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Currently legislated decreases in nitrogen deposition will yield only limited plant species recovery in European forests

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Keywords: LTER, forest ecosystem, air pollution, modelling, climate change, LRTAP Convention

Supplementary material for this article is available online

Abstract

Atmospheric nitrogen (N) pollution is considered responsible for a substantial decline in plant species richness and for altered community structures in terrestrial habitats worldwide. Nitrogen affects habitats through direct toxicity, soil acidification, and in particular by favoring fast-growing species. Pressure from N pollution is decreasing in some areas. In Europe (EU28), overall emissions of NO_x declined by more than 50% while NH_3 declined by less than 30% between the years 1990 and 2015, and further decreases may be achieved. The timescale over which these improvements will affect ecosystems is uncertain. Here we use 23 European forest research sites with high quality long-term data on deposition, climate, soil recovery, and understory vegetation to assess benefits of currently legislated N deposition reductions in forest understory vegetation. A dynamic soil model coupled to a statistical plant species niche model was applied with site-based climate and deposition. We use indicators of N deposition and climate warming effects such as the change in the occurrence of oligophilic, acidophilic, and cold-tolerant plant species to compare the present with projections for 2030 and 2050. The decrease in N deposition under current legislation emission (CLE) reduction targets until 2030 is not expected to result in a release from eutrophication. Albeit the model predictions show considerable uncertainty when compared with observations, they indicate that oligophilic forest understory plant species will further decrease. This result is partially due to confounding processes related to climate effects and to major decreases in sulphur deposition and consequent recovery from soil acidification, but shows that decreases in N deposition under CLE will most likely be insufficient to allow recovery from eutrophication.

Introduction

Human emissions of reactive Nitrogen (N) have caused numerous environmental problems (Gruber and Galloway 2008). Excess deposition of reduced and oxidized N is considered responsible for a substantial decline in plant species richness (Bobbink *et al* 2010). N-related changes in forest understory plant species composition and loss are driven by increased N availability in N-poor conditions or indirect effects from altered tree stand cover and litter N content (Gilliam 2006, Dirnböck *et al* 2014, Simkin *et al* 2016). Although there has been recovery from acidification (Cools and De Vos 2011, Johnson *et al* 2018) in response to large reductions in sulphur (S) emissions, this recovery has been slowed by the acidifying effects of N deposition and the simultaneous decrease in base cation deposition in some regions (Hedin *et al* 1994, Johnson *et al* 2018). N deposition rates are decreasing, but remain too high in many countries across Europe (EMEP 2017) with respect to the deposition thresholds (critical loads) used to describe the sensitivity of ecosystems to air-borne pollution (Amann *et al* 2011, Amann *et al* 2018). In Europe (EU28), overall emissions of NO_x declined by more than 50% while NH_3 declined by less than 30% between the years 1990 and 2015 (EMEP 2017). A further decrease in N deposition can be achieved in Europe with emission reduction requirements under the EU National Emission Ceilings Directive (2016/2284/EU). Since these measures can be costly, policymakers require assessments of their potential benefits for ecosystems. These have mainly been quantified through assessing reduced future exceedances of ecosystem-specific critical loads (De Vries *et al* 2015) and show that measures would still leave more than 50% of the area of the EU Natura2000 nature protection zones at risk (Amann *et al* 2018). Studies investigating the potential benefits for biodiversity taking into account lags in soil recovery are just emerging (Storkey *et al* 2015). Also studies addressing climate change as a factor influencing recovery from soil acidification as well as plant available N through its impact on decomposition and N mineralization are rare (Bernal *et al* 2012, Butler *et al* 2012, McDonnell *et al* 2014, Gaudio *et al* 2015, Rizzetto *et al* 2016, Dirnböck *et al* 2017). This highlights a critical need for further research and continuous observation to appreciate the biodiversity benefit of reduced N deposition in European forests (Schmitz *et al* 2019).

Some evidence exists that forest understory vegetation has responded to decreasing acidifying S deposition with a decrease in acidophilic and an increase in basiphilous species (Dirnböck *et al* 2014) but soil recovery from acidification did not generally occur in Europe (Schmitz *et al* 2019). However, no observational study on forest understory diversity recovery in response to recently decreasing N deposition in Europe has been carried out to our knowledge. Stevens (2016) provided a review on the recovery from NITREX and other experiments, concluding that these studies have failed to find signals for recovery of species composition, richness and diversity even 48 years after the last N addition. Experiments of N addition (De Schrijver *et al* 2011) show that effects on plant diversity occurs faster at low cumulative N values. Cumulative N deposition turned out to render significant legacy effects for observed long-term forest understory changes (Bernhardt-Römermann *et al* 2015). Recently, Rowe *et al* (2017) proposed using a 30 year cumulative N deposition above the critical load as an ecosystem pressure metric to reflect the persistence of excess N in the environment. These studies suggest that a significant recovery of vegetation from eutrophication may require substantial reductions in N emissions.

In order to explore expected plant response to currently legislated reductions in N emission, we used 23 ecosystem research plots in sites of the European Long-Term Ecological Research network (LTER-Europe, Mirtl *et al* (2018)) and the International Cooperative Programs Integrated Monitoring and Forests under the Long-Range Transboundary Air Pollution (LRTAP) Convention, with high quality long-term data on deposition, climate, soil recovery, and understory vegetation. A dynamic soil model coupled to a statistical plant species niches model was applied with site-based climate (12 regional climate model ensemble members for each of the Representative Concentration Pathways RCP 4.5 and RCP 8.5) and N and S deposition scenarios (Current Legislation Scenario from EMEP scaled with site specific measurements and a baseline scenario with no further emissions reductions after the year 2010). We used occurrence changes in indicator species of N and S deposition and climate warming effects to compare the present with projections for 2030 and 2050. Specifically, we quantified the expected change in the occurrence probability of (1) oligophilic species, (2) acidophilic species, and (3) cold-tolerant species.

