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Abstract

Climate change and air pollution, interact with altering forest management and land-use change to produce short and long-term changes to forest in Europe. The impact of these changes on the forest greenhouse gas (GHG) balance is currently difficult to predict. To improve the mechanistic understanding of the ongoing changes, we studied the response of GHG (N_2O , CH_4) exchange from forest soils at twelve experimental or natural gradient forest sites, representing anticipated future forest change. The experimental manipulations one or more per site included nitrogen (N) addition (4 sites), changes of climate (temperature, 1 site; precipitation, 2 sites), soil hydrology (3 sites), harvest intensity (1 site), wood ash fertilization (1 site), pH gradient in peat (1 site) and afforestation of cropland (1 site).

In most of the investigated treatments N_2O emissions increased by 7 ± 3 (range 0–30) $\mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ across all treatments on mineral soils, but by up to 10 times the mineral soil maximum on an acidic organic soil. Soil moisture together with mineral soil C/N ratio and pH were found to significantly influence N_2O emissions across all treatments. Emissions increased with N availability and decreased with soil C/N ratio, especially in interaction with increased soil moisture. High pH reduced the formation of N_2O , even under otherwise favourable soil conditions.

Oxidation (uptake) of CH_4 was reduced from 16 ± 2 to 4 ± 6 $\mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ by the investigated treatments. The CH_4 exchange was significantly influenced by soil moisture and soil C/N ratio across all treatments, and CH_4 emissions occurred only in wet or water-saturated conditions.

For most of the investigated forest manipulations or natural gradients, the response of both N_2O and CH_4 fluxes was towards reducing the overall GHG forest sink. The most resilient forests were dry Mediterranean forests, as well as forests with high soil C/N ratio or high soil pH. Mitigation strategies may focus on (i) sustainable management of wet forest areas and forested peat lands, (ii) continuous forest cover management,

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(iii) reducing atmospheric N input and, thus, N availability, and (iv) improving neutralisation capacity of acid soils (e.g. wood ash application).

1 Introduction

European forests sequester atmospheric carbon in biomass and soil at an estimated annual net rate of 109 Tg (Luyssaert et al., 2010), which is about 10 % of the European fossil fuel emissions. Moreover, compared to agricultural soils, forest soils generally function as a net sink for the strong greenhouse gas (GHG) methane (CH₄) and emit less of the even stronger GHG nitrous oxide (N₂O), hence, having a net total GHG mitigation effect.

The radiative forcing of CH₄ and N₂O on a time horizon of 100 yr is 25 and 298 times stronger than CO₂, respectively. The atmospheric concentration of both gases has constantly risen since the late 1890's, amounting presently to a 158 % and 19 % increase, respectively, compared to pre-industrial levels (WMO, 2010). At present, these two greenhouse gases constitute 18 % (CH₄) and 6 % (N₂O) of the global radiative forcing in the atmosphere (not accounting for water vapour), and their role in the global warming is expected to increase in the future (WMO, 2010).

Recently, the first European Nitrogen Assessment (Sutton et al., 2011) stated that European forests were responsible for a net cooling effect, although the magnitude of this phenomenon is still associated with considerable uncertainty (Schulze et al., 2009; Butterbach-Bahl et al., 2011b). These studies have also pointed to the fact that enhanced C sequestration in European forests is in part a consequence of increased N deposition. However, the largest uncertainty on the net GHG balance of these ecosystems is related to the determination of annual budgets of N₂O and CH₄ and to feedback mechanisms between changes to forests and CH₄ and N₂O soil-atmosphere fluxes. Currently, the forested area in Europe is increasing annually by 0.3 % and is expected to continue to increase by natural succession after abandonment of agricultural land or

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by active afforestation. Thus, the importance of forests for the European GHG balance will increase.

Current and future management strategies, such as replacement of coniferous with broadleaf species, restoration of natural water regime to conserve and foster biodiversity, modified and intensified management strategies towards use of wood for bioenergy, will contribute to altering the present GHG balance of CH₄ and N₂O for forests in combination with climate change (i.e. temperature increase and altered precipitation patterns) and air pollution. Limited scientific evidence is available to allow for an accurate prediction of forest changes in Europe and subsequent impacts on the balance of CH₄ and N₂O (Schulze et al., 2009).

The present work aims to contribute to filling this knowledge gap. We compiled annual fluxes of N₂O and CH₄ from forest soils at twelve sites across Europe ranging from Sweden to Portugal where manipulation or natural gradient effects on non-CO₂ GHG fluxes were investigated.

The conceptual frame of our study is visualised in Fig. 1. The *external drivers* of forest change will alter soil conditions, which we call the *internal drivers*, leading to responses in N₂O and CH₄ fluxes (Fig. 1). Based on recent literature reviews we expect soil pH, diffusion properties, N availability, soil temperature and water content to be the most important internal drivers affecting the exchange of these gases (Ball et al., 1997; Butterbach-Bahl et al., 2011a,b; Liu and Greaver, 2009; Machefert et al., 2002). The goal of this paper is to synthesise how changes of the external and internal drivers are connected to the exchange of N₂O and CH₄ in European forests. Based on this conceptual frame, the objectives of this study are: i) to present the responses of CH₄ and N₂O to changes in external drivers; ii) to identify interactions between external and internal soil drivers of CH₄ and N₂O fluxes including feedback to external changes; iii) to identify potential risks for increased emissions of CH₄ and N₂O due to expected future forest change as well as their sources and relative importance, stratified by area, forest type and management; iv) to propose mitigation options by managing external and internal drivers.

