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 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 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). 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 criterias resulted in sample of 129 sites.

For each survey (a survey conists 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

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). 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
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

43 Ellenberg nutrients values of recorded species (community nutrients index) and (5) the community mean of the
44 Ellenberg light values of recorded species (community light index). The Ellenberg values were obtained from
45 the recalibrated indicator values for the Swiss Flora (Landolt et al. 2010). Additionally to these five community
46 measures that describe the state of plant communities for each site at a given time point, we also estimated the
47 temporal turnover (i.e. species exchange ratio sensu Hillebrand et al. (2018)) as the proportion of species that differ
48 between two time points to describe the community change between two time points.

Environmental gradients
50 • Mean annual temperature
51 • Mean annual precipitation
52 • Nitrogen deposition
53 • Inclination: The steeper the site the less intensive a site.
54 • Environmental variables were standardized.

Statistical analyses
56 To estimate the linear trend over time for each of the five community measures we applied linear mixed models with
57 normal distribution (except for alpha-diversity with Poisson distribution and the logoraithm as link function). We
58 used the year as predictor variable and site-ID as random intercept and slope variable to account for the fact that
59 every site was sampled three times. Model parameters were estimated in a Bayesian framework using the R-Package
60 *rstanarm* (Stan Development Team 2016, Muth, Oravecz, and Gabry (2018)).

61 • Comparision of colonizating and disappearing species with randomly selected species (refer to Appendix A).

62 To estimate the effect of N deposition at a given time point . We described the plant species richness at the
63 sites using a generalized linear model with Poisson distribution and the logarihm as link function. The selection
64 of predictor variables was based on an earlier study in Swiss mountain grasslands (Roth et al. 2013). Except for
65 N deposition we thus used elevation (linear and squared term), inclination (linear and squared term), mean annual
66 precipitation (linear and squared term), pH, average moisture value, average light value and the aspect. For the
67 analyses the variables were standardized.

RESULTS

Temporal change in community structures
70 The five measures of plant community structure suggested that plant communities in mountain hay meadows were
71 rather stable between 2003 and 2017 and did not show a clear increase or decrease over time (Table 1): for each of
72 the three 5-year survey periods the averages of alpha-diversity and the average Ellenberg values for temperature,
73 huminity, nutrients and light did not vary much among the three sampling periods and the estimated trends were
74 rather small. Except for average Ellenberg value for temperature, the 90% credible-interval of the temporal trend
75 contained zero. The results from the linear mixed models suggest that a linear temporal change was most likely for the
76 community mean of the Ellenberg value for temperature (probability of increase: 0.97), followed by the community
77 mean of the Ellenberg light value (probability of decrease: 0.93) and it was least likely for the alpha-diversity

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

78 (probability of increase: 0.53). The chance that the community mean of the nutrient value decreased between 2003
79 and 2017 was 0.67.

80 **Different drivers of species turnover**
81 This temporal stability as inferred from the community measures was, however, in contrast to a rather large observed
82 temporal turnover of species. The average percentage $\pm$ SD of species that differed between the first and second
83 survey at a site was NaN $\pm$ NA% and the percentage of species that differ between the second and third survey was
84 NaN $\pm$ NA%. Thus, it seemed that the turnover from the first/second survey to the turnover of the second/third survey
85 moderately decreased (90% Credible interval of the change in turnover estimated from the Binomial generalized
86 linear mixed model: -0.15 - -0.02). Variation in species turnover was largest along the Nitrogen deposition gradient
87 with highest species turnover at sites with low Nitrogen deposition (Table 2). The other three gradients were less
88 inportant to explain the variation in species turnover among sites.
89   High species turnover at a site is the result of species that disappeared from the site and species that newly
90 colonized the site. To better understand the factors that drive these changes we are particularly interested whether
91 the species that disappeared or colonized the sites differed in Ellenberg values compared to what would be expected
92 if the same number of species randomly disappeared or colonized the sites (i.e. random disappearance and random
93 colonization) and whether there is a change along the gradients. It seems that the Ellenberg values of newly
94 colonizing species differened more from random colonization than the Ellenberg values of disappearing species
95 (Table 3). For colonizing species, we found the largest differences from random colonization in the Ellenberg value
96 for nutrients: at sites with nitrogen deposition of 10 kg ha^{-1} yr^{-1} the newly colonizing species had in average a
97 lower Ellenberg value for nutrients than species under random disappearance (column "Difference from random"
98 in Table 3), but this differences between colonizing species and random colonization decreased with increasing N
99 deposition (column "Change along gradient" in Table 3). Thus at high Nitrogen deposition colonizing species did
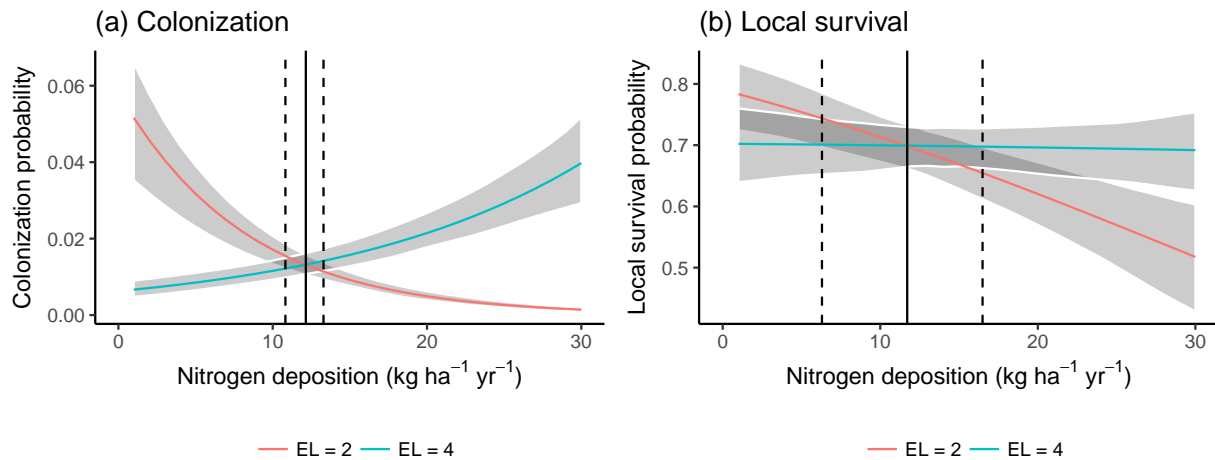
Figure 1. Colonization (a) and local survival (b) of oligotrophic (Ellenberg N = 2; red line) and eutrophic (Ellengerg N = 4) species along the N deposition gradient. Given are means and 95%-Credible Intervals from logistic linear mixed models. The vertical lines indicate the deposition rate with equal colonization or survival probabilities for oligotrophic and eutrophic species with the solid line indicating the median and the dashed lines the 5% and 95% quantiels of the marginal posterior distribution.

