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

Tobias Roth[1, 2] and Lukas Kohli[2]

[1]**Zoological Institute, University of Basel, Basel, Switzerland**
[2]**Hintermann Weber AG, Austrasse 2a, 4153 Reinach, 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 (N) deposition is a major threat to biodiversity. The recent introduction of cleaner technologies has let 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 recovey 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 infered 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

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). Data collection was carried out by qualified botanists who visited each sampling site twice per 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).

In the present study, we analysed the 129 sampling sites in mountain hay meadows (EUNIS E2.3).

The sampling sites were circles with a size of 10 m^2 that were arranged on a regular sampling grid covering the whole of Switzerland. Each sampling site was surveyed once in each survey period: first survey period lasted from 2003 to 2007, the second from 2008 to 2012 and the third from 2013 to 2017.

- Selection of sample sites based on 1366 K_Standort.csv column "E23_1366". The site with exceptionally high nitrogen deposition was excluded from that list.
- Three surveys 2003 - 2007, 2008 - 2012 and 2013 - 2017.

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 alpha-diversity with Poisson distribution and a log-link function) with site-ID as random intercept and slope effect. The measure of precision for the temporal trend is given as the 5% and 95% quantiles of the marginal posterior distribution. Finally, the probability that the linear trend is > 0 is given. Linear mixed models were not applicable for beta-diversity because measures for beta-diversity were not available for the single sites.

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
Beta-diversity	0.60	0.60	0.60				
Temperature value	3.11	3.13	3.13	0.01	0.00	0.02	0.97
Huminity value	2.99	2.98	2.99	0.01	-0.01	0.02	0.78
Nutrients value	3.20	3.20	3.20	-0.01	-0.02	0.01	0.32
Light value	3.56	3.55	3.55	-0.01	-0.02	0.00	0.09

Community measures

To describe the plant communities we used the following measures:

- Species richness: number of recorded species per $10m^2$.
- Spatial turnover (beta-diversity): Average turnover between all pair-wise combinations of study plots.
- gamma diversity: Total number of species recorded in all study plots.
- The temporal turnover (i.e. species exchange ratio sensu Hillebrand et al. (2018)) is the proportion of species that differ between two time points calculated as

$$\text{Temporal turnover} = \frac{\text{Species gained}+\text{Species lost}}{\text{Total species observed in both timepoints}}.$$

Ellenberg values and gradients

Ellenberg indicator values:

- T: Temperature
- F: Huminity
- N: Nutrient contentent
- L: light

Gradients among studied sites:

- Mean annual temperature
- Mean annual precipitation
- Nitrogen deposition
- Inclination: The steaper the site the less intensive a site.
- Environmental variables were standardized.

Statistical analyses

- Comparision of colonizating and disappearing species with randomly selected species (refer to Appendix A).
- Gradient study applied at diffferent time steps (describe covariates used in Roth et al. (2013)).

RESULTS

Temporal change in community structures

The different measures of total 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- and beta-diversity and the average Ellenberg values for temperature, huminity, 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

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 with the proportion of species that differed between two surveys as dependent variable and the site gradients and period as predictors and site-ID as random effect.

Gradient	Estimate	5%	95%
Annual mean temperature	0.06	0.00	0.11
Annual mean precipitation	-0.02	-0.11	0.08
Nitrogen deposition	-0.20	-0.35	-0.05
Inclination	-0.04	-0.10	0.03

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 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	-0.034	0.009	0.007	-0.002	0.016
Humidity	Annual mean precipitation	-0.003	-0.038	0.033	0.008	-0.012	0.029
Nutrients	Nitrogen deposition	-0.012	-0.052	0.028	0.000	-0.046	0.046
Light	Inclination	-0.022	-0.047	0.004	-0.002	-0.024	0.022
(b) Plants that newly colonized a site							
Temperature	Annual mean temperature	0.018	0.001	0.034	-0.001	-0.008	0.006
Humidity	Annual mean precipitation	0.023	-0.010	0.054	-0.004	-0.023	0.014
Nutrients	Nitrogen deposition	-0.082	-0.117	-0.048	0.062	0.024	0.102
Light	Inclination	-0.039	-0.062	-0.016	0.010	-0.009	0.031

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: 0.91) 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 0.68.

