Species turnover reveals hidden effects of decreasing Nitrogen deposition in mountain hay meadows

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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 inferred different drivers of community change (i.e. Nitrogen deposition, climate warming, land-use change) in Swiss mountain hay meadows using data from the Swiss biodiversity monitoring. While oligotrophic species were more likely to colonize compared to random expectation, we found only weak shifts in plant community structure. Particularly, the average nutrient value of plant communities remained stable over time. Apparently, the community effects of the replacement of eutrophic species with oligotrophic species was outweighed by climate warming. Our results add to the increasing evidence that inferring species turnover will generate a far more reliable understanding of the biotic response to changing environments than solely tracking average community composition.

INTRODUCTION

Nitrogen deposition is the entry of reactive nitrogen compounds into water and soil via deposition through the air. Since Nitrogen is an essential plant nutrient and many species-rich communities are adapted to conditions of low Nitrogen availability (Vitousek et al. 1997), the addition of Nitrogen is likely to alter these communities. Indeed, Nitrogen deposition together with land-use and climate change is one of the major threats to biodiversity (Sala et al. 2000; Bobbink et al. 2010). While there is strong evidence for the reduction in diversity of species-rich grasslands due to increased Nitrogen deposition (Stevens et al. 2004; Duprè et al. 2010; Maskell et al. 2010; Wesche et al. 2012), mountain grasslands have received less attention (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; Fowler et al. 2007). However, there are a number of factors that may prevent the recovery of plant communities that suffered from increased Nitrogen deposition. First, even if Nitrogen deposition is reduced, large areas might still be above the critical load (Slootweg, Posch, and Hettelingh 2015; Rihm and Achermann 2016). Second, there is a potential that communities reach an alternative stable state after decades of increased Nitrogen deposition and these species are unlikely to disappear again after the reduction of Nitrogen deposition (Stevens 2016). Therefore, it is an open question whether and how fast the reduction in Nitrogen deposition rates will lead to the recovery of extant plant communities.

Recovery of extant plant communities from high Nitrogen deposition would imply that the state of communities measured at different time points is improving over time (i.e. improving biodiversity endpoints sensu Rowe et al. (2017)). Species richness is an easy to measure and communicate biodiversity endpoint and it is often negatively

correlated with Nitrogen deposition (Maskell et al. 2010; Field et al. 2014; Rowe et al. 2017). Other metrics that are potentially more useful to reflect favourable changes can be derived from the traits of the species in a community. In Europe, environmental preference has often been expressed using indicator values assigned to each plant species (Ellenberg et al. 1992). Examples of such metrics would be the number of oligotrophic species or the average indicator value of the species in a community (Roth et al. 2013; Rowe et al. 2017). However, the lack of a temporal trend in such biodiversity endpoints – particularly in species richness – does not necessarily mean that species composition remains unchanged. This is because immigration and extinction might be equally frequent and may cancel each other out (Hillebrand et al. 2018). Thus a useful approach to understanding biodiversity change is through estimates of biodiversity turnover reflecting both colonization and local extinction (Hillebrand et al. 2018), especially if colonization and local extinction is compared to random expectation (Chase and Myers 2011).

In Switzerland, grassland accounts for 70% of the agricultural land. With extensive cultivation, permanent grassland has a very high biodiversity. This applies in particular to the meadows in the alpine region, where meadows with a high plant diversity are also of importance agronomically (Leiber et al. 2006). In mountain hay meadows, the spatial variation of species richness in vascular plants is negative correlated with Nitrogen deposition (Roth et al. 2013), suggesting that mountain grasslands suffered from increased Nitrogen deposition. However, between 1990 and 2010 NO_x emissions in Switzerland decreased by 46% and NH_3 emissions by 14% (Maas and Grennfelt 2016) and we expect plant communities to recover.