Materials and methods

Study sites and observation data

We used data from 23 intensively studied forest plots in LTER sites from LTER Europe, the International

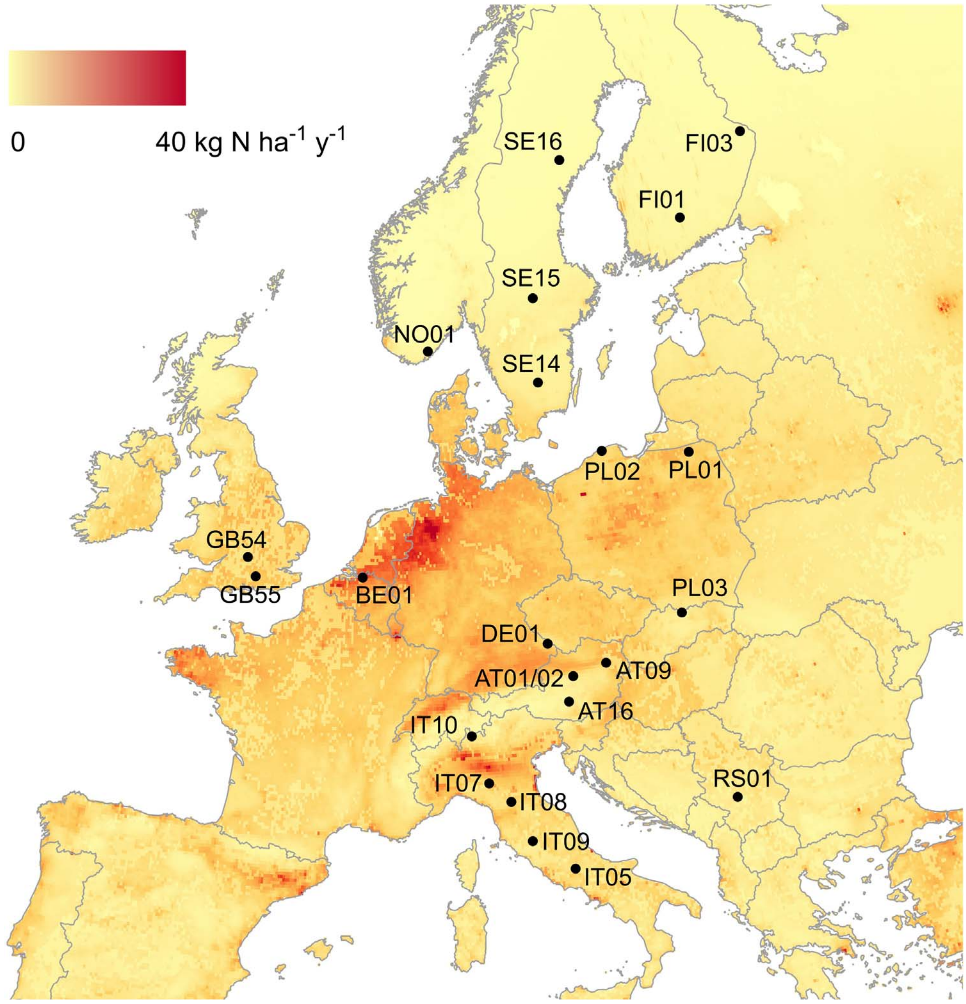

Figure 1. Study site locations on a map of the total N deposition from EMEP MSC-W (forest receptor, year 2015, http://www.emep.int/mscw/mscw_data.html).

Co-operative Programs on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), and on Integrated Monitoring of Air Pollution Effects on Ecosystems (ICP IM) under the LRTAP Convention. The plots are located in Atlantic, continental, Mediterranean, alpine and boreal regions in 10 countries across Europe and cover major continental N pollution and climate gradients (figure 1, S1 table 1 is available online at stacks.iop.org/ERL/13/125010/mmedia). Our assessment was based on a previous model calibration study using the same sites as Holmberg *et al* (2018), where a detailed description of the climate and soil input parameters for the soil model VSD+ can be found.

Scenario data

N and S Deposition

Site-specific values for deposition of S and N were obtained through a combination of modelled and measured data (see S2). The current legislation scenario (CLE) includes the pre- and post-2014 regulations implemented in the GAINS Integrated Assessment Model (http://gains.iiasa.ac.at/gains/). In addition to the CLE scenario a baseline scenario with no further change in N deposition after the year 2010 was used for comparison (B10 scenario). We have not implemented climate effects into future deposition scenarios because emission changes dominate over trends induced by climate change (Engardt and Langner 2013, Simpson *et al* 2014).

Total annual N deposition in the CLE scenario in 2030 was on average 1.7 ± 1 kg N ha^{-1} lower than in 2015 when assuming emission reductions according to current legislation. In 2030 annual N deposition was 8.9 ± 8.1 kg N ha^{-1} lower than in 1980, with only small differences between scenarios CLE and B10 (figures 2(a) and (b)). No further reduction after 2030 was assumed in the scenarios. Annual S deposition in the CLE scenario in 2030 was 28.9 ± 20.2 kg S ha^{-1} lower than in 1980 and 1.5 ± 1.6 kg S ha^{-1} lower than in 2015 (S2 figure 1).

