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Historic nitrogen deposition determines future climate change effects on nitrogen retention in temperate forests

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Abstract Nitrogen (N) cycle processes in terrestrial ecosystems are highly sensitive to temperature and soil moisture variations. Thus, future climate change may affect the degree to which N deposited from the atmosphere will be retained in forest ecosystems. We evaluated the effect of future changes in climate and N deposition on ecosystem N cycling using the model LandscapeDNDC forced with historical data from eight long-term forest ecosystem monitoring stations in Austria and downscaled future N deposition and climate scenarios. With every 1 °C of warming, annual N uptake in biomass increased by +0.03 to +0.54 kg N ha^{-1}, total soil organic matter (SOM) increased annually by +0.003 to +0.08 kg N ha^{-1}, and mean annual N leaching was between −0.09 and −2.03 kg N ha^{-1} lower. The magnitude of N deposition in the years from 1990 to 2010 was by far the most important determinant of the response of nitrogen cycling to future warming, including statistically significant relationships with humus N content and N leaching. We conclude that climate change will likely increase ecosystem N retention in temperate forest ecosystems, and even more so at forest sites with high past N deposition.

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1 Introduction

Nitrogen deposition has led to changes in carbon and nitrogen dynamics in forest ecosystems (Butterbach-Bahl and Gundersen 2011), causing changes in C sequestration (Thomas et al. 2010; Yue et al. 2016), increased nitrate leaching (Gundersen et al. 2006), increased gaseous N emissions (van Groenigen et al. 2015) and the loss of plant species susceptible to high nutrient availability (Dirnböck et al. 2014). N deposition effects are predominantly discussed in the conceptual framework of ecosystem N saturation where an oversupply of N is thought to gradually diminish N retention, and surplus N leaves the ecosystem via leaching or gaseous emissions (Aber et al. 1998; Lovett and Goodale 2011).

A variety of factors affect N cycling in terrestrial ecosystems. Soil organic matter (SOM) decomposition is temperature sensitive (Davidson and Janssens 2006) and soil warming leads to enhanced N mineralization and nitrification (Butler et al. 2012), though the latter strongly depends also upon the availability of NH_4^+ (Butterbach-Bahl and Gundersen 2011). Furthermore, soil water content affects the temperature sensitivity of SOM decomposition (Davidson and Janssens 2006) and controls gaseous N efflux (Butterbach-Bahl et al. 2013). In addition to climatic conditions, N processes depend to a large extent upon soil characteristics, management and vegetation type. Soil properties such as soil texture and porosity can affect N turnover in soils, via their impacts on soil hydrology, N adsorption and soil organic carbon concentrations (Butterbach-Bahl and Gundersen 2011). Low topsoil C:N ratios (<20–25) have been shown to indicate increased nitrate leaching and gaseous N loss (Gundersen et al. 2006). Apart from the N losses the C:N ratio also relates to N availability because N immobilisation dominates at high C:N ratios while net mineralisation increases and net nitrification occurs at low C:N ratios (Aber et al. 2003; Dannenmann et al. 2007). Soil acidity also controls N transformation by generally reducing the abundance and activity of fine roots and microorganisms (Brumme and Khanna 2008). Vegetation type has major effects on ecosystem N cycling controlling litter quality, root distribution and canopy structure that affect soil moisture, temperature and substrate availability, microbial N turnover as well as nitrate leaching and gaseous N loss (Brumme et al. 1999; Butterbach-Bahl et al. 2002; Rothe et al. 2002).

N uptake by trees is sensitive to climate change because tree growth is related to temperature. Enhanced tree growth has been observed during the last decades (Fang et al. 2014; McMahon et al. 2010; Pretzsch et al. 2014a; Pretzsch et al. 2014b). Warming can increase tree growth directly or via the enhancement of N availability by increasing rates of N mineralization and nitrification (Butler et al. 2012). Enhanced tree growth can cause soil nutrient depletion (N, phosphor and base cations) rendering limitations in tree growth (Jonard et al. 2015; Templer 2013). Increasing drought conditions may also counteract growth acceleration that is caused by warming (Charru et al. 2014).

Though combined effects of N deposition and climate change are studied more often, so far it still remains elusive as to how forest ecosystem N retention might be affected in future (Porter et al. 2013). Here, we use data from eight long-term forest ecosystem monitoring stations in Austria with different N status to calibrate a physiologically oriented ecosystem model (LandscapeDNDC) with a detailed soil process description (Haas et al. 2013; Molina-Herrera et al. 2015). We hypothesise that in temperate forest ecosystems, climate warming will increase tree growth and will enhance N mineralization and nitrification. In sum, climate change will compensate N saturation by increasing N retention, resulting into less N leaching and gaseous losses. The temporal dynamics and magnitude of this offsetting process will strongly depend upon site conditions, but also on historic and future N deposition and climate change trajectories.