100   not differ from random species (see Figure 3b in Appendix A).

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

Potential effects of reduction in Nitrogen emmissions

112   In Fig. 1 we compare the colonization and local survival probability of oligotrophic (Ellenberg value of nutrients =
113   2) and eutrophic (Ellenberg value of nutrients = 4) species along the Nitrogen deposition gradient. Local survival
114   probability was the same for oligotrophic and euthrophic species at a deposition rate of 11.89 kg N ha^{-1} yr^{-1};
115   colonization probability was the same for for oligotrophic and euthrophic species at a deposition rate of 12.15 kg N
116   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
117   eutrophic with oligotrophic species is likely.

118   While we could not detect a consistent decrease in average Ellenberg value for nutrients (Table 1), the higher
119   colonization rate of species with low nutrient value at sites with low deposition rate seems to affect the spatial
120   variation of species richness: sites with low Nitrogen deposition are likely to become more species rich over time
121   likely resulting in steeper slope of the negative relationship between N deposition and species richness. Indeed, if
122   we apply at different time points a similar model as in Roth et al. (2013) to infer the effects of N deposition on the
123   spatial variation of species richness, the resulting effect size (i.e. the slope) becomes more negative over time (Fig.
124   2).

DISCUSSION

126   • *General points*: Altough N deposition considerabely declinded between 2005 and 2015, we could not detect
127   major shifts in plant community structure during the same time period.

128   • *Replacement of oligotrophic with eutrophic species is faster than the oposite direction*: Eutrophic species have
129   rather high local survival across the entire deposition gradient, while oligotrophic species have much reduced
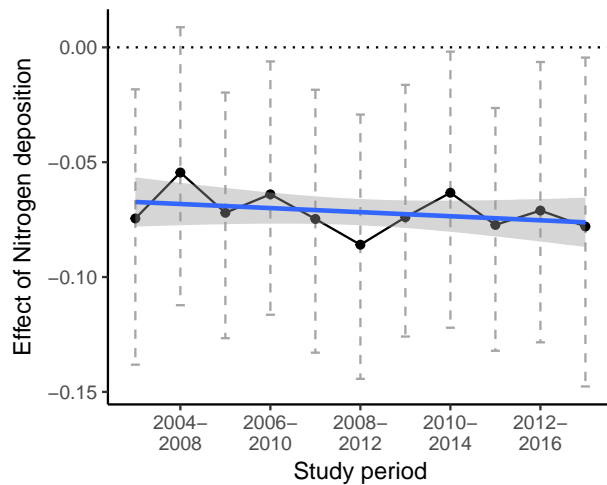
Figure 2. Effect size of Nitrogen deposition on total species richness estimated from applying the Poisson-GLM with species richness as dependend variable and Nitrogen deposition plus other site covariates as predictors using only the surveys from one five-year interval. Note that within every five-year interval all plots were sampled once.

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

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ACKNOWLEDGEMENTS

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