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2 Methods

2.1 Sites with forest change

Results of the annual GHG exchange were compiled from 12 sites with manipulation experiments or observational gradients (Table 1) selected to represent multiple aspects of forest change across Europe (Fig. 2). Long term experiments and well characterised sites were preferred where possible to avoid transient responses and due to the availability of soil and vegetation data. Field measurements of soil GHG exchange were established at all sites and treatments as part the NitroEurope project (C2 sites) and designed specifically to address the objectives of this study. For studies over soil gradients, plots were established along the gradients according to soil characteristics to form treatments (e.g. in a soil hydrological gradient, separate plots were installed in a dry upland treatment (control) and a wetter lowland treatment). In total, 39 treatments (including controls) and 74 plots were investigated. Main site characteristics are presented in Table 1 along with references to more detailed site information and in depth descriptions of the manipulation treatments.

The climate ranged from hemi-boreal in Sweden with a mean annual air temperature (MAT) of 5 °C to Mediterranean climate in Portugal with a MAT of 15.5 °C. Mean annual precipitation (MAP) ranged from a maximum of 2300 mm at Alptal (AT) to a minimum of 594 mm at Vestskoven (VS). Ambient N deposition ranged from 8 to 29 kg N ha⁻¹ yr⁻¹ at Gårdsjön (GS) and Höglwald (HW), respectively.

2.1.1 Nitrogen addition

For the study of responses to elevated N deposition, four ongoing N addition experiments were available (Table 1). Three of them – GS, Sweden, Klosterhede (KH), Denmark and AT, Switzerland – were originally a part of the NITREX project (Wright et al., 1995). The selected forest stands were Norway spruce (*Picea abies* (L.) Karst.) stands with an age spanning 80 to 200 yr. N addition started in 1991–94 with a monthly or

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event-based application rate of 25–35 kgN ha⁻¹ yr⁻¹ (NH₄NO₃). Soils at GS and KH were acidic (pH < 4.3) nutrient poor podzols, whereas AT had a less acidic (pH 5.5) Gleysol. The fourth experiment – Klausenleopoldsdorf (KL), Austria – comprised a similar treatment with addition of 50 kgN ha⁻¹ yr⁻¹ since 2006 in a 65-year-old beech (*Fagus sylvatica* L.) stand on an acidic (pH 4.6) Cambisol. Ambient N deposition was 10–20 kgN ha⁻¹ yr⁻¹ at the four sites leading to a total N deposition on the manipulated plots between 45 and 65 kgN ha⁻¹ yr⁻¹. The experiment at KH had a paired plot design, whereas at KL a block design with six replicates was implemented. The experiments at AT and GS were paired catchment studies. At AT the studied catchments were 0.15 ha and at GS they were > 0.5 ha. At both sites, wet and dry areas were included and sampled as separate treatments at GS.

2.1.2 Climate change

The response to changes in precipitation regime were studied by throughfall manipulations at two Mediterranean sites initiated in 2004: Tolfa Allumiere (TA), Italy (with GHG sampling between 2006–2007) and Herdade da Mitra (HM), Portugal (with GHG sampling between 2008–2009) with evergreen woodlands dominated by strawberry tree (*Arbutus unedo* L.) and cork oak (*Quercus suber* L.), respectively. At TA and HM a dry treatment with an exclusion of 20–26 % of the annual throughfall was established, using partial roofs and plastic covers installed 0.3–1.6 m above the soil surface. Throughfall collected at the dry treatment was redistributed by suspended sprinklers or irrigation pipes with drip emitters on other plots to obtain a wet treatment at HM and to keep soil water content above 10 % during dry summer at TA. Both sites were established as a block design with three replicates including also ambient control treatments. The soil was an Andisol at TA with pH 4, and a Cambisol at HM with pH 5.5.

The response to elevated temperature was studied in a soil warming experiment established in 2004 at Achenkirch (AK), Austria in a 130-yr-old Norway spruce (*Picea abies*) dominated stand. Soil warming +4 °C at 5 cm depth was maintained in the

vegetation period by heating cables installed at 3 cm depth 7.5 cm apart. Paired warmed and controls plots (2 × 2 m) were established in three replicates. Soils were shallow Chromic Cambisols with pH slightly above 6 on Dolomite bedrock.