Different drivers of 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: -0.15 - -0.02). 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 inportant 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 differened 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 kg ha^{-1} yr^{-1} the newly colonizing species had in average a

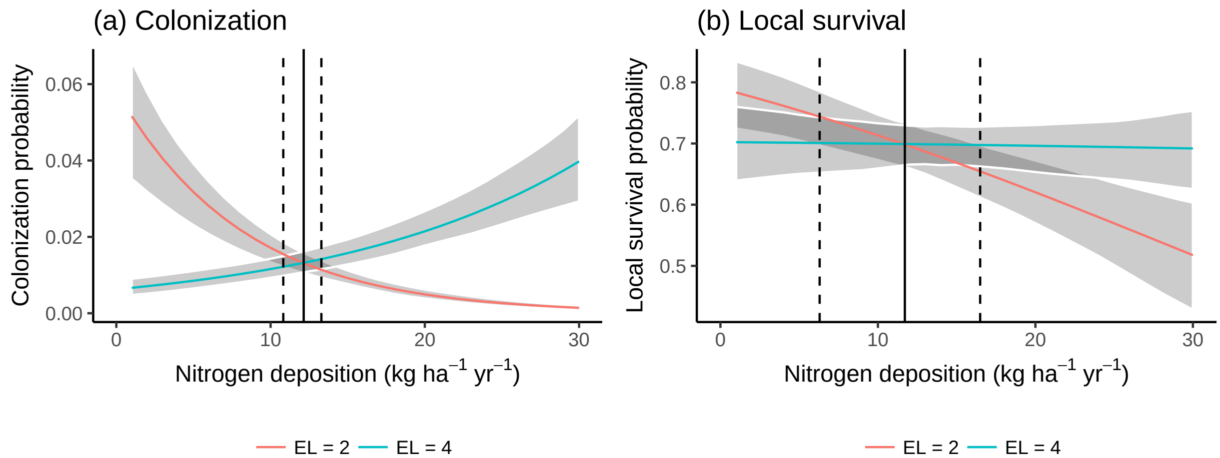

Figure 1. Colonization (a) and local survival (b) of oligotrophic (Ellenberg N = 2; red line) and eutrophic (Ellengerg N = 4) species along the N deposition gradient. Given are means and 95%-Credible Intervals from logistic linear mixed models. The vertical lines indicat the deposition rate with equal 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.

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 impportant 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 hihger 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 were we present detailed results for the comparision between colonizing or disappearing species with randomly selected species.

Potential effects of reduction in Nitrogen emmissions

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 euthrophic species at a deposition rate of 11.89 kg N ha^{-1} yr^{-1}; colonization probability was the same for for oligotrophic and euthrophic species at a deposition rate of 12.15 kg N ha^{-1} yr^{-1}. In only 0.30% of the sites the deposition rate was below 11.5 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 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 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*: Altough N deposition considerabely declinded between 2005 and 2015, we could not detect major shifts in plant community structure during the same time period.

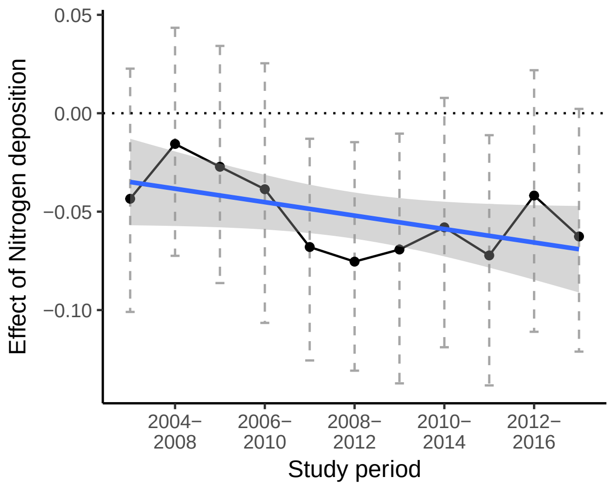

Figure 2. Effect size of Nitrogen deposition on total species richness estimated from applying the Poisson-GLM with species richness as dependend variable and Nitrogen deposition plus other site covariates as predictors using only the surveys from one five-year interval. Note that within every five-year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

- *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 thant 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 infered from anlysing 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

xxx

ACKNOWLEDGEMENTS

We thank the dedicated and qualified botanists who conducted fieldwork. The Swiss Federal Office for the Environment (FOEN) kindly provided biodiversity monitoring data and topographic data. This work was supported by the FOEN, the Swiss National Science Foundation (grant no. 31003A_156294), the Swiss Association Pro Petite Camargue Alsacienne, the Fondation de bienfaisance Jeanne Lovioz, and the MAVA Foundation.

REFERENCES

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." *Google Scholar*.

Delarze, Raymond, and Yves Gonseth. 2008. *Lebensräume Der Schweiz: Ökologie - Gefährdung - Kennarten*. Ott. `https://books.google.ch/books?id=8kFrAAAACAAJ`.

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

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

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

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

Weber, Darius, Urs Hintermann, and Adrian Zangger. 2004. "Scale and Trends in Species Richness: Considerations for Monitoring Biological Diversity for Political Purposes." *Global Ecology and Biogeography* 13 (2): 97–104.