Climate scenarios

We used 12 combinations per RCP 4.5 and RCP 8.5 of bias-adjusted regional climate model (RCM) data

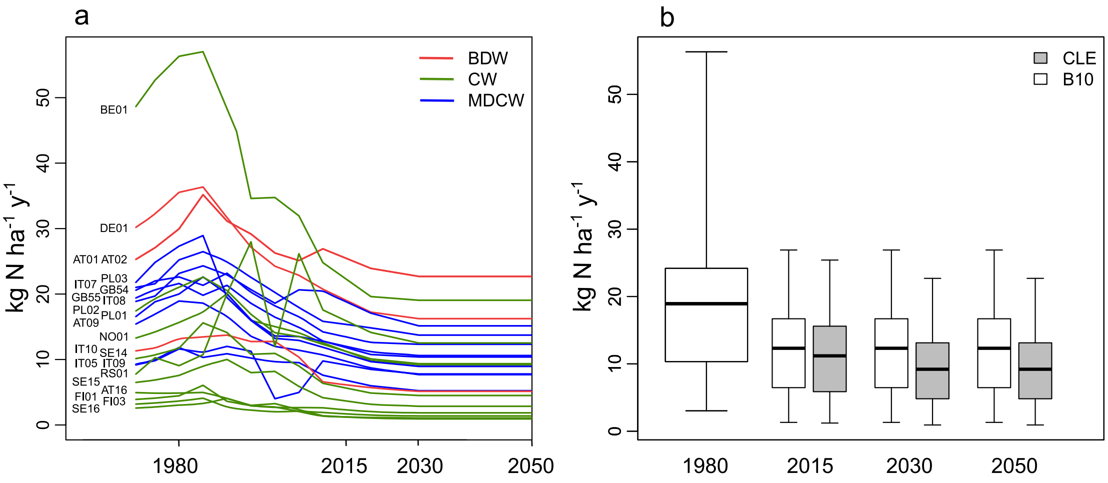

Figure 2. Trends in (a) total N deposition in the study sites assuming the current legislation (CLE) scenario and (b) distribution of N deposition in the two scenarios (CLE, B10: no further reduction after 2010) and in the assessment years 2030 and 2050 in comparison with 1980 and 2015. BDW: broadleaved deciduous woodland, CW: coniferous woodland, MDCW: mixed deciduous and coniferous woodland.

from the EURO-CORDEX initiative, the European branch of the Coordinated Regional Downscaling Experiment (CORDEX) project (Giorgi *et al* 2009, Gutowski Jr *et al* 2016), available through the data nodes of the Earth System Grid Federation model data dissemination system (Cinquini *et al* 2014). RCP 4.5 assumes that global annual greenhouse gas emissions peak around the year 2040 whereas RCP 8.5 assumes emissions to rise throughout the 21st century (see S2 for more details).

The climate scenario RCP 4.5 ensemble mean projected an average increase in temperature for all sites of 0.41 °C ± 0.08 °C between 2015 and 2030 and of 0.86 °C ± 0.14 °C between 2015 and 2050 respectively. In RCP 8.5 these increases were 0.28 ± 0.13 and 1.01 °C ± 0.25 °C (figure 3(a)). The precipitation RCP 4.5 ensemble mean decreased slightly from 2015 to 2030 and to 2050 (on average 10 ± 30 and 20 ± 38 mm), whereas the RCP8.5 ensemble mean increased (on average 4 ± 40 and 30 ± 50 mm). In both RCPs we observed high variability among sites (figure 3(b)).

Model setup

We used the dynamic geochemical soil model VSD + (version 5.6.3) and its pre-processing software MetHyd Version 1.9.1 (Bonten *et al* 2016) together with the plant response model PROPS (Reinds *et al* 2014). The VSD+ model includes cation exchange (Gaines-Thomas or Gapon) and organic C and N dynamics according to the RothC-Model version 26.3 (Coleman and Jenkins 2005). VSD+ is driven by time series of N and S deposition as well as temperature and hydrology to predict soil solution chemistry and soil C and N pools. The VSD+ calibration was taken from Holmberg *et al* (2018) apart for AT02 where the model was calibrated using an identical procedure. The start year of the model runs was set to 1971. Since tree growth is sensitive to climate and N deposition, we scaled the calibrated model parameters (C and N in litterfall, base cation and N uptake) to future changes in temperature, carbon use efficiency, drought (using the ratio between potential and actual evapotranspiration), and N deposition according to Dirnböck *et al* (2017). In its current version, the PROPS model is a database holding statistical niche functions for 4053 plant species occurring in Europe that were derived from a very large set of vegetation relevés (approx. 800 000 plots) together with associated soil data (10 804 plots with soil pH; 7281 plots with soil C:N) (Reinds *et al* 2014). The outputs of PROPS are probabilities of species occurrences as a function of precipitation, temperature, N deposition, soil C:N ratio and soil pH.

Data analysis

Methods and results for model validation see S2.

Biodiversity metrics

In order to assess impacts of N deposition as well as climate change on biodiversity, endpoint metrics recommended by Rowe *et al* (2017) and an additional climate change impact metric were used. We analysed the temporal change in positive and negative plant species indicator groups: oligo- versus eutrophilic species, acidophilic versus basiphilous species, and thermophilic versus cold-tolerant plant species. These groups were defined by the use of Ellenberg indicator values (Ellenberg *et al* 1992), empirical values assigned to each species according to its ecological niche preference. Species-specific indicator values for nitrogen (N), soil reaction (*R*) and temperature (*T*) were assigned to long-term vascular plant and bryophyte species records. Species with intermediate indicator values and non-rated species were excluded from subsequent analyses. Regional Ellenberg indices were used for Atlantic study plots (Fitter and Peat 1994) and