2.1.3 Land use change

5 We considered “land use change” as the changes of long-term influences (rotation length or longer) on soil processes such as afforestation on cropland, the choice of tree species and changes in drainage. Two chronosequences of afforestation on cropland were studied in Denmark, one with Norway spruce (*Picea abies*) and one with pedunculate oak (*Quercus robur* L.) at Vestskoven (VS1), where young (12–15 yr) and
10 older (40 yr) stands of each species were compared. Soils were Luvisols still affected by previous liming and fertilisation. In the same area, another oak stand planted on a gentle slope comprising a hydrological gradient was studied (VS2). After agricultural activities had ceased, the drainage system gradually failed and a small temporary pond emerged at the low end of the slope. A similar slope was selected at Strødam (ST),
15 Denmark in a 200-yr-old beech (*Fagus sylvatica*) forest (unmanaged since 1945) and used to represent a natural undisturbed hydrological gradient. The soil type at ST was an Arenosol with pH ranging from < 4 to 6. At these two sites (VS2, ST) measurements were done in transects along the hydrological gradients and were delineated for this study to form dry (well-drained upland) treatments (control) and wet treatments
20 (permanently moist soils). Due to soil pH differences probably caused by groundwater inflow versus outflow zones, the wet treatment at ST could be further separated to wet-pH < 4 and wet-pH > 4.

2.1.4 Forest management

25 We included two aspects of forest management, harvest intensity and fertilisation/re-use of wood ash, both relevant in scenarios with increased bioenergy extraction from forests. At Höglwald (HW), Germany, clear-cut and selective cutting were compared

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in a 100-year-old Norway spruce (*Picea abies*) stand. In February 2000, one plot was clear-cut while a second plot was selectively cut with approx. 20 % of the basal area removed. The clear-cut and the gaps formed underneath the remaining spruce trees in the selective-cutting treatment were planted with beech seedlings. A third intact Norway spruce stand remained as control. The soil at HW is an acidic (pH < 4) Dystric Cambisol and N-saturated due to long-term high atmospheric nitrogen input of c. 30 kg N ha⁻¹ yr⁻¹ (Huber et al., 2004). As the treatment response we report a mean for the first 3 yr after the disturbance since that period exhibits a clear response to the clear-cut treatment.

Stabilised wood ash was applied in two doses (3.3 and 6.6 t ash ha⁻¹) in a random block design at Skogaryd (SR), Sweden, on a drained Histosol afforested with Norway spruce (*Picea abies*) 60 yr ago after abandonment of agricultural use. Wood ash was spread by hand in August 2006 and measurements of GHG fluxes were conducted between July 2006 and June 2008. Due to an apparent difference in water table among the plots the highest wood ash treatment was excluded from our analysis. Wood ash clearly affected soil pH. To further illustrate the long term effect of pH differences, another drained Histosol site at Falköping (FK), Sweden, with a Silver birch (*Betula pendula* Roth) forest was studied. Here, soil GHG fluxes were measured in plots along a natural occurring pH gradient, ranging from 3.6–5.8, with the high pH taken as the control treatment in our analysis.

2.2 Gas exchange measurements

A common minimum protocol for gas sampling in the field, gas analysis and criteria for conversion of gas concentration to fluxes was agreed on among the participants of the NitroEurope Component 2 (C2) on manipulation experiments. All GHG fluxes were measured using manually operated closed static chambers measured at weekly to monthly intervals except at the HW site where automated closed static chambers were sampled on a 2-hourly basis. An overview of the gas sampling protocol at all sites is given in Table 2. In total, soil GHG exchange was measured from 248 chambers.

Some sites continued gas flux measurements that started prior to the NitroEurope project period, but at most sites chambers were installed according to the protocol after 2006 and measurements started a couple of months later. Measurements were done for one year at three sites and two or more years at the other sites. In our analyses we used the average flux of N₂O and CH₄ ($\mu\text{g m}^{-2} \text{h}^{-1}$) per treatment calculated on an annual basis (Table 3), along with site and soil characteristics determined in each treatment. The original flux data obtained were uploaded to a common database (<http://nitroeuropedata.ceh.ac.uk>).

2.3 Calculations and statistics

Treatment responses are reported here as the absolute difference in gas exchange fluxes between control and treatment. Response ratios were difficult to use due to control fluxes being close to zero at several sites. Treatment responses were tested for each treatment year with measurements by the statistical method appropriate for the design of each experiment and are reported in Table 3.

The influence of site and soil characteristics on mean annual gas exchange fluxes were explored by stepwise regression with the SAS procedure REG, first using data from control treatments and then from all treatments on mineral soil. In the first analysis the land use change sites were represented by the oldest stands and those on upland dry soils as control treatments. In stepwise regression analyses we considered the influence of MAT, MAP, throughfall precipitation, N deposition and the following soil parameters: bulk density, pH, and C/N ratio from the top mineral soil (0–20 cm), soil organic carbon (SOC; 0–30 cm) as well as soil moisture and soil temperature (at c. 5 cm depth). Log-transformed N₂O and CH₄ fluxes and reciprocal values of mineral soil C/N ratios were used in order to fulfil the assumptions of the stepwise linear regression analyses. Time series data were represented as mean values over the gas exchange measurement period.

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3 Results

3.1 N₂O responses

All the investigated forest soils acted as sources of N₂O, except for a small net negative flux of $-0.5 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ at the wet treatment in GS (Table 3). The maximum emission of $77 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ occurred from the drained organic soil at FK, Sweden (Table 3). The other Swedish site on organic soil (SR) had emission rates ranging from 17 to $30 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$. For mineral upland soils, the mean (\pm standard error of the mean) was $3 \pm 1 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$, with a maximum of $8 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ at KL. Stepwise regression analysis including only control treatments on mineral soil revealed a significant negative correlation between mineral soil C/N ratio and N₂O flux (Table 4).