2 Methods

2.1 Site description

We used eight long-term forest monitoring and research sites (Table 1) spanning altitudinal ranges between lowland (290 m a.s.l.) and montane to subalpine areas (1540 m a.s.l.). Mean annual temperature (T) variation is mostly related to this altitudinal gradient and ranges between 4.2 and 10.8 °C with a pronounced seasonal pattern typical for temperate forest ecosystems. Lowland sites in eastern Austria experience the lowest mean annual precipitation (600–700 mm y^{-1}) whereas sites in the Northern Limestone Alps receive around 1500 mm y^{-1}. N deposition is highest at sites with high precipitation (15–28 kg N ha^{-1} y^{-1}) and at sites in eastern Austria (12–18 kg N ha^{-1} y^{-1}). Norway spruce (*Picea abies* (L.) H. Karst.) is the dominant tree species except at two sites where either European beech (*Fagus sylvatica* L.) (KL09) or oak species (*Quercus petraea* Liebl., *Qu. cerris* L.) (UP02) dominate. The soils range from acidic (pH < 4) to neutral (pH 6–7). Three sites have carbonate bedrock with high soil pH and base saturation (AK22, MG15 and ZB00). Whereas AK22 and ZB00 has mull type humus characterized by low C:N ratios of 16.8–17.0, MG15 has a moder type humus with a C:N ratio of 25.6. Three sites, JO17, KL09 and UP02, have acidic soils (pH 3.9–4.6), high base saturation (70–90%) and similar A-horizon C:N ratios (12.8–13.9). JO17 has a mixed moder-mull humus type, KL09 and UP02 had a mull humus. Two sites are characterised by very acidic soils (pH 3.6–3.7), low base saturation, moder type humus with C:N ratios of 20.4 and 23.7 (Table 1).

2.2 LandscapeDNDC model

LandscapeDNDC is a modular ecosystem model that combines detailed soil C, N and water process representations with physiologically oriented vegetation descriptions. It is designed for simulating ecosystem C and N turnover and losses including associated changes in the C and N stocks of soils (Haas et al. 2013). A particularly strong part of the model is the detailed description of ecosystem nitrogen processes, including trace gas emission and leaching. Generally process descriptions are based on Li et al. (1992) and Li et al. 2000). LandscapeDNDC was evaluated to represent the water, C and N cycling of various forest ecosystems under different weather and soil conditions (Holst et al. 2010; Molina-Herrera et al. 2015) and used successfully to simulate nitrate leaching for one of the forest sites (Dirnböck et al. 2016). For the current analysis, we used a more detailed forest growth model within LandscapeDNDC (Grote et al. 2011a; Grote et al. 2011b; Grote et al. 2009).

2.3 Input data

LandscapeDNDC was initialized using site-specific information on longitude, latitude, annual precipitation, slope, aspect and vertically distributed physical and chemical soil properties and profile information: soil texture, soil organic carbon and nitrogen, bulk density, saturated hydraulic conductivity, stone fraction, pH, field capacity and wilting

Table 1 Study site characteristics

	Site code	Site name	Alti (m)	Lat	Lon	T (°C)	P (mm y^{-1})	N_{dep} (kg N ha^{-1} y^{-1})	Tree species	Soil type	Humus type	Soil C:N[a]	Soil pH[b]	BS[c]
Carbonate, high base saturation	AK22	Achen-kirch	896	47.58	11.94	7.0	1454	15.5	S (90%); B (10%)	Shallow chromic Cambisols and rendzic Leptosols	Mull	17	6.5	100
	MG15	Mürz-zuschlag	715	47.63	15.66	7.6	1148	9.4	S (100%)	Eutric calcaric Endoskeletic cambisol	Moder	25.6	6.9	100
	ZB00	Zöbel-boden IP1	900	47.84	14.44	8.0	1565	27.9	S (75%); B (25%)	Shallow chromic Cambisols and rendzic Leptosols	Mull (mode-r)	16.8	6.7	100
Acid soil, high base saturation	JO17	Jochberg	1050	47.33	12.41	7.3	1200	6.6	S (100%)	Eutric stagnic Episkeletic fluvisol	Moder (mull)	13.9	4.6	70
	KL09	Klausen-Leopolds-dorf	510	48.12	16.05	8.7	689	12.5	B (100%)	Endostagnic Endoskeletic Luvisol	Mull	13.2	4	70
	UP02	Unter-pullendorf	290	47.49	16.56	10.8	631	17.8	SO (50%); AO (50%)	Eutric stagnic vertic Cambisol	Mull	12.8	3.9	90
Acid soil, low base saturation	MO11	Mondsee	860	47.88	13.35	9.7	1568	16.0	S (100%)	Hyperdystric Endoskeletic cambisol	Moder	20.4	3.6	11
	MU16	Murau	1540	47.06	14.11	4.2	1155	4.2	S (80%); L (20%)	Hyperdystric Endoskeletic cambisol	Moder	23.7	3.7	3

T annual mean temperature, *P* annual precipitation, *S* Norway spruce, *B* European beech, *L* European larch, *SO* Sessile oak, *AO* Austrian oak

[a] All A horizons

[b] Mean value in mineral soil $CaCl_2$

[c] Base saturation average in mineral soil

point. For the sites simulated, soil input data was taken from Mutsch et al. (2013) and Dirnböck et al. (2016). LandscapeDNDC uses daily climate data of air temperature, precipitation, solar radiation, N deposition and atmospheric CO_2 concentration. Since the focus of this study was to disentangle climate effects on N cycling, we kept CO_2 concentrations constant at the value of the year 2000 (370 ppm). Soil moisture in 15 and 30 cm soil depth was used for model evaluation.