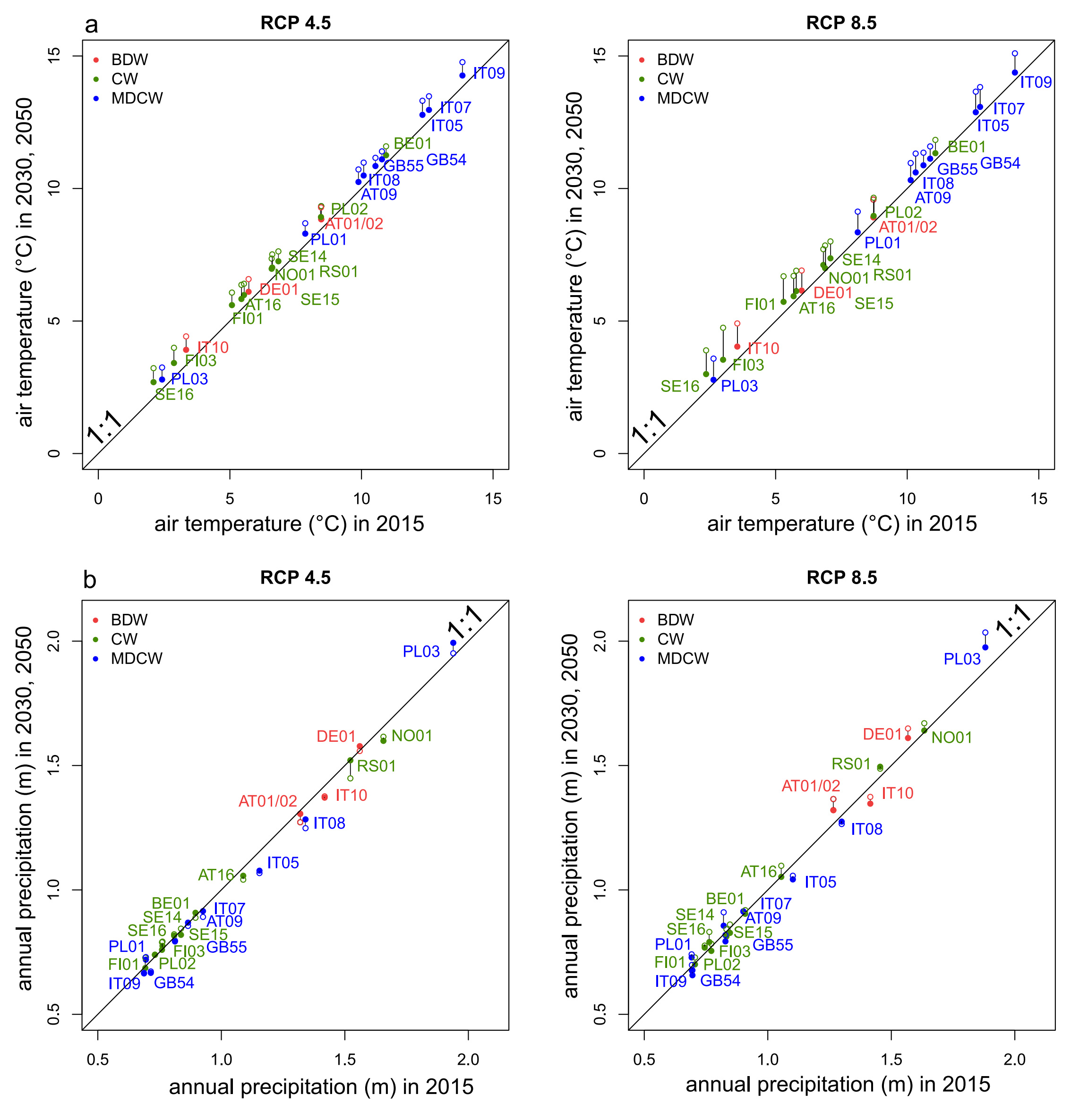

Figure 3. Mean annual temperature (a) and annual precipitation (b) according to RCP 4.5 and RCP 8.5 in 2030 (closed symbol) and 2050 (open symbol) on vertical axis, versus corresponding values for 2015 on horizontal axis. The length of the line joining the symbols is a measure of the change from 2030 to 2050 and the vertical distance of the symbols from the 1:1 line shows the change with respect to 2015. BDW: broadleaved deciduous woodland, CW: coniferous woodland, MDCW: mixed deciduous and coniferous woodland.

Mediterranean study plots (Pignatti *et al* 2005) by using the *R* package 'TR8' version 0.9.18 (Gionata 2015). Species with low Ellenberg *N* and *R* value (<5) were deemed oligophilic and acidophilic, species with high *N* and *R* value (>5) were deemed eutrophilic and basiphilous, respectively. Species with high Ellenberg *T* value (>5) were defined as being thermophilic, those with low *T* value (<5) were defined cold-tolerant.

Instead of modelling all species described in PROPS, we used phytosociological plant community descriptions to define distinctive plant species for each of the forest plots. This approach is based on the floristic composition of vegetation stands (Braun-Blanquet 1964, Dengler *et al* 2008) and allowed us to define distinctive plant species for each of the forest plots. These distinctive species were either characteristic (diagnostic) species or constant attendant species taken from literature or defined by vegetation experts for the sites (S3). The conservation habitat characterization of the European Union Nature 2000 protected area network is based on the same approach (Rodwell *et al* 2018). In addition, the distinctive species considered for the analysis had to be present in the observations. The resulting suites of species are ecologically suitable for undisturbed soil and climate conditions at each of the sites, and do not depend on long-range in-migration because they are part of the regional species pool. Subsequently, species' group mean occurrence probability resulting from the PROPS model was calculated for each scenario combination, plot and year.

Temporal change in indicator group mean probability of occurrence (*X*) were characterized by calculating the mean of the response ratios (RR) of each species belonging to the group, as the natural logarithm of the ratio between the first year (t_1) and the last year (t_2) of the observation period, i.e. $\ln RR = \ln(Xt_2/Xt_1)$ (Hedges *et al* 1999). The periods considered were between the reference year 2015 and 2030 and 2050, respectively.