Overall, the response of N₂O fluxes to treatments was generally positive (Table 3, Fig. 3), and again the organic soils at FK (with the highest flux in the control treatment) exhibited the highest flux changes (up to $291 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$) over a soil pH gradient. The responses increased with the level observed on the control ($R^2 = 0.64$, $p < 0.001$). The mean N₂O emission from mineral upland soils for all treatments was $7 \pm 3 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$, and the response of N₂O to treatments ranged from no significant change at several sites to $30 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ (Fig. 3). Even within groups of similar manipulation types, e.g. N addition, responses varied by orders of magnitude (Fig. 3). The responses on mineral soils alone also increased with the level observed on the control ($R^2 = 0.31$, $p < 0.03$) when excluding GS wet where the response was exceptionally strong, see later. The largest treatment response on mineral soil occurred after clear-cut at HW, but this was a transient response. After reaching the highest emission in the second year after the cut, emissions gradually declined to pre-cut levels in the sixth year (data not shown).

The stepwise regression analysis including all control and treatment plots on mineral soils showed that a combination of soil moisture, mineral soil C/N ratio (reciprocal) and soil pH had a significant positive effect on N₂O emissions (Table 4).

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3.2 CH₄ responses

At all control plots, except the AT site (Table 3), mean CH₄ fluxes were negative ($-15 \pm 2 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$), i.e. the soil generally acted as a sink of atmospheric CH₄ and ranged from a maximum uptake of $-38 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ at the drained organic soil at SR to a small net emission of $3 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ at the wet AT site. The stepwise regression including only control treatments on mineral soils indicated that soil moisture was the most important factor although not statistically significant ($p > 0.05$) (Table 4).

With the exception of three sites, treatments generally increased net CH₄ exchange, meaning that either CH₄ oxidation was reduced or CH₄ emission increased (Fig. 4). The mean CH₄ flux for the treatment sites was $-4 \pm 6 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$, indicating an overall four-fold reduction of CH₄ uptake. The response to manipulations was minor at several sites, but reached $80 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$ (Fig. 4) at the hydrological gradient site, ST. In fact, major responses to manipulation, excluding the organic soils, were all observed at the sites with wet soil conditions (AT, GS, VS1 and ST), where a switch from net CH₄ uptake in upland soils (control plots, except at AT) to net CH₄ emission in the wet parts occurred. Even within groups of similar manipulation types, e.g. N addition or pH gradients, responses varied markedly (Fig. 4) and the responses were not related to the level observed on the control treatments. The treatments that stimulated CH₄ uptake were additional precipitation at HM, selective cutting at HW and wood ash addition at SR, though not significantly (Fig. 4).

The stepwise regression analysis for CH₄ on all plots included a combination of soil factors similar to N₂O (Table 4). Soil water content and mineral soil C/N ratio could explain the variation in CH₄ fluxes observed at a significant level (Table 4).

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4 Discussion

4.1 Factors controlling N₂O emissions from forest soils

Our data (Table 3, Fig. 4) emphasise the large variability encountered when dealing with N₂O fluxes from soils reported in numerous studies (e.g., Pilegaard et al., 2006, Skiba et al., 2009). Based on the diverse assemblage of forest sites and treatments we discuss the main soil factors (and their interaction) that may control the large variability in N₂O emission. The two Swedish organic soil sites investigated (SR, FK) had much greater N₂O emission (a factor of 5 to 10) and greater treatment responses than sites on mineral soils (Table 3). High N₂O emissions from organic soils are known, and a recent review discussed controlling factors on this soil type across many sites in boreal climate (Maljanen et al., 2010). We thus focus on the mineral soil sites that are better represented in our dataset.

4.1.1 Nitrogen availability

As expected, N addition had a positive effect on N₂O emission across all four experiments (GS, KH, AT, KL), which was statistically significant at 3 out of 5 sites (Fig. 3). This suggests that N deposition could enhance N₂O emissions, but the regression analysis did not give any explanatory power to N deposition (control treatments, Table 4), as also observed by Pilegaard et al. (2006) for another European-wide dataset. Even the stepwise regression across all treatments including the relative large N additions (35 to 50 kg N ha⁻¹ yr⁻¹) did not reveal an overall effect of N input (Table 4), since the responses in N₂O emissions to N addition were low compared to responses to other changes.