However, Swiss mountain ecosystems are threatened also by other global change drivers. In Switzerland, temperatures increased from 1959 to 2008 at all altitudes, with an average warming rate of 0.35°C per decade, which is about 1.6 times the northern hemispheric warming rate (Ceppi et al. 2012). This climate warming is likely to directly affect or interact with Nitrogen deposition to drive plant community changes (Humbert et al. 2016). Indeed, in an earlier study we found that at the landscape scale plant communities responded to climate warming even within a comparably short time period (Roth, Plattner, and Amrhein 2014) and particularly the shift of plant communities at mountain summits are the result of recent climate warming interacting with airborne nitrogen deposition (Steinbauer et al. 2018). Furthermore, traditional management regimes are currently changing, which also has major impacts on plant communities in mountainous regions of Europe (Niedrist et al. 2009; Homburger and Hofer 2012). Management regimes of accessible mountainous areas are frequently intensified, while poorly accessible mountainous areas are being abandoned (Tasser and Tappeiner 2002; Strebel and Bühler 2015).

Here, we used the data from the Swiss biodiversity monitoring (Weber, Hintermann, and Zangger 2004) and addressed the following questions: (1) Did biodiversity endpoints that are likely to reflect temperature, precipitation, Nitrogen deposition or land-use intensity change over the last 15 years, (2) was species turnover correlated with the average temperature, precipitation, Nitrogen deposition or inclination (we expect steep areas to be less intensively managed), and (3) did species that newly colonized or disappeared (local extinction) from sites differ from random expectation according to their indicator values for temperature, humidity, nutrients or light.

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

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). 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 biodiversity endpoints (Rowe et al. 2017): (1) The number of recorded species (species richness), the community mean of indicator values of recorded species for (2) temperature, (3) humidity, (4) nutrients and (5) light. The indicator values were obtained from the recalibrated indicator values for the Swiss Flora (Landolt et al. 2010). Additionally, to these five biodiversity

endpoints 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.

To test data quality, independent replicate surveys are routinely performed within the BDM program by botanists who were not involved in the regular BDM surveys. The regular surveyors did not know if and which sites were replicated (Plattner, Birrer, and Weber 2004). We used the data from 14 such replicated surveys that were available to calculate the pseudo-turnover, which is the proportion of species that differed between two surveys that were conducted by two different surveyors during the same year on the same site.

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 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 Nitrogen 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 Nitrogen deposition see also Rihm and Achermann (2016) 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 biodiversity endpoints we applied linear mixed models (LMM) with normal distribution except for species-richness with Poisson distribution. 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, Gelman and Hill 2006). 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 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 values of colonizing species were lower than the indicator values of 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 if they were observed or not observed (then Occ = 0) during the third 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

Table 1. Average measures of the biodiversity endpoints 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
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

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 (i.e. biodiversity endpoints) 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 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

The average $\pm$ SD percentage of species that differed between replicated surveys was $28.96 \pm 8.43\%$. This pseud-turnover was lower than the observed temporal turnover: the average percentage 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

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 disappeared/colonized species and random species as dependent variable and the site-measure (gradient) as predictor variable.

Ellenberg value	Gradient	Difference from random			Change along 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

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 were 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 spatial variation 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).

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 where 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 (Fig. 1a). In 2000 only 11.63% 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 2015 the Nitrogen deposition decreased in average -2.70 $\pm$ 1.74 kg N ha^{-1} yr^{-1} with slightly higher net decreases at lower elevation (Fig. 1a).