Assessing future biodiversity benefits

The 12 combinations within each RCP and two N deposition scenarios resulted in 48 scenarios for which we calculated those biodiversity metrics that were selected for scenario assessment. For each model run the temporal change using lnRR was calculated between the reference year 2015 and 2030, and 2015 and 2050. Metaregression analyses using a random effects model with Sidik-Jonkman estimator were used to test for a significant deviation of lnRR from zero (metafor R package version 2.0–0 (Viechtbauer 2017)).

Thereafter, the effect of the CLE deposition scenario was calculated by subtracting the lnRRs of each indicator group at each site from the lnRRs resulting from the B10 deposition scenario. This was done with the lnRRs for the periods 2015–2030 and 2015–2050 respectively. Significant differences from zero were determined with a Wilcoxon test and exact *p*-values. Since plant species' Ellenberg indicator values are not independent from each other (Diekmann 2003), we analysed the correlation of N deposition reduction effects on acidophilic, oligophilic, and cold-tolerant groups by means of Spearman's rho correlation coefficient.

Results

Soil chemistry changes until 2030 and 2050

The CLE deposition resulted in a small increase in soil pH values by an average of +0.06 ± 0.05 between 2010–2020 and 2025–2035 and by 0.07 ± 0.08 between 2010–2020 and 2045–2055 respectively when running VSD+ with the RCP 4.5 climate scenarios (figure 4(a)). Until 2025–2035 only at one site and until 2045–2055 only at three sites decreasing pH values were found. For RCP 8.5, both magnitude and direction of trends were very similar (S4 figure 1(a)).

The CLE deposition scenarios resulted in various trends in the soil C:N ratio. At 14 sites the C:N ratio increased, at 9 it decreased between the periods 2010–2020 and 2025–2035 and 2045–2055, respectively, in the RCP 4.5 and RCP 8.5 climate scenario ensemble means. On average, the C:N ratio increased by 0.29 ± 1.43 (until 2025–2035) and by 1 ± 3.24 (until 2045–2055) in the RCP 4.5 (figure 4(b)) and by 0.4 ± 1.57 (2025–2035) and 1.1 ± 3.46 (2045–2055) in the RCP 8.5 (S4 figure 1(b)), respectively.

Indicator species group changes until 2030 and 2050

With only one exception, we found significant negative mean trends in the three indicator groups ranging between 35% and 80% lower occurrence probabilities (corresponding to the lowest and highest significant lnRR in table 1) in 2030 compared to 2015 assuming CLE deposition and either RCP 4.5 or RCP 8.5 climate (table 1). These trends continued until 2050, with some exceptions (e.g. oligophilic species increased in the RCP 4.5 scenario at PL01; S5 table 1).

The mean lnRR under the CLE and RCP 4.5 scenario in oligophilic species was −0.47 ± 0.45. Under the RCP 8.5 climate scenario the magnitude of the lnRR in oligophilic species was lower (−0.29 ± 0.56). Acidophilic species decreased with lnRR −0.43 ± 0.49 (RCP 4.5) and lnRR −0.36 ± 0.45 (RCP 8.5). Cold-tolerant species were rare in broadleaved deciduous forests (only PL03 hosted more than one of these species). At the other sites, the lnRR indicated a decrease with −0.5 ± 0.51 (RCP 4.5) and −0.32 ± 0.45 (RCP 8.5).

Effects of N deposition reductions under current legislation

Differences in lnRR between climate scenarios ($\ln RR_{RCP8.5} - \ln RR_{RCP4.5}$) and between deposition scenarios ($\ln RR_{CLE} - \ln RR_{B10}$) were used to single out climate versus deposition effects. These effects were not independent between indicator groups. Foremost, effects on acidophilic species correlated significantly positively with effects on cold-tolerant species ($r_s = 0.83$, $p < 0.05$). Effects on acidophilic species also correlated with effects on oligophilic species ($r_s = 0.44$) but not significantly ($p > 0.05$). Effects on oligophilic species showed a weak and non-significant negative correlation with effects on cold-tolerant species ($r_s = -0.10, p > 0.05$).

The CLE deposition reduction between 2015 and 2030 as compared to constant deposition after 2010 (B10) showed significant negative changes in oligophilic species in broadleaved deciduous and coniferous woodland, but no effect in mixed deciduous and coniferous woodland (figure 5). The CLE scenario as compared to the B10 scenario resulted in significantly stronger negative lnRR of acidophilic species in coniferous woodland. Owing to the correlation between species groups, cold-tolerant species lnRRs also differed between deposition scenarios. In the CLE scenario as compared to the B10 scenario, cold-tolerant species experienced more negative lnRR in coniferous woodland. In deciduous forests only PL03 could be assessed and there the trend was more positive. Climate effects on the lnRR resulting from the RCP 8.5 versus the RCP 4.5 scenario either were not relevant (differences in lnRR < 0.08) or positive in the range from 0.12 to 0.69 in all three species groups.