In the dataset compiled by Pilegaard et al. (2006), the C/N ratio of the top mineral soil was the best predictor of N₂O emissions from forests on mineral soils. Likewise, our stepwise regression analyses for controls as well as for all plots underlined the role of mineral soil C/N as a significant predictor of N₂O fluxes (Table 4). In Fig. 5 we plotted

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control (filled symbols) and treatment (open symbols) data for N₂O emission vs. mineral soil C/N ratio (with sites identified by numbers) along with the relationship observed by Pilegaard et al. (2006). The relationship of the N₂O emission to C/N ratio in our data does not show up clearly in Fig. 5, probably due to interaction with other factors, mainly soil moisture and pH. However, small N₂O emissions were observed at C/N ratio above 30 and N₂O emissions were higher and more responsive to change at sites with lower C/N ratios. No or low emissions were observed at some plots with C/N below c. 20, if these plots were dry (TA), or with high soil pH (AT, VS1, VS2) or both (HM). One of the largest responses to change (dry to wet) was seen at the afforested site (VS2) with a C/N ratio of 11. A relationship between soil C/N ratio on N₂O emission was also found across a number of organic soils with a threshold for increased N₂O emission at C/N ratios around 20 to 25 (Klemedtsson et al., 2005; Maljanen et al., 2010). The emission level at the SR site with a C/N ratio of 23 is in line with that relationship for organic soils, and the FK site was represented in the Klemedtsson et al. (2005) dataset with the lowest C/N ratio (13) and the highest emission.

The C/N ratio can be seen as a proxy for N availability. At high C/N ratio N immobilisation is dominating, but as C/N ratio decreases net mineralisation increases, and below C/N 24–27 net nitrification occurs (Aber et al., 2003; Dannenmann et al., 2007; Kriebitzsch, 1978). With N₂O emissions mainly coupled to nitrification and denitrification, the highest N₂O fluxes should be expected when nitrate is formed and available at lower soil C/N ratios (< 25) where also losses by nitrate leaching usually increases (Gundersen et al., 1998).

In forests N losses to the atmosphere by N₂O emission and N losses to the hydrosphere as leaching below the root zone are both preferentially occurring at low soil C/N ratios (high mineral N availability). Therefore, a correlation between the two types of N losses from the soil should be expected. We plotted N₂O emissions and nitrate leaching data (where available) from our sites with other published data in Fig. 6. At low leaching rates (< 5 kg N ha⁻¹ yr⁻¹) N₂O emissions are mainly less than 5 µg N₂O-N m⁻² h⁻¹, and above this leaching rate the N₂O emissions are above 5 µg N₂O-N m⁻² h⁻¹. Within

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individual sites a clear relationship between N leaching and N₂O emission was found for VS2 (Christiansen and Gundersen, 2011) and for the treatments with similar forest cover at HW (control and selective cut) plotted here for three individual years (2000–2002), where N₂O emission doubled as nitrate leaching increased from 45 to 70 kg N ha⁻¹ yr⁻¹. However, the relationship across sites is not clear. The N losses from the clear-cut treatment at HW were obviously in another category especially for the first two years with N leaching > 100 kg N ha⁻¹ yr⁻¹ and N₂O emission around 50 μg N₂O-N m⁻² h⁻¹. After the clear-cut, N availability was exceptionally high (no plant uptake), and soil moisture as well as seepage water flux was high due to low evapotranspiration, leading to large N losses to both air and water.

4.1.2 Soil pH

We observed a significant effect of soil pH together with soil moisture and C/N ratio in the stepwise regression for all plots on mineral soil (Table 4). It is well known that N₂O emissions increase at lower soil pH because the nitrous oxide reductase enzyme is inhibited resulting in an increased N₂O/N₂ ratio in the product of denitrification (Šimek and Cooper, 2002) and consequently leading to higher N₂O production. Our data did not suggest a threshold soil pH for enhanced N₂O emission, but treatment responses were larger at soil pH below 4 as it was observed at the ST and FK sites (Christiansen et al., 2012; Weslien et al., 2009). The noticeable decline in emissions on the organic soil over the natural increasing pH gradient at FK and the decline after wood ash application at SR (increasing soil pH) again emphasises the importance of pH, even if other parameters correlated more strongly with the N₂O emission as well (Weslien et al., 2009).

4.1.3 Soil moisture

Soil moisture levels are known to control the magnitude of N₂O emission originating from denitrification (e.g., Firestone and Davidson, 1989; Schaufler et al., 2010).

Evidently, the temporal variation of soil moisture is an important factor for variability of N_2O emissions (Kitzler et al., 2006; Christiansen et al., 2012), often with higher emissions in wet periods than dry (at the same temperature) as we also observed (data not shown). However, our study focused on whether forest change, as we defined earlier, leads to long-term effects or if it changes the average soil moisture content rather than the short-term effects of soil moisture variability.

In agreement with the existing knowledge, the stepwise regression revealed mean soil moisture as the most important parameter affecting N_2O emissions (Table 4) across all treatments including wet forest areas. High emissions at wet, but not saturated, conditions are expected since the conditions for the anaerobic process of denitrification are favoured, as in the wetter soil oxygen consumption exceeds the supply due to inhibition of gas diffusion. For example, N_2O emissions were reduced during very wet periods compared to the usual moist conditions at the AT site (data not shown). It is important to note that wet conditions (up to a certain level) may also indirectly increase the release of substrates (NH_4^+ , NO_3^- and organic N) for N_2O production. Furthermore, soil water content can control soil pH through the limitation of weathering processes and subsequent proton release. Thus, soil moisture, rather than being only a direct effect, can also act as an indirect effect, influencing other important biogeochemical drivers of N_2O exchange.