Tree species-specific volume, height and diameter for the entire rotation period were taken from species-specific yield tables (Marschall 2011) taking into account the site-specific yield classes that were defined by using tree age and maximum tree height from the years 1995, 2000, 2005 and 2009. To ensure comparability among sites, simulations were based on forest plantation in 1950, a spin up time of 40 years (until 1990), and covered a simulation period of 110 years (1990–2100). Tree harvest was defined according to common procedures without implementing a clear-cut.

By using the weather generator ClimGen (Stöckle et al. 1999) and measured data (20–27 years, see S1), we derived the baseline climate time series for 1950–2100. Then, scenario data were synthesized by means of anomalies gathered from the A1B, A2 and B1 scenarios (IPCC AR4 WG1 2007). Parameter-specific monthly climate change anomalies for each of the study sites were derived from the respective grid cell of the regional climate model COSMO-CLM (Loibl et al. 2011). The A1B, A2, and B1 scenarios were based on the global circulation model ECHAM5, and the A1B scenario was also available from the HadCM3 model (see S1 T1 for differences between scenarios). We ran LandscapeDNDC with each of these scenarios and the results, if not mentioned otherwise, are presented as averages over scenarios.

Daily total dry and wet N deposition for 1950–2100 was derived from retrospective modelling and considered three future scenarios: the current legislation (CLE) scenario with revised Gothenburg Protocol emissions and the technically maximum feasible emission reduction scenario (MFR). CLE and MFR scenarios assume no change in deposition after 2030. A baseline scenario was defined by the 2010 deposition values with no further reductions (B10) (see S1 for more details).

2.4 Model optimization

According to Molina-Herrera et al. (2015), we optimized for each site three forest structure development and growth parameters: HDMAX which regulates the height diameter ratio for mature trees in dense stands, HREF which defines the canopy depth where full foliage is developed and the KM20 maintenance respiration coefficient at reference temperature following (Thornley and Cannell 2000). The optimization was based on a Markov Chain Monte Carlo calibration minimizing the Euclidian distance (Molina-Herrera et al. 2015) between simulation results for tree volume, height and diameter and every 20–30 year values according to the yield tables. The optimization routine performed several thousand site simulations for 150 years for each parameter. Parameter ranges were defined a priori for each species based on literature data (Molina-Herrera et al. 2015). The calibration was performed for all sites independently.

2.5 Data analysis and statistics

By following Lovett and Goodale (2011), we focused on the temporal dynamics of N in plant biomass, N in the forest floor (humus N), N in the mineral soil, soil N loss via gaseous emissions (N_2O, N_2 and NO) and via leaching in seepage water (NO_3^- and NH_4^+). First, we characterised the current state and direction of N fates by calculating mean annual vegetation and soil pools and fluxes of the period 1990–2010. Differences in the fluxes between sites were tested separately for each group with a non-parametric Kruskal-Wallis test. Second, we inferred whether the sites accumulated or lost SOM N under the different combinations of climate and N deposition scenarios ($n = 15$ for each site). For this, we tested if simulated annual changes in humus N, mineral soil N and the sum of both (total SOM N) were different from zero during the period 2010–2100 with a Wilcoxon rank sum test. And third, we quantified effects of N deposition and climate on all N fates for each site by comparing mean N pools and mean annual N fluxes of all combinations of scenarios ($n = 15$ for each site) considering time periods of 1990–2010 and 2080–2100, respectively, assuming that differences between the two time periods are representative for changes in N fates. In order to separate N deposition and climate effects on N fates, we used the baseline climate scenario and the MFR N deposition (the lowest N deposition) scenario as a reference. We subtracted the changes in mean annual N increments resulting under the MFR N deposition scenario from those derived under the B10 and CLE N deposition scenarios (and all climate scenarios), and we subtracted the N changes resulting under the A1B, A2 and B1 climate scenario from those derived under the baseline climate scenarios (and all N deposition scenarios). Whether these effects were significantly different from zero was tested with a Wilcox rank sum test. In order to compare sites, we also calculated these effects per 1 kg N deposition and per 1 °C warming by dividing changes of N fates with changes in N deposition and temperature, respectively, and tested differences between sites with a post-hoc multi-comparison Nemeneyi test (Pohlert 2014). Whether these standardized effects on N fates were related to past N deposition, climate (means between 1990 and 2010), soil pH-values and A-horizon C:N ratios (measurements between 2005 and 2007), were tested with linear least square regression.