Discussion

The expected decrease in N deposition under current legislation emission reduction targets until 2030 will

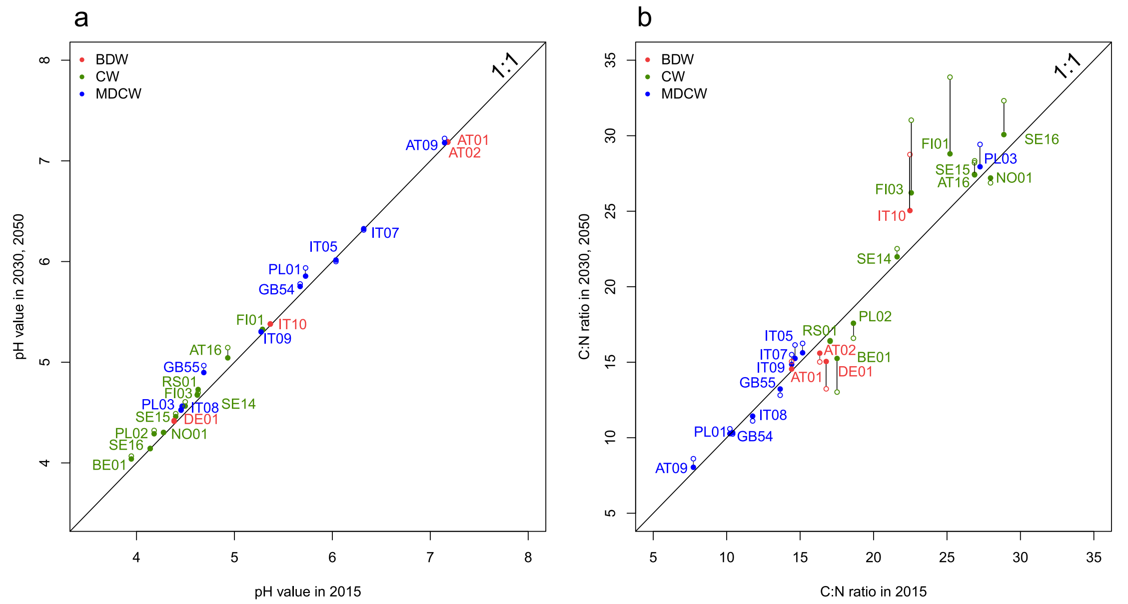

Figure 4. Changes in (a) soil pH value and (b) soil C:N ratio between 2015, 2030 (closed symbol), and 2050 (open symbol) under the current legislation deposition scenario (CLE) and RCP 4.5 climate scenario. The length of the line joining the symbols is a measure of the change from 2030 to 2050 and the vertical distance of the symbols from the 1:1 line shows the change with respect to 2015. BDW: broadleaved deciduous woodland, CW: coniferous woodland, MDCW: mixed deciduous and coniferous woodland.

Table 1. Changes (=response ratios) in the oligophilic ($N < 5$), acidophilic ($R < 5$) and cold-tolerant indicator species groups between 2015 and 2030 assuming current legislation deposition (CLE) and RCP 4.5 and RCP 8.5 climate scenarios. Significant changes with $p < 0.05$ are shown in bold. Sites with <2 species per group were not assessed.

		Oligophilic ($N < 5$)		Acidophilic ($R < 5$)		Cold-tolerant ($T < 5$)	
	Site	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Broadleaved deciduous woodland	AT09	—	—	—	—	—	—
	GB54	**−0.93 ± 0.44**	**−1.27 ± 0.45**	−0.45 ± 0.41	−0.35 ± 0.41	—	—
	GB55	−0.54 ± 0.35	−0.45 ± 0.35	−0.49 ± 0.28	**−0.56 ± 0.28**	—	—
	IT05	—	—	—	—	—	—
	IT07	0.16 ± 0.18	0.03 ± 0.18	0.24 ± 0.2	0.12 ± 0.2	—	—
	IT08	—	—	—	—	—	—
	IT09	0.29 ± 0.24	−0.17 ± 0.25	0.27 ± 0.36	−0.13 ± 0.38	—	—
	PL01	−0.41 ± 0.38	0.41 ± 0.52	−0.37 ± 0.4	0.48 ± 0.55	—	—
	PL03	—	—	**−1.3 ± 0.41**	**−1.23 ± 0.46**	**−0.93 ± 0.41**	−0.46 ± 0.4
	mean ± SD	−0.29 ± 0.45	−0.29 ± 0.56	−0.16 ± 0.34	−0.09 ± 0.36		
Coniferous woodland	AT16	−0.3 ± 0.41	−0.03 ± 0.41	**−1.36 ± 0.32**	−0.59 ± 0.38	**−1.62 ± 0.4**	**−1.15 ± 0.41**
	BE01	**−1.01 ± 0.1**	**−0.78 ± 0.09**	**−0.99 ± 0.12**	**−0.85 ± 0.12**	—	—
	FI01	—	—	−0.37 ± 0.23	−0.29 ± 0.21	−0.2 ± 0.11	−0.14 ± 0.08
	FI03	0.05 ± 0.29	−0.02 ± 0.29	0.1 ± 0.19	0.03 ± 0.19	−0.01 ± 0.32	−0.05 ± 0.32
	NO01	−0.13 ± 0.4	−0.39 ± 0.4	0.04 ± 0.14	−0.24 ± 0.15	0.08 ± 0.13	−0.21 ± 0.13
	PL02	**−0.59 ± 0.19**	**−0.44 ± 0.19**	**−0.59 ± 0.16**	**−0.44 ± 0.16**	—	—
	RS01	**−0.62 ± 0.24**	0.06 ± 0.22	**−0.57 ± 0.18**	0 ± 0.15	**−0.53 ± 0.14**	0 ± 0.1
	SE14	—	—	**−0.54 ± 0.15**	**−0.46 ± 0.14**	−0.39 ± 0.25	−0.34 ± 0.25
	SE15	—	—	−0.1 ± 0.22	−0.2 ± 0.22	−0.14 ± 0.22	−0.39 ± 0.22
	SE16	—	—	−0.05 ± 0	−0.22 ± 0.18	0 ± 0.41	−0.1 ± 0.41
	mean ± SD	−0.43 ± 0.35	−0.27 ± 0.30	−0.50 ± 0.43	−0.33 ± 0.25	−0.40 ± 0.53	−0.34 ± 0.25
Mixed woodland	AT01	—	—	0.13 ± 0.41	0.15 ± 0.41	−0.24 ± 0.23	0.28 ± 0.22
	AT02	**−1.2 ± 0.35**	**0.66 ± 0.23**	—	—	**−0.66 ± 0.3**	0.26 ± 0.3
	DE01	—	—	**−0.95 ± 0.19**	**−0.72 ± 0.13**	**−1.37 ± 0.15**	**−1.23 ± 0.14**
	IT10	**−0.86 ± 0.33**	**−1.34 ± 0.32**	**−0.86 ± 0.33**	**−1.34 ± 0.32**	−0.53 ± 0.27	**−0.7 ± 0.24**
	mean ± SD	−1.03 ± 0.17	−0.34 ± 1.00	−0.56 ± 0.49	−0.64 ± 0.61	−0.70 ± 0.42	−0.35 ± 0.65
mean ± SD		−0.47 ± 0.45	−0.29 ± 0.56	−0.43 ± 0.49	−0.36 ± 0.45	−0.50 ± 0.51	−0.32 ± 0.45