The interaction between enhanced soil moisture and N availability was most prominent at the three mineral soil sites with the largest treatment responses (GS wet, VS1, HW clear-cut; Fig. 3). As discussed above, increased N availability and higher soil moisture after clear-cut at HW gave the highest N_2O response. A response almost as high as at HW clear-cut was observed over the hydrological gradient on a former fertilised arable soil (VS1). While we cannot directly assess how soil moisture and N availability interacted at that site, we can directly deduce how the addition of N, at certain hydrological conditions, stimulated N_2O production. Addition of N at GS gave a minor increase in the drier parts of the catchment, but a major increase in N_2O emission from the wetter parts (Fig. 3).

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4.1.4 Climate change

Even though the climatic conditions of the experimental sites of this study spanned from hemi-boreal in Sweden to Mediterranean in Portugal, the large variation in treatment responses overshadowed any climatic effects. There was no influence of mean annual precipitation or mean annual air temperature on N₂O fluxes. In contrast, increasing the soil temperature by 4 °C in the growing season at the only site with experimental soil warming (AK) led to persistently elevated annual N₂O emissions (Table 3, Fig. 3), probably related to enhanced microbial activity (Schindlbacher et al., 2009) and N turnover (Verburg et al., 1999).

At the water addition/exclusion sites (HM, TA), emulating changing precipitation patterns, only small and non-significant effects on N₂O emission were found. However, addition of water temporarily stimulated N₂O production at HM, but the effect was not persistent throughout the measurement period (Shvaleva et al., 2011). As mentioned earlier, low emissions at HM may be an effect of high pH. The TA site was acidic (pH 4), but a detailed process study at the site showed a chemical inhibition of nitrification and denitrification as a reason for minor N₂O emissions across all treatments (Castaldi et al., 2009).

4.1.5 Synthesis

Most of the considered forest change treatments increased N₂O emission through changes in soil conditions (internal drivers) and their interactions (Fig. 7). Nitrogen availability – and especially NO₃⁻ availability – was, as expected, a prerequisite for significant N₂O emission. However, emissions were not related to N deposition, although N additions increased the emissions. The mineral soil C/N ratio (proxy for N availability) was a weak predictor of N₂O emission with low emissions and moderate treatment responses at C/N ratios > 25 (Fig. 5), but the interactions with other soil conditions were important. High pH (above ≈ 5 in mineral soil) limited N₂O emission, regardless of other favourable soil conditions. High soil water content is a key condition for the

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highest N₂O emissions observed often in interaction with high N availability. However, as soil water content approached saturation, the effect on N₂O emission ceased, either due to reduced gas diffusion and/or due to complete reduction to N₂ (Fig. 7). Soil temperature increased N₂O emission – an effect that may in part be caused by stimulating N mineralisation and thus N availability rather than just the temperature effect on microbial activity alone (Fig. 7).

4.2 Emission factors for N₂O

Quantification of the N deposition effect on N₂O emission remains difficult, since other environmental conditions may also play a significant role. A default N₂O emission factor of 1 % of the N introduced to the system has been suggested for soils following N deposition in IPCC reporting guidelines (IPCC, 2006). Although a large variability in emissions from our assemblage of sites and treatments on mineral soils was detected, median and range of emission factors were 1.2 % and 0–5 % in control plots, and 1.7 % and 0–32 % for all plots, respectively. For the organic soils from Sweden emission factors were 20–400 %, indicating that N deposition was not an important source of the N₂O at these sites. In N addition sites, only 0.1 % (KH) to 1 % (KL) of N input was emitted as N₂O, with the exception of the wet parts of GS, where 5 % of the added N was emitted back to the atmosphere. In a previous study along N deposition gradients from an ammonia source (poultry farm) it was estimated that 1.4 % and 5.4 % of the N deposition was returned to the atmosphere as N₂O in coniferous and deciduous forest, respectively (Skiba et al., 2006).

Our data show that N₂O emission factors vary considerably in both controls as well as across the entirety of plots. The variability of N₂O emission factors was clearly increased by the manipulations, where the largest factor of 32 %, although transient, was found after the clear-cut at HW. A precise estimate of the emission factor from (semi-)natural ecosystems in a landscape or a region would have to take into account the extent of wet areas and organic soils with high emission strength as well as areas with wide C/N ratio with low emission strength. Furthermore, temporary emission

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extremes would also have to be included. The 1 % default N₂O emission factor can only be taken as a rough estimate of indirect N₂O emissions, but it is probably too low by a factor two in comparison to what was measured at our sites as well as based on other estimation approaches (Butterbach-Bahl et al., 2011b). Our findings underline the fact that default N₂O emission factors are not able to capture the intrinsic feedback mechanisms between biogeochemical processes, especially when interacting with soil water and N availability, which can result in dramatic increases in N₂O emissions.

4.3 Factors controlling CH₄ uptake or emission

Much of the efforts in measuring and understanding CH₄ exchange have been devoted to organic soils that often exhibit major emissions, but many forested organic soils show a net uptake of CH₄ (Maljanen et al., 2010). This was also the case for the two Swedish organic soils investigated (SR, FK; Table 3). As for N₂O, in the following we focus on the results from mineral soils and the factors affecting CH₄ exchange across our diverse assemblage of forest sites and treatments.