3 Results

3.1 Current (1990–2010) N status of the study sites

Among the sites with carbonate bedrock, simulated N stored in trees between 1990 and 2010 was 1.5 and 1.9-fold higher in ZB00 than in AK22 and MG15, respectively. The SOM N pool was 2.6–2.7-fold in AK22 than ZB00 and MG15 (Table 2). N loss via leaching ($NO_3^- + NH_4^+$) and in gaseous (N_2O, N_2 and NO) form was 15.1 and 3.4 kg N ha^{-1} y^{-1} at ZB00, summing up to 68% of the N deposition (54% leaching, 14% gaseous). MG15 lost 3.7 kg N ha^{-1} y^{-1} via gaseous efflux (39% of N deposition) and 1 kg N ha^{-1} y^{-1} via N leaching (11%). N loss via leaching was 3.6 kg N ha^{-1} y^{-1} (32% of N deposition) and gaseous N efflux was 1.4 kg N ha^{-1} y^{-1} in AK22 (23% leaching, 9% gaseous) (Table 2, S2 F1). Annual N fluxes between 1990 and 2010 were different between the sites (Kruskal-Wallis X^2 = 39.2–52.5, df = 2, $p < 0.001$).

At sites with acidic soils and high base saturation, the amount of simulated N stored in the trees between 1990 and 2010 was 1.7 and 1.3-fold in KL09 than in JO17 and UP02, respectively. Though these three sites had similar mineral soil N pools (6405–8821 kg N ha^{-1}) in the period 1990–2010, humus N pool was 1.8 and 1.5-fold in JO17 than in KL09 and UP02, respectively (Table 2). Simulated N leaching was <2% of N deposition at JO17 and KL09 but was 5.6 kg N ha^{-1} y^{-1} at UP02 (31% of N deposition). In JO17, simulated gaseous N efflux was low (0.8 kg N ha^{-1} y^{-1}) but KL09 and UP02 showed 30 and 26% losses, respectively (3.7 and 4.7 kg N ha^{-1} y^{-1}) (Table 2, S2 F1). N fluxes between 1990 and 2010 were different between the sites (Kruskal-Wallis $X^2 = 39.4–52.5$, df = 2, $p < 0.001$).

Among the two sites with acidic soils and low base saturation N stored in trees was twofold in MO11 than in MU16. Mineral soil N and humus N were similar (Table 2). Simulated N leaching loss was 4.9 and 1.3 kg N ha^{-1} y^{-1} at MO11 and MU16, respectively, amounting to 31% of the N deposition at both sites. Simulated gaseous N losses were 0.9 kg N ha^{-1} y^{-1} at MO11 and 1.4 kg N ha^{-1} y^{-1} at MU16 (MO11: 6%, MU16: 33% of N deposition) (Table 2, S2 F1). N fluxes between 1990 and 2010 were different between the sites (Kruskal-Wallis $X^2 = 22.2–29.3$, df = 1, $p < 0.001$).

3.2 Long-term changes in climatic conditions, N deposition, and SOM N pools

Mean annual temperature increased by 1.7–4.3 °C between 1990–2010 and 2080–2100 (S1 T1). Temperature increase was lowest in the B1 and highest in the A2 scenarios. Precipitation in the climate scenarios of the sites tended to decrease (by up to −192 mm y^{-1}) but varied considerably between sites and scenarios. The scenarios A2 (ECHAM5) and A1B (HADCM3) showed the strongest decrease while at some sites precipitation even increased, particularly under the B1 scenario (S1 T1). In 2080–2100, simulated mean annual deposition was 5.4 and 3.2 kg N ha^{-1} lower than for the period 1990–2010 in the MFR and the CLE scenario, respectively (S1 T1).

Simulated mean annual total SOM N budgets between 2010 and 2100 were predominantly negative (S3 F1). Simulated total SOM N decreased less in JO16, MG15 and UP02 (from −0.6 to −1.3 kg N ha^{-1} y^{-1}) than in ZB00, AK22, MU16 and MO11 (from −2.1 to −2.7 kg N ha^{-1} y^{-1}) (Wilcox rank sum test for differences from zero, $p < 0.001$). At KL09, total SOM N increased in the CLE scenario (+0.5 kg N ha^{-1} y^{-1}, Wilcox $p < 0.001$) decreased in the MFR scenario (−0.2 kg N ha^{-1} y^{-1}, Wilcox $p < 0.001$) but showed no significant trend in the B10 scenario (Wilcox $p = 0.131$). At UP02, total SOM N had no trend in the MFR scenario (Wilcox $p = 0.128$). At all sites changes in total SOM N were dominated by changes in mineral soil N, ranging from −0.1 to −2.8 kg N ha^{-1} y^{-1} (Wilcox $p < 0.001$).