In Fig. 2 we compare the colonization and local survival probability of oligotrophic (indicator value of nutrients <3) and eutrophic (indicator value of nutrients > 3) species along the Nitrogen deposition gradient. Local survival probability was the same for oligotrophic and euthrophic species at a deposition rate of 13.07 kg N ha^{-1} yr^{-1}; colonization probability was the same for oligotrophic and eutrophic species at a deposition rate of 12.41 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
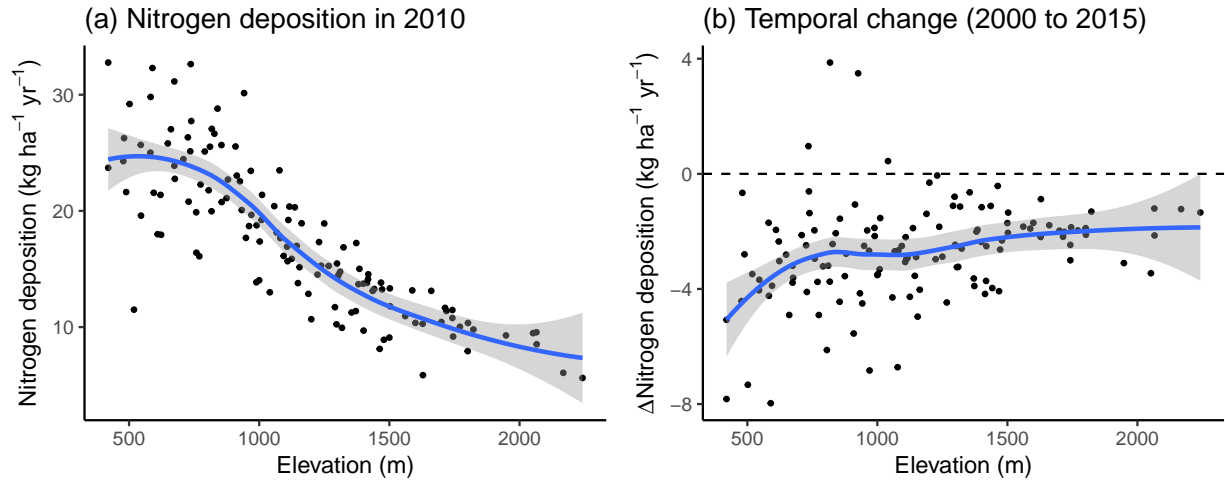
Figure 1. (a) The nitrogen deposition in 2000 and (b) the change in Nitrogen deposition between 2000 and 2015 along the elevational gradient of the study sites.
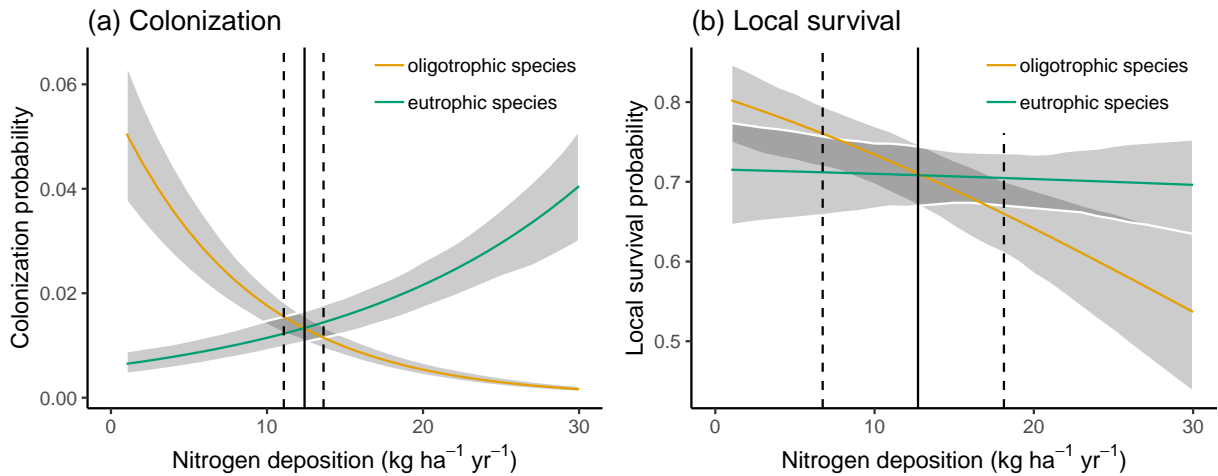
Figure 2. Colonization (a) and local survival (b) of oligotrophic (indicator value for nutrients < 3; red line) and eutrophic (indicator value for nutrients > 3) species along the Nitrogen deposition gradient. Given are means and 95%-Credible Intervals from logistic linear mixed models. The vertical 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.
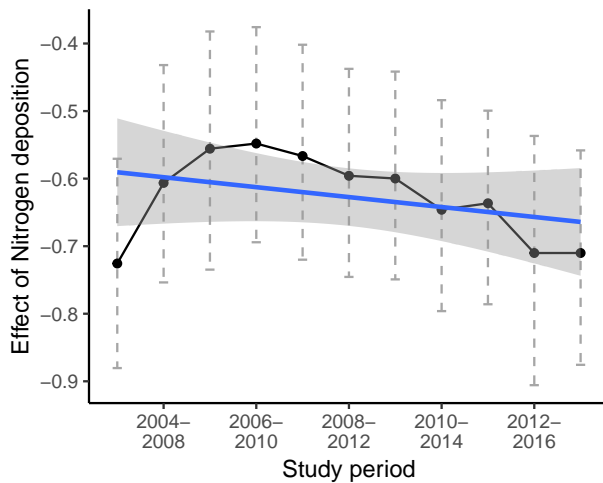
Figure 3. Effect size of Nitrogen deposition on oligotrophic species richness estimated from applying the Poisson-GLM with species richness as dependent variable and Nitrogen deposition plus other site covariates as predictors using only the surveys from one five-year interval. Note that within every five-year interval all plots were sampled once.