4.3.1 Nitrogen availability and soil pH

Similar to previous studies on the effect of nitrogen addition (Stuedler et al., 1989; Liu and Greaver, 2009), all sites receiving additional N experienced a decrease in CH₄ oxidation in the soil, although at only two of the sites responses were significant (Fig. 4). Ammonium can compete with the enzyme methane mono-oxygenase in the soil, effectively lowering the oxidation of CH₄ by methanotrophs (Hanson and Hanson, 1996). The variable reduction of CH₄ oxidation across the N addition sites indicates that other soil factors may be important as well. The significant influence of C/N ratio on CH₄ fluxes across all treatments (Table 4; positive influence on the reciprocal C/N ratio) also suggests an overall negative effect of N availability on CH₄ oxidation.

Acidic conditions are assumed to be suboptimal for methanotrophs (Hanson and Hanson, 1996) but CH₄ oxidation was observed in quite acidic soils such as the ST

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(Christiansen et al., 2012) and the HW (Butterbach-Bahl and Papen, 2002) sites. A positive effect of increasing pH was observed for the organic soils at the wood ash addition site (SR) as well as at the pH gradient site (FK), but for the mineral soils no clear pH effect could be identified (Table 4).

4.3.2 Soil moisture and climate

Soil moisture is one of the most important factors controlling CH₄ dynamics in soils (Le Mer and Roger, 2001) due to the effect on both diffusion of CH₄ within the soil matrix as well as the physiological stress excess or limited water exerts on methanotrophic bacteria and promotion of CH₄ production at anaerobic conditions following saturation.

We thus observed the largest response of CH₄ fluxes in treatments involving water, and our stepwise regression analyses confirmed this (Table 4). Emissions of CH₄ were, as expected, confined to very wet or water-saturated sites/treatments. A recent reassessment of the European CH₄ budget showed that the inclusion of wet forest soils in the assessment doubled the estimated CH₄ emissions from natural ecosystems (Grunwald et al., 2012) emphasising the importance of these soil types.

In the upland forest soils, higher soil water content might not per se reduce CH₄ oxidation. Gas diffusion is proposed as one of the most important factors limiting CH₄ uptake, and diffusivity is directly linked to soil water content by blocking pathways within the soil matrix (Dubbs and Whalen, 2010). Thus, it is likely that increased soil water content in soils that normally act as sinks, as after clear-cut at HW and in the gradient at VS1, limits CH₄ oxidation simply by lowering the transport of atmospheric CH₄ to the soil pore system. At HW, increased N availability in combination with lower gas diffusion may explain the observed reduction in CH₄ oxidation after clear-cut.

No consistent effect of precipitation or temperature could be observed across the sites, although the wettest site, AT with a MAP of 2300 mm, was the only site showing a net CH₄ emission. Changed precipitation regimes at the two Mediterranean sites (HM, TA) showed inconsistent and insignificant responses (Fig. 4). However the

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measured uptake rates ($20\text{--}28\ \mu\text{g CH}_4\text{-C m}^{-2}\ \text{h}^{-1}$; Table 3) stress that in dry ecosystems methanotrophs are present and active.

Increasing the soil temperature ($+4\ ^\circ\text{C}$ during the growing season) at the AK site significantly reduced CH_4 oxidation (Table 3). However, considering that elevated soil temperatures may have stimulated N turnover it is plausible that part of the reduction in CH_4 oxidation represents a similar effect as observed for the N addition sites.

4.3.3 Synthesis

Most of the forest change treatments investigated led to reduced uptake (lower CH_4 oxidation) except for the wet-dry gradients (ST, VS1), where emission occurred at high soil moisture. Overall, our results indicate that soil water dynamics (through effects on gas diffusion) are crucial to CH_4 fluxes (Fig. 7), and change of hydrological conditions is the single most important factor that controls the magnitude and direction of CH_4 fluxes into and out of the soil. Increased N availability by forest change treatments (and between sites as indicated by an effect of soil C/N ratio) also reduces the CH_4 uptake (Fig. 7).

4.4 Hot spots and hot changes – mitigation perspectives

Prediction of GHG exchange in time and space as well as upscaling to national or continental scale remains challenging (e.g., Schulze et al., 2009). This challenge has been described to arise from the fact that hot spots (small areas) and hot moments (brief periods) frequently account for much of the N_2O gas exchange (Groffman et al., 2009), and the same is true for CH_4 (Grunwald et al., 2012). Our study added short- and long-term effects of forest change to this complexity, and some of our forest treatments (hot changes) even altered the GHG exchange orders of magnitude compared to the control (Table 3). “Hot changes” are much related to the wet and temporary wet areas that are also “hot spots” within forests, but also N deposition, forest management and soil warming affected soil GHG exchange significantly.