Table 2 Simulated soil organic matter N pools in in the humus and the mineral soil, N in plant biomass, annual N leaching and gaseous N efflux between 1990 and 2010 (mean ± SEM). N loss is the percentage of N deposition lost to N leaching and gaseous N efflux

	Site	Humus (kg N ha^{-1})	Mineral soil (kg N ha^{-1})	Plant (kg N ha^{-1})	Leaching[a] (kg N ha^{-1} y^{-1})	Gas efflux[a] (kg N ha^{-1} y^{-1})	N loss (%)
Carbonate,	AK22	546 ± 2	22,779 ± 1	293 ± 9	3.6 ± 0.8	1.4 ± 0.05	32
high base	MG15	148 ± 4	8638 ± 2	228 ± 7	1.0 ± 0.2	3.7 ± 0.3	50
saturation	ZB00	328 ± 2	8226 ± 3	433 ± 11	15.1 ± 1.4	3.8 ± 0.2	68
Acid soil,	JO17	299 ± 1	6761 ± 2	183 ± 6	0.1 ± 0.01	0.8 ± 0.02	14
high base	KL09	165 ± 3	8821 ± 3	317 ± 9	0.1 ± 0.01	3.7 ± 0.2	30
saturation	UP02	199 ± 1	6405 ± 2	245 ± 8	5.6 ± 0.9	4.7 ± 0.4	58
Acid soil,	MO11	417 ± 2	13,076 ± 2	429 ± 11	4.9 ± 0.6	0.9 ± 0.03	36
low base saturation	MU16	371 ± 3	15,878 ± 1	216 ± 5	1.3 ± 0.1	1.4 ± 0.1	64

[a] N fluxes are different between the sites in each of the groups (Kruskal-Wallis $p < 0.001$)

3.3 Climate and N deposition effects on N fates at different forest sites

Temperature increase significantly affected all N fates in the carbonate sites (Wilcoxon rank sum test $p < 0.05$) apart from mineral soil N at ZB00 and humus N at MG15. There was a particularly strong effect of temperature on simulated plant N uptake (AK22, ZB00) and on mineral soil N (AK22, MG15). Gaseous efflux of N decreased in MG15 and increased in AK22 and ZB00 (S2 F1). The two carbonate influenced sites with mull humus (AK22, ZB00) showed pronounced N deposition effects on N leaching but small effects on the N pools (Wilcoxon rank sum test $p < 0.1$) (S2 F1). There, every additional kilogram N per hectare per year deposited caused between +0.7 and +0.9 kg N ha^{-1} higher mean annual N leaching and 0.1 kg N ha^{-1}additional tree N uptake. At MG15, changes per each additional kilogram N per hectare per year were small (+0.12 and +0.3 kg N ha^{-1} y^{-1} for N leaching and tree N uptake, respectively) but gaseous N loss and total SOM N increase was substantially higher (+0.35 and +0.2 kg N ha^{-1} y^{-1}) as compared to the other two sites. At AK22 and ZB00, every degree Celsius warming decreased mean annual N leaching by −1.2 to −2 kg N ha^{-1} and additional tree N uptake by +0.2 to +0.5 kg N ha^{-1}. Climate change led to higher gaseous N efflux at these sites. At MG15, annual mean effects on N fates with every degree Celsius warming were small (<0.17 kg N ha^{-1}) besides gaseous N loss decreasing by −0.25 kg N ha^{-1} which was the highest value among all sites (Fig. 1).

Among the three sites with acidic soils characterised by higher base saturation, KL09 showed very small climate effects on N fates whereas effects were significant at UP02 and JO17 (Wilcox rank sum $p < 0.05$, S2 F1). KL09 and JO17 exerted strong positive effects per kg N deposition in tree N uptake and in total SOM N being between +0.3 and +0.4 kg N ha^{-1} y^{-1}, respectively (Wilcox rank sum $p < 0.05$, S2 F1). For all three sites mean annual gaseous N loss was between +0.1 and +0.3 kg N ha^{-1} higher with every kg N. UP02 was specific as to its lower effect in tree N uptake but higher effects in mean annual N leaching (+0.4 kg N ha^{-1}). Warming effects on mean annual tree N uptake were either low (UP02, JO17, <0.09 kg N ha^{-1}) or even negative (KL09). Whereas JO17 showed no substantial temperature effects, at UP02 and KL09 every degree Celsius warming caused mean annual N leaching and N gas efflux to decrease by −0.2 to −0.6 and by −0.2 kg N ha^{-1}, respectively (Fig. 1).

The two sites with acid soils and with low base saturation experienced different N deposition and corresponding effects. At MU16, the difference between the deposition scenarios was marginal so that all effects on N fates but on plant N uptake were insignificant (Wilcox rank sum test $p > 0.05$, S2 F1). At MO, the deposited N led to significantly higher uptake of N in plants and SOM, and higher N effluxes (Wilcox rank sum test $p > 0.05$). Mean annual N leaching was +0.6 kg N ha^{-1} higher and mean annual tree N uptake was +0.2 kg N ha^{-1} higher per kilogram N deposition. The strongest climate change effect was on N leaching. Every degree Celsius warming decreased N leaching by between −0.3 and −0.6 kg N ha^{-1} y^{-1} and increased tree N uptake by +0.1 and +0.2 kg N ha^{-1} y^{-1} in MU16 and MO11, respectively (Fig. 1).