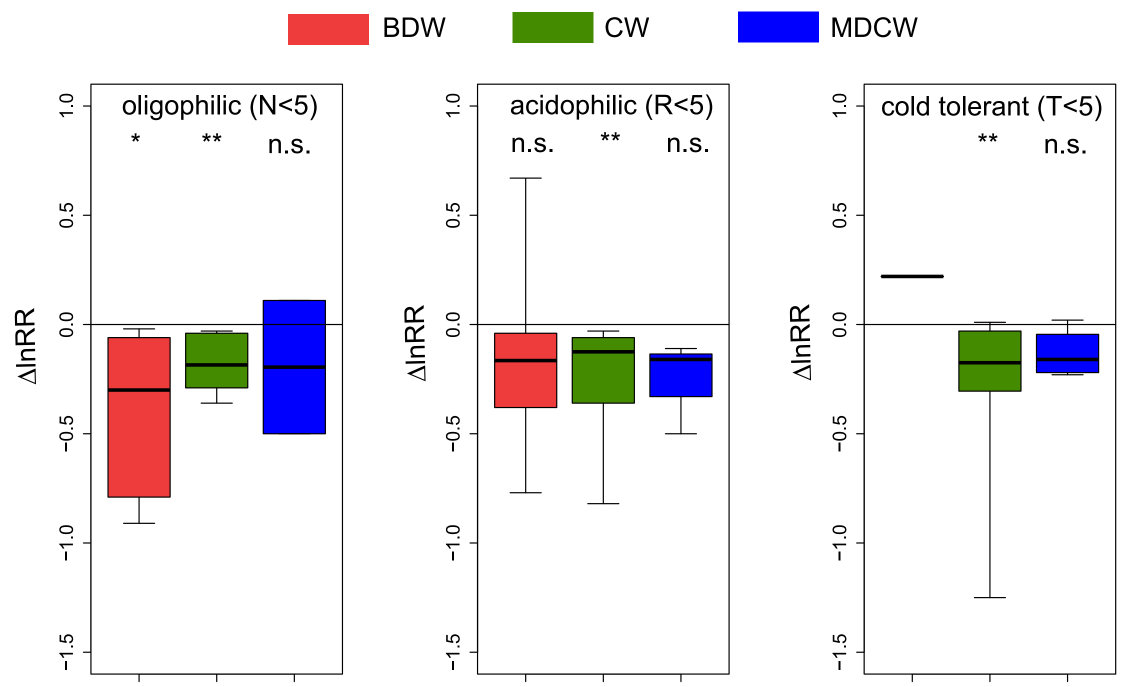

Figure 5. Effects of current legislation deposition (CLE) on trends in oligophilic ($N < 5$), acidophilic species ($R < 5$), and cold-tolerant ($T < 5$) plant species until 2030. Effects were calculated as $\Delta \ln RR = \ln RR_{CLE} - \ln RR_{B10}$ (both with RCP 8.5 climate scenario). Significant differences from zero are indicated with * ($p < 0.1$), ** ($p < 0.05$), *** ($p < 0.001$). The boxplots show the median, the first and third quartile, and the total range of values. BDW: broadleaved deciduous woodland, CW: coniferous woodland, MDCW: mixed deciduous and coniferous woodland.

most likely be insufficient to result in a release from eutrophication across 23 European forest plots. This is in line with the conclusions of a recently published review about effects of reduced N deposition in forests (Schmitz *et al* 2019). Oligophilic forest understory plant species will unlikely increase by 2030 and only scarcely by 2050 according to our modelling results. This result was partially also due to confounding processes related to climate effects and to increases in soil pH values in response to the decrease in acid deposition, after reaching its peak in the 1970s. The latter will offer less chance for acidophilic plant species to occur. Since these species are very often also oligophilic, a general improvement in this indicator group is prevented. The negative effect of climate change on the probability of species being cold-tolerant and acidophilic, will additionally counteract an improvement in the oligophilic species group. Climate change will result in a number of soil chemical changes, with general and site-specific effects on trends in plant species occurrence probability. Climate changes until 2030 and 2050 in general will accelerate the decrease in soil acidity, but will prevent a decrease in N availability in some plots through various effects (detailed below) on soil C:N ratios. In summary, these effects will worsen rather than improve the habitat suitability for oligophilic plant species in these forests. Note that implementing plant response into soil chemical models is still fraught with considerable prediction uncertainty which should be considered when interpreting our results.