215 eutrophic with oligotrophic species is likely.

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

DISCUSSION

224 Although Nitrogen deposition considerably declined between 2000 and 2015 (Fig. 1), we could detect only weak
225 shifts in plant community structure (i.e. biodiversity endpoints sensu Rowe et al. (2017)) during the same time
226 period (Table 1). While the slight increase in average temperature value suggests that plant communities adopted
227 to increasing temperatures, the constant average nutrients value suggests that the decrease in Nitrogen deposition
228 did not yet affect plant communities. However, this apparent stability in community structure was accompanied by
229 marked temporal turnover in species identities. It seems unlikely that this temporal turnover can entirely be explained
230 by methodological issues such as overlooked species. First, pseudo-turnover of species entities in independent
231 surveys of the same site during the same season was smaller than the observed temporal turnover between two
232 surveys from different years. Second, spatial variation of turnover showed patterns that can hardly be explained by
233 methodological issues. For instance species turnover varied along the Nitrogen deposition gradient with highest
234 species turnover at sites with low Nitrogen deposition (Table 2). Taken together, our results add to the increasing
235 evidence that contemporary communities are often relatively stable at community level, but this apparent stability is
236 often accompanied by marked turnover of species (Vellend et al. 2013; Dornelas et al. 2014; Hillebrand et al. 2018).

237   Species communities are shaped by a range of factors, including deterministic processes such as environmental
238 filtering or competitive interactions (Götzenberger et al. 2012; Janeček et al. 2013). Such factors select for species
239 with specific characteristics. Community assembly theories thus suggest that the factors that drive the composition
240 of species in a community can be inferred from comparing the characteristics of the species in the community with
241 random expectation (Chase and Myers 2011). We adopted this idea and compared the indicator values of species
242 that disappeared or colonized a site with the indicator values from randomly chosen species from the same site
243 (Appendix A). We found that the nutrient values of colonization species showed largest deviations from random
244 expectation suggesting that Nitrogen deposition or other factors that change the nutrient content of soils were the
245 most important drivers of the change in species composition over the last 15 years in Swiss mountain hay meadows.

246   Nitrogen deposition at our plots decreased by -2.70 kg ha^{-1} yr^{-1} on average between 2000 and 2015. This is

only about one tenth of the decrease in England, where Nitrogen deposition decreased by 24 kg ha^{-1} yr^{-1} from 1996 to 2011 (Storkey et al. 2015). This comparatively low change in Nitrogen deposition in Swiss mountain hay meadows might explain why we observed no change in average nutrient value of communities. Additionally, other anthropogenic pressures such as climate change might have overruled Nitrogen depositing effects on community structure. Particularly, we found that the species disappearing from the sites tend to have below average indicator values for temperature, while species that newly colonize sites have above average indicator values for temperature (Table 3). Thus, the effect of disappearing and the effect of colonizing species on the community mean for temperature is additive resulting in increasing average temperature values (Tab. 1). This is in contrast to how Nitrogen deposition is affecting disappearing and colonization of species: It seems that both species disappearing from the sites as well as species colonizing the sites tend to have below average indicator values for nutrients (Table 3). Thus, the effect of disappearing and colonizing species on the average community value for nutrients partially cancel each other out. Furthermore, eutrophic species had rather high local survival across the entire deposition gradient, while oligotrophic species have much reduced local survival at higher Nitrogen deposition rates. This suggests that mountain hay meadow communities can reach alternative stable states with eutrophic species that are unlikely to disappear even if Nitrogen deposition is reduced (Stevens 2016). Taken together, these reasons might explain why the response of mountain hay meadow communities responded stronger to climate warming than to Nitrogen reduction, although the reduction in Nitrogen resulted in above average colonization of oligotrophic species.

