity Change Is Uncoupled from Species Richness Trends:

215 Consequences for Conservation and Monitoring.” *Journal of Applied Ecology* 55 (1): 169–84. doi:10.1111/1365-
 216 2664.12959.

217 Landolt, Elias, Beat Bäumler, Andreas Erhardt, Otto Hegg, Frank Klötzli, Walter Lämmli, Michael Nobis, et al.
 218 2010. *Flora Indicativa. Ecological Indicator Values and Biological Attributes of the Flora of Switzerland and the*
 219 *Alps*. Haupt Verlag.

220 Muth, Chelsea, Zita Oravecz, and Jonah Gabry. 2018. “User-Friendly Bayesian Regression Modeling: A Tutorial
 221 with Rstanarm and Shinystan.” *The Quantitative Methods for Psychology* 14 (2): 99–119.

222 Plattner, Matthias, Stefan Birrer, and Darius Weber. 2004. “Data Quality in Monitoring Plant Species Richness
 223 in Switzerland.” *Community Ecology* 5 (1): 135–43.

224 Rihm, Beat, and Daniel Kurz. 2001. “Deposition and Critical Loads of Nitrogen in Switzerland.” In *Acid Rain*
 225 *2000*, 1223–8.

226 Roth, Tobias, Lukas Kohli, Beat Rihm, and Beat Achermann. 2013. “Nitrogen Deposition Is Negatively Related
 227 to Species Richness and Species Composition of Vascular Plants and Bryophytes in Swiss Mountain Grassland.”
 228 *Agriculture, Ecosystems & Environment* 178: 121–26. doi:10.1016/j.agee.2013.07.002.

229 Roth, Tobias, Lukas Kohli, Beat Rihm, Reto Meier, and Beat Achermann. 2017. “Using Change-Point Models
 230 to Estimate Empirical Critical Loads for Nitrogen in Mountain Ecosystems.” *Environmental Pollution* 220: 1480–7.

231 Roth, Tobias, Matthias Plattner, and Valentin Amrhein. 2014. “Plants, Birds and Butterflies: Short-Term
 232 Responses of Species Communities to Climate Warming Vary by Taxon and with Altitude.” *PloS One* 9 (1): e82490.

233 Stan Development Team. 2016. “Rstanarm: Bayesian Applied Regression Modeling via Stan.” [http:](http://mc-stan.org/)
 234 [//mc-stan.org/](http://mc-stan.org/).

235 Strebel, Nicolas, and Christoph Bühler. 2015. “Recent Shifts in Plant Species Suggest Opposing Land-Use
 236 Changes in Alpine Pastures.” *Alpine Botany* 125 (1): 1–9.

237 Weber, Darius, Urs Hintermann, and Adrian Zangger. 2004. “Scale and Trends in Species Richness: Consid-
 238 erations for Monitoring Biological Diversity for Political Purposes.” *Global Ecology and Biogeography* 13 (2):
 239 97–104.