Future decline in all three indicator groups

The general negative future trend in all three indicator groups corroborates results from re-survey of historical data and from studies modelling future trends. A number of environmental changes have affected forest understory species composition in the past. Verheyen *et al* (2012) showed that 30% of plant species in central European forest plots have been replaced during the 20th century in response to changes in N and S deposition, forest management, and grazing by large herbivores. Climate niches of forest understory plant species have been affected by climate change (Lenoir *et al* 2008) and plant species optima in France have shifted 29 m upwards in altitude per decade during the 20th century. In a study covering central Europe and some sites in the USA, De Frenne *et al* (2013) could clearly show a decline in forest species adapted to cooler conditions and increases in species adapted to warmer conditions. According to our results the anticipated reductions in N deposition by 2030 and 2050 will not reverse this trend, at least not on a broad, continental scale.

Recovery from soil acidification

The partial effect of N and S deposition emission reductions on the trend in acidophilic species by 2030 and 2050 was clearly negative. Though not in general across Europe, partial soil recovery from acidification has been found in a number of studies in response to significantly lower acid deposition after its peak in the 1970s (Schmitz *et al* 2019). We show that the current legislation reduction in acid deposition will very likely contribute to further recovery of forest soils from acidification, thereby reducing the habitat suitability for acidophilic species, which were formerly favoured by more acidic soils. Apart from a decrease in acidophilic species, recovery in basiphilous species was also found in a European study on long-term forest vegetation trends (Dirnböck *et al* 2014). However, we could not assess basiphilous species recovery because they were either very rare at our sites or modelled responses did not reproduce the long-term vegetation observations well enough.

No recovery in oligophilic species

Contrary to our hypothesis, lower N deposition in the CLE scenario will not improve the oligophilic species indicator group. We are confident that our results are not a result of sampling bias as found by McDonnell *et al* (2018) because the European PROPS data is representative for large gradients in N deposition, climate and soil conditions. Strengbom *et al* (2001) used two Swedish forest plots to show that vascular plant species composition changed until at least 9 years after cessation of N fertilization. Pine forest understory plant community response to drastic emission reductions from a nearby fertilizer plant in Lithuania caused a decrease in nitrophilic species within 16 years (Sujetovienė and Stakėnas 2007). Although these are only two examples, strong N reduction can cause recovery in vegetation. However, a considerable response lag in N sensitive species is very likely (Stevens 2016, Schmitz *et al* 2019). Together with the modest reduction in N deposition under currently legislated emission cuts (EMEP 2017), major recovery in sensitive forest habitats is not to be expected, as shown in our results.

The various future responses of the soil C:N ratios in the climate and deposition scenarios will also cause variation in oligophilic species trends. As an example, coniferous forests mostly had soil C:N ratios $>$ 16 in 2015, i.e. relatively nutrient poor soils, rendering considerable, though positive and negative, changes until 2030 and 2050. Northern European coniferous forest's soil N status was, in comparison to sites in western and central Europe, not as dramatically affected due to much lower N deposition in the past (Holmberg *et al* 2013). According to our modelling results, these forests will experience increased C:N ratios until 2030 and 2050, hence less soil N availability which is likely a double effect from climate warming increasing tree growth and from less N deposition. In comparison, the sites BE01, DE01, and PL02 have all been exposed to high N (and S) loads and showed substantial decrease in soil C:N ratios until 2030 and 2050. The response of soil C:N ratio to increased N inputs can hence be an increase (where productivity is stimulated and inputs of fresh litter, with relatively high C:N ratio, increase) or a decrease (where the extra N is mainly immobilized into existing soil organic matter). These results corroborate the findings of Simkin *et al* (2016) regarding N driven plant diversity changes in the US. They show that on acid soils, and under warm and dry climates the relationship between N deposition and richness decline can be obscured.

The overlap in the plant species between the three indicator groups, and hence the correlation in their temporal changes, is further deemed partly responsible for no recovery of oligophilic species. Many acidophilic forest understory species are also oligophilic and cold-tolerant (e.g. the common forest species *Luzula sylvatica* (Huds.) Gaudin, *Calamagrostis villosa* (Chaix) JF Gmel, *Vaccinium myrtillus* L). Hence, when, climate warming directly reduces the probability of the cold-tolerant species group and when soil recovery from acidification reduces the occurrence probability of acidophilic species, improvement in the oligophilic species group becomes less likely. The relationship between soil acidity and nutrient availability as well as between indicator values for acidity (*R*), nutrient availability (*N*), and temperature (*T*) has long been known (Schmidt 1970) confounding the signals of acidification and eutrophication, as well as climate warming (Naaf and Kolk 2016). The strong functional relationship between nutritional determinants and plant species *R* values is due to abilities such as preferences for NH_4 in acid sites or the ability to use phosphorous and iron from soils on carbonate bedrock (Bartelheimer and Poschlod 2016). Hence, the number of species benefiting from both soil recovery from acidification and increasing N limitation is limited in general. Moreover, some of these species may have gone locally extinct during conversion of deciduous to coniferous forests and soil acidification (as at PL03). We found too few basiphilous or thermophilic species occurring in the plots to allow for a sound evaluation in their performance. Although our study plot sample is by no means representative for all European forest types, we think that pauperization in forest understory diversity may hinder fast recovery.

Conclusion

We show that long-term research and monitoring sites are reference systems for developing and validating ecological models. Environmental policies may increasingly take advantage of Research Infrastructures such as eLTER RI and of the integrated ecosystem models they are enabling (Mirtl *et al* 2018). From our study, we learned that oxidized and reduced N emission reductions need to be considerably greater to allow recovery from chronically high N deposition. Legislative efforts should also focus on limiting N saturation in parts of the world, that have so far avoided the extreme amounts of cumulative N deposition that have occurred across large areas of Europe.

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