

No sign of recovery

Tobias Roth^{1, 2} and Lukas Kohli²

¹Zoological Institute, University of Basel, Basel, Switzerland

²Hintermann 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 led to reductions in the emissions of nitrogen oxides, with affiliated decrease in N-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. Species gain and losses were best explained by differences in Ellenberg value for temperature suggesting that climate warming was the most important driver of community change in Mountain hay meadows.

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).

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

- Selection of sample sites based on 1366 K_Standort.csv column "E23_1366".
- Three surveys 2003-2007, 2008-2012 and 2013 - 2017.

Plant traits

Functional traits:

- SLA: specific leaf area
- CH: canopy height
- SM: Seed mass

Ellenberg indicator values:

- L: light
- N: Nutrient content
- T: Temperature
- F: Humidity

Community measures:

- Species richness: number of recorded species per 10m².
- 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.

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
Humidity 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

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

Community measures

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

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

Statistical analyses

Environmental variables were standardized.

RESULTS

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 consistent 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, 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 for an increase: 0.97), followed by the community mean of the Ellenberg light value (probability for a decrease: 0.91) and it was least likely for the alpha-diversity (probability for an increase: 0.53). The chance that the community mean of the nutrient value decreased between 2003 and 2017 was 0.68.

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

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	-0.003	-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
<i>(b) Plants that newly colonized a site</i>							
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

the Binomial generalized linear mixed model that also contained site variables: -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 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 from random disappearance (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 decreases 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 be expected 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 randomly disappearing species leading 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: it was also species with lower nutrients values that tended to be more likely to disappear than randomly disappearing species (Table 3). See also Appendix A where we present detailed results for the comparison between colonizing or disappearing species with randomly selected species.

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. Colonization probability is the same

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 affects the spatial variation of species richness: sites with low Nitrogen deposition become more species rich over time resulting in steeper slope of the negative relationship between N deposition and species richness. Consequently, if we apply a model as in Roth et al. (2013) to infer the effects of N deposition on the spatial variation of species richness at different time points, the resulting effect size (i.e. the slope) becomes more negative over time (Fig. 2).

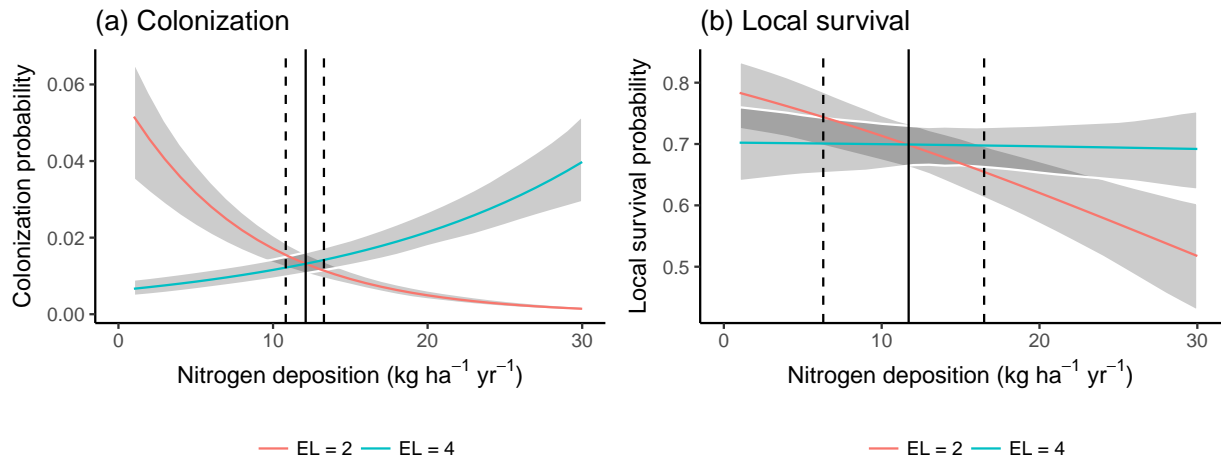


Figure 1. Colonization (a) and local survival (b) of oligotrophic (Ellenberg N = 2; red line) and eutrophic (Ellenberg N = 4) species along the N deposition gradient. Given are means and 95%-Credible Intervals from logistic linear mixed models.

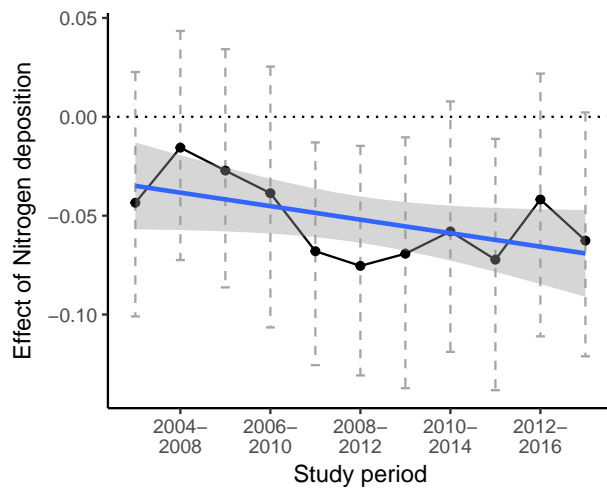


Figure 2. Effect size of Nitrogen deposition on total species richness estimated from applying the Poisson-GLM with species richness as dependend variable and Nitrogen deposition plus other site covariates as predictors using only the surveys from a five-year interval. Within every five-year interval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

DISCUSSION

- Any empty space that could be caused by any disturbance that led to the local disappearance of species is likely to be filled by eutrophic species. Disturbance depends on the site, while colonization depends on species characteristics.
- The rather large spatial turnover might be partly explained by species that remained undetected in one of the surveys, but it might also be the result of species that newly colonized sites (species gains) and species that truly disappeared from sites (species losses).
- Although N deposition considerably declined between 2005 and 2015, we could not detect major shifts in plant community structure during the same time period.
- 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 much more time to replace eutrophic by oligotrophic species than replacing oligotrophic by eutrophic species.
- 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.
- Local survival is higher for low temperature plants → This could explain the decrease in community change along elevation. This could also explain the differences at mount summits where space was empty in the beginning.
- Climatic effects are more likely to be reversed than effects due to fertilization.

0.0.1 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 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 decades was likely due to the species rich vegetation surrounding the experimental plots, from where immigration was easily feasible.

Hier sagen, dass der CRL identisch wie der CRL von räumlichen Zusammenhängen ist.

CONCLUSIONS

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REFERENCES

- 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.
- Roth, Tobias, Lukas Kohli, Beat Rihm, and Beat Acherhmann. 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.