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Most of the investigated treatments increased the net loading of GHG to the atmosphere (cf. Figs. 3 and 4) because of the increased emissions or the reduced uptake for N_2O and CH_4 , respectively. Only for three treatments the responses had the opposite direction for the two gases, but in these cases the responses were relative small. For example, older afforested stands emitted more N_2O than younger stands (site VS2), but older stands had a higher CH_4 uptake rate. Another more important trade-off between the gases was observed in the dry-wet gradients (site ST, VS1): Emissions of N_2O did increase in the wet parts of these gradients but became negligible at water-saturated conditions (Christiansen et al., 2012), where in contrast CH_4 emissions increased considerably.

The similarity in response to treatments indicate a correspondence in the soil factors regulating the soil-atmosphere exchange of these two gases as illustrated in Fig. 7. A synergistic effect of N availability and soil water content on N_2O emission was shown by N addition in the wet parts of GS, and was also demonstrated by the major response of N_2O emissions to clear-cutting at HW.

Considering the 12-fold larger warming potential of N_2O compared to CH_4 , most emphasis should be on N_2O with respect to controls on emissions and to mitigation efforts. However, for the majority of forest change treatments investigated, the direction of the response was the same for both gasses, reducing (or, in a few cases, increasing) the overall GHG sink strength of forests.

The two organic soils studied confirm that peatlands, and particularly those on afforested former agricultural soils, are hot spots (Maljanen et al., 2010) and are highly sensitive to changes in soil conditions. The fertile FK site with some of the highest fluxes of both gases may be a special example, however, confirming the importance of C/N ratio and pH (Klemedtsson et al., 2005) in controlling the GHG exchange from organic soils. Forests with complex topography may have wet and temporary wet areas that may comprise a major part of the GHG exchange even though they only represent a small fraction of the area (Christiansen et al., 2012; Grunwald et al., 2012). Increased winter precipitation, as foreseen for this century at northern latitudes in Europe, may

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enhance this phenomenon by increasing the endurance of wet areas especially in poorly and moderately drained soils. Moreover, increasing soil moisture in some periods may increase the overall soil GHG emissions.

The most responsive sites, next to those on wet soils, were those with low soil C/N ratio and low soil pH. Thus, resilient ecosystems with respect to soil GHG exchange are forests with high soil C/N ratio (> 25) or high soil pH (> 5). Much of the boreal forests and forests planted on heathlands in NW Europe have high C/N ratio and thus persistently low N₂O emissions are expected. Also, the dry Mediterranean forests are resilient ecosystems concerning GHG emissions, since the rainfall exclusion/addition had no effects on GHG exchange although water was expected to be a limiting factor.

Mitigation strategies may focus on (i) management of wet forest areas and forested peatlands, (ii) continuous forest cover management, (iii) reducing N availability, and (iv) avoiding anthropogenic soil acidification e.g. by acid inputs or excessive biomass removal.

Management of the water level or restoration of natural hydrology may be used to reduce N₂O emissions from drained peatlands and other wet areas by increasing the area of water saturated zones. However there may be a trade-off with increasing CH₄ emissions. A better knowledge of the hydrological interactions with GHG dynamics in forests will be imperative to foster wise management.

In N-saturated (such as HW) or naturally fertile forests clear-cuts should be avoided by using continuous forest cover management systems. We recommend this, even though the observed effects on GHG exchange of a clear-cut were transient, but with the magnitude of the responses they still have importance on a rotation scale. In N-rich systems, an increase in biomass removal (harvesting whole trees or more of the N-rich parts of the trees) may alleviate the N excess in the soil and reduce GHG emissions. However, care should be taken not to deplete other nutrients or they should be returned by wood ash application. Wood ash application, slightly increasing the pH (Klemedtsson et al., 2010) is yet again a mitigation option. For example, it was the one treatment that mitigated emission of both gases the most. Thus, management of forest bioenergy

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production systems in N-rich sites should aim at removing excess N and compensating other nutrients through addition of ash products thereby not only reducing the GHG emissions by substituting fossil fuels but also by reducing the non-CO₂ GHG fluxes from forest soils.

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Table 1. NitroEurope C2 sites (ordered north to south) – characteristics and treatments.

Site	Code	Latitude	Longitude	Tree species	Soil type	MAP (mm)	MAT (°C)	Forest change treatment or factor	Reference for site and treatment details
Falköping, SE	FK	58°76' N	13°32.7' E	Silver birch	Histosol	620	5	pH gradient	Weslien et al., (2009)
Gårdsjön, SE	GS	58°40' N	12°30' E	Norway spruce	Podzol	1145		N addition Soil hydrology	Moldan and Wright (2011)
Skogaryd, SE	SR	58°23' N	12°09' E	Norway spruce	Histosol	881	8.4	Wood ash	Klemetsson et al. (2010)
Klosterhede, DK	KH	56°29' N	8°24' E	Norway spruce	Podzol	769	8.0	N addition	Gundersen, 1998
Strødam, DK	ST	55°57' N	12°16' E	Beech	Arenosol	657	7.8	Soil hydrology	Christiansen et al. (2012)
Vestskoven, DK (1)	VS1	55°42' N	12°21' E	Oak	Luvisol	594	7.9	Soil hydrology	Christiansen et al. (2012)
(2)	VS2			Oak, N. spruce				pH gradient Tree species /Stand age	Hansen et al. (