3.4 Drivers of future changes in N fates

The post hoc multi-comparison Nemeneyi test showed that effects on N fates were site dependent (Fig. 1). We found that per kilogram effects of future N deposition on tree N uptake were significantly related with the mean annual N deposition between

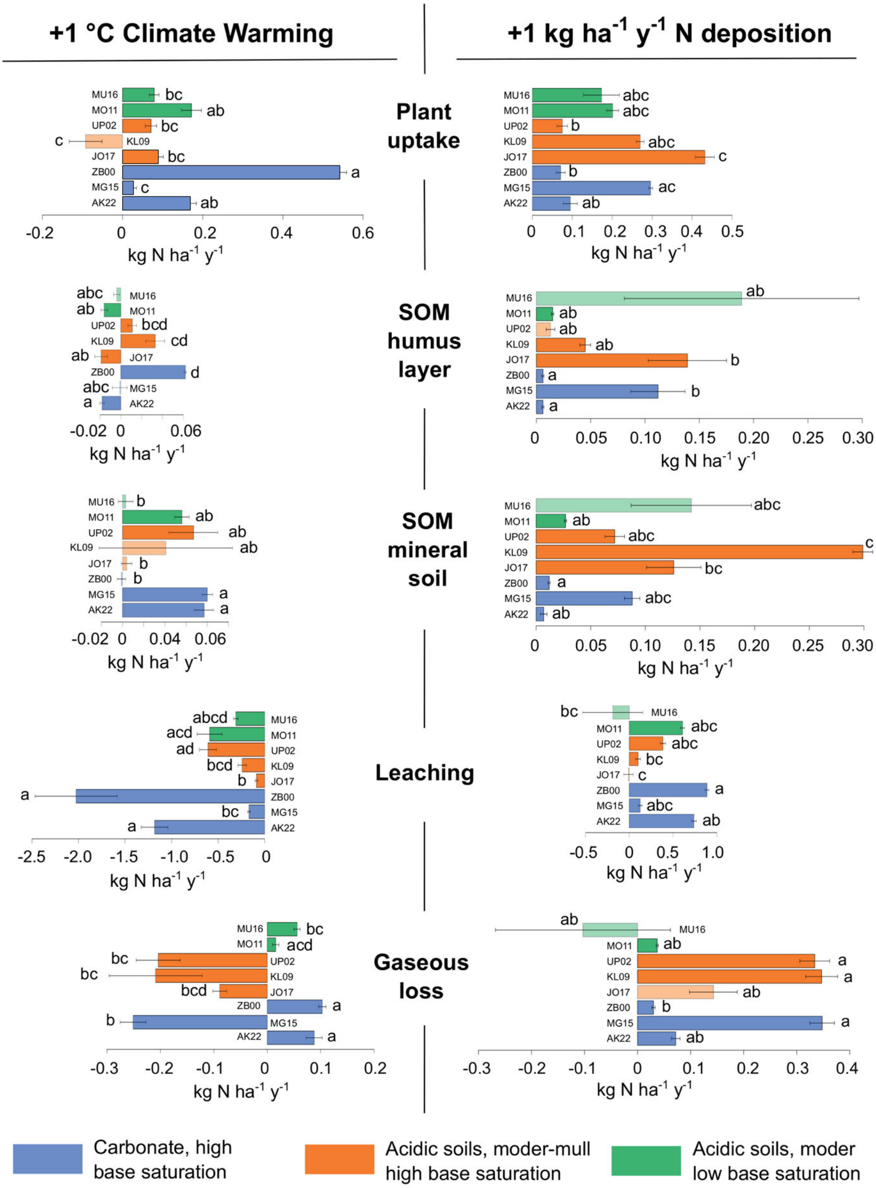

Fig. 1 Effects of 1 °C warming in annual mean temperature and 1 kg N ha^{-1} increase in annual deposition rates on N pools and N fluxes. Effects are shown as mean annual increases or decreases (plus SEM) in the period between 2080 and 2100 in the N uptake by plants, SOM N pool, N leaching with seepage water, and N loss in gaseous forms. *Dark colour bars* significantly different effects from zero (Wilcox rank sum test $p < 0.05$). *Letters a–d* differences between sites (post hoc multi-comparison Nemeneyi test $p < 0.05$)

1990 and 2010 (Fig. 2a, R^2 = 0.52, p = 0.044) and future gaseous N emissions with mean annual precipitation between 1990 and 2010 (Fig. 2b, R^2 = 0.7, p = 0.009).