Observational studies along a gradient of Nitrogen deposition often infer how the spatial variation in species richness is related to Nitrogen deposition (Stevens, Thompson, et al. 2010; chapter 4 in Vries, Hettelingh, and Posch 2015). They assume that the spatial variation in species richness (or other metrics of community structure) arose because over time some areas lost more species than others because they chronically experienced higher Nitrogen deposition. Although there is evidence supporting the use of such a 'space for time substitution' for detecting the effects of Nitrogen deposition on plant diversity (Stevens, Duprè, et al. 2010), they can not replace studies that relate temporal patterns in species with Nitrogen deposition (De Schrijver et al. 2011). There are only a limited number of studies inferring temporal trends of plant species diversity related to varying amounts of Nitrogen deposition in extant communities (Clark and Tilman 2008; Storkey et al. 2015; Stevens 2016). In a recent study, we used the mountain hay meadow data from a single survey only and estimated the critical load along the Nitrogen deposition gradient at which species richness of oligotrophic species richness start to decrease with increasing Nitrogen deposition (Roth et al. 2017). Using this spatial variation in species richness and nitrogen deposition we estimated a critical load for mountain hay meadows of 13.1 kg ha^{-1} yr^{-1}. In the current study we estimated the rate of Nitrogen deposition at which local survival probability or colonization probability was equal for oligotrophic and eutrophic species. This rate could also be interpreted as a critical load. With this temporal approach we obtained very similar results as the spatial approach. Our results are thus validating the space for time approach, at least for Swiss mountain hay meadows.

However, the results of Fig. 3 also shows that the results of spatial comparisons must be interpreted carefully. When we used the same model to infer how oligotrophic species richness is decreasing along the Nitrogen deposition gradient at different time points, except for the first two study periods the decrease became steeper (more negative) over time. Our first interpretation was that the Nitrogen deposition effect became stronger over time. This contradicted our prediction that the Nitrogen deposition should become weaker over time since Nitrogen deposition decreased. Only then we realized that species turnover was highest in low deposition sites (Tab. 2) where the colonizing species were species with below average indicator values for Nutrients. It seems that the decrease in Nitrogen deposition resulted in oligotrophic species replacing eutrophic species especially at sites with low deposition, thus leading to a steeper spatial decline in oligotrophic species richness from sites with low to sites with high Nitrogen deposition. The increasingly steeper decline over time in the eutrophic species richness along the spatial Nitrogen deposition gradient is thus a sign of the recovery of plant communities in low deposition sites rather than a sign that the negative Nitrogen deposition effects became stronger over time.

CONCLUSIONS

Comparing the indicator values of colonizing and disappearing species with random expectation we found that oligotrophic species are currently more likely to colonize mountain hay meadows than oligotrophic species, which might be the results of the recently decreasing atmospheric Nitrogen deposition. However, our results also caution that re-transferring mountain hay meadows to oligotrophic species communities after high nitrogen deposition might take much longer than transferring an oligotrophic into an eutrophic community. This is because eutrophic species have high local survival probabilities also when Nitrogen deposition becomes lower again. All these results were, however, hidden when only inferring the temporal trends of species communities. Our study thus adds to the

understanding of contemporary biodiversity change that is currently not well understood (Magurran et al. 2018), and it supports the notion of Hillebrand et al. (2018) that inferring species turnover will generate a far more reliable understanding of the biotic response to changing environments than solely tracking community composition.

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