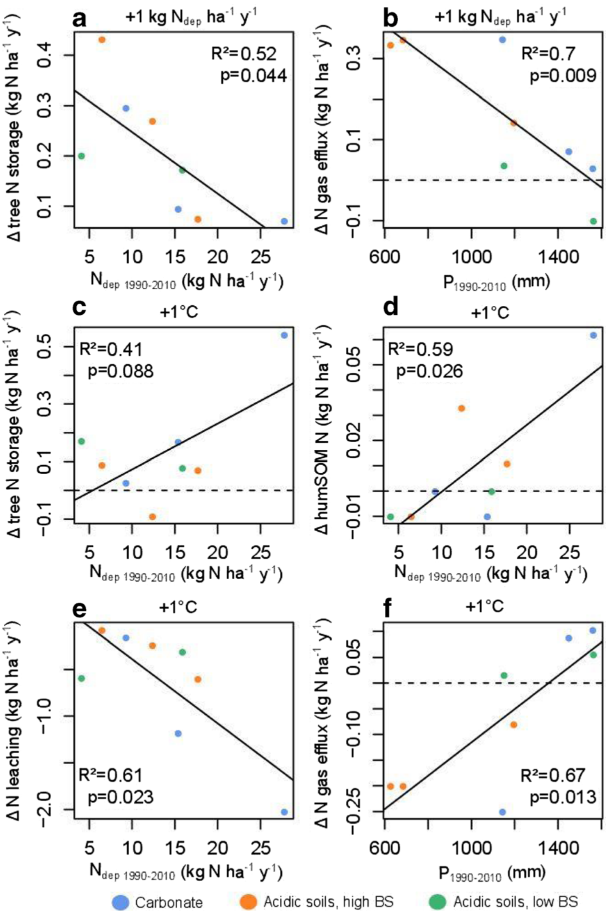

Fig. 2 Relationships between mean N deposition and precipitation (P) in the period 1990 to 2010 and effects of future N deposition and climate change on N fates in the eight study sites. Shown are mean annual effects in the period between 2080 and 2100 in climate and N deposition scenarios on N fates per kilogram N per hectare additional N deposition (**a**, **b**) and per 1 °C warming (**c**–**f**). *Dashed horizontal line* no effect, *positive values* increasing pools and flux rates, and *negative values* decreasing pools and flux rates

In addition, per degree Celsius effects of climate warming on humus N and N leaching were significantly related with the mean annual N deposition between 1990 and 2010 (Fig. 2d–e, R^2 = 0.59–0.61, p = 0.023–0.026). Also tree N uptake was, though not significantly, higher in sites with high historic N deposition (Fig. 2c, R^2 = 0.41, p = 0.088). None of the other site conditions (T, soil pH, soil C:N) had a significant ($p < 0.05$) relation with standardized future effects of N depositions or climate change.

4 Discussion

The magnitude of N deposition between 1990 and 2010 was by far the most significant determinant of future warming effects on forest ecosystem N retention explaining 59–61% of the variation in N leaching and humus N changes. Hence, climate warming caused higher SOM N storage and lower N leaching in sites where N deposition was high in the past compared to sites where it was low. Those sites experiencing water shortage in future were an exception because soil water limitations inhibited tree N uptake and SOM decomposition while continuously high N deposition caused higher N accumulation in SOM, increased N leaching and gaseous N losses.

We could show that LandscapeDNDC was capable of modelling soil water dynamics and forest growth of the investigated sites and the resulting N budgets were in line with measurements (see details in S4). Nevertheless, not all factors have been taken into account. Particularly, we neglected future increase in atmospheric CO_2 concentration despite its effect on N mineralization and biomass (Reich and Hobbie 2013).

In most sites higher rates of N deposition caused significantly higher tree growth and related uptake of N in plant biomass, which was accompanied by higher rates of N mineralization and nitrification in soils. We found a significant mean annual increase of +0.07 to +0.43 kg N ha^{-1} y^{-1} in plant biomass with every additional kilogram N input via atmospheric N deposition. This corresponds to a mean annual biomass increase of approximately 50–150 kg ha^{-1} when using mean N concentration of 2.8 g N kg^{-1} (Jacobsen et al. 2002). By the end of the twenty-first century the forest stands would have 5–15% more biomass under the B10 deposition than the MFR deposition scenario. This result corresponds quite well with estimated 1% growth increase with every kilogram N per hectare as in Laubhann et al. (2009) and Solberg et al. (2009). We can neglect any age-dependent difference in N uptake between sites because all model runs were initiated in the year 1950 and forests reached maturity by the end of the model runs. Nevertheless, future N deposition did not result in the same relative changes in tree growth among sites. In the three sites with the highest N deposition between 1990 and 2010 (AK22, UP02, ZB00) uptake increased by only +0.07 to +0.1 kg N ha^{-1} per 1 kg N ha^{-1} deposition while in sites with low historic deposition (MG15, JO17) tree N uptake increased by +0.3 to +0.4 kg N ha^{-1} per 1 kg N ha^{-1} deposition. This is in line with empirical evidence showing that chronic N deposition stimulates tree growth only to a certain level (de Vries et al. 2014) and may even be adverse at high levels of N deposition (Magill et al. 2004).

Significant retention of additional N in SOM occurred together with tree N uptake and was between +0.02 and +0.3 kg N ha^{-1} y^{-1} with every additional kilogram N per hectare in deposition. This results in a ratio of approx. 3:2 between plant and soil N retention and corroborates well with ecosystem partitioning of C sequestration with N deposition (De Vries et al. 2014). It is notable that some processes responsible for soil N retention are not fully captured by the model. Kaiser et al. (2010) demonstrated efficient N retention processes for KL09 by seasonal switches in soil microbial communities preferably feeding on soil organic matter in summer and on plant litter in autumn. Hence, we may have underestimated whole year soil N retention to some extent. In contrast to tree N uptake, we did not find a relation between historic N deposition and future N deposition effects on SOM N retention which might be controlled by a combination of factors which we cannot test because of the small number of sites. As an example, at sites where low C:N ratios of 17 were combined with mull type humus and high soil pH (AK22, ZB00), SOM N retention was particularly limited, as was also shown in Brumme and Khanna (2008), and much lower than at the third site on carbonate bedrock (MG11) characterized with a much higher A-horizon C:N ratio of 25. However, SOM N retention at MG11 was similar to sites such as JO17 and KL09 which are characterised by even lower C:N ratios (13–14) than AK22 and ZB00. At ZB00 and AK22, high precipitation and coarse textured soils cause high percolation and leaching losses (Jandl et al. 2012; Jost et al. 2011), contributing to the variation in N retention between these and other sites.

Long-term mean annual precipitation explained 70% of the variation in effects of N deposition on future gaseous N effluxes, which were predominantly positive. Simulated gaseous N efflux was particularly sensible to N deposition at the two driest study sites (KL09, UP02) but also at MG15. Both, tree N uptake and N immobilization in SOM are low in the dry sites due to chronic N deposition. N leaching is low because of low percolation, hence leaving disproportional amounts of N being prone to gaseous efflux. Higher bulk densities at these two sites, leading to lower porosity and thus generally higher anaerobic volume fractions causing denitrification, might explain the sensitivity of gaseous N loss to N deposition (Butterbach-Bahl et al. 2013).

Similar to N deposition, we found significantly increased tree N uptake with expected future climate change. The impact of climate warming on the increase in temperate forest tree growth over the last decades is well documented (Laubhann et al. 2009; Pretzsch et al. 2014a; Pretzsch et al. 2014b; Solberg et al. 2009; Thomas et al. 2010). Mean annual future rates of tree N uptake caused by each °C warming were between +0.03 to +0.5 kg N ha^{-1} y^{-1}. N deposition between 1990 and 2010 explained 41% of this variation showing that future warming induced tree growth might be higher in sites with high N deposition in the past. Though this relationship was only marginally significant (p = 0.088) and strongly controlled by only one site (ZB00) tree fertilization due to enhanced N mineralization rates under warming has been shown experimentally (Butler et al. 2012), and it is likely that the stimulation of tree growth is higher in sites with low N limitation as a result of higher N loads in the past. N deposition during the period 1990–2010 also controlled future N retention in humus. Reduced organic matter decomposition due to N deposition as shown in Frey et al. (2014) together with higher litter input may add to the increased SOM N retention. Hence, future climate change increases N retention particularly in sites in an advanced state of N saturation, which would otherwise lose N in gaseous form or as nitrate via seepage water. Indeed, past N deposition explained 61% of the variation in the future N leaching decrease across sites caused by warming.

Relative to the climate effects on plant N uptake, SOM N retention and leaching, the effects on gaseous N loss were small and idiosyncratic. Depending upon the annual sum of precipitation, N efflux was either positively or negatively affected. Future climate warming led to decreasing N gas efflux but only in the driest sites, which might be related to a decrease in rates of denitrification due to evapotranspiration. Mean annual precipitation in fact was a good predictor for the variation in gaseous N efflux effects of warming (R^2 = 0.67, p = 0.017). This agrees well with findings at one of the study sites characterised by high precipitation (AK22). Experimental soil warming by 4 °C in the growing season led to persistently elevated annual N_2O emissions (Gundersen et al. 2006) which may have been related to higher microbial activity as mineral nitrogen concentrations did not increase at the warmed plots (Schindlbacher et al. 2009). Hence, these observations corroborate our findings at the humid sites, but require caution because changes in N_2O emissions do not necessarily reflect changes in total N gas efflux.

5 Conclusions

Our study indicates that while N deposition weakens N retention in Austrian temperate forest ecosystems, expected future climate change will likely have a strong offsetting effect by increasing N immobilization in tree biomass and SOM. However, the future magnitude of this compensation will be strongly site dependent. We identified magnitude of historic N deposition to be most important but could also show climatic constraints with sites of low annual precipitation being less affected when becoming drier in future. Anticipated reduction in N deposition under a current legislation scenario will additionally lower N availability in these forest ecosystems very likely causing a lower net N loss to the atmosphere and the groundwater than we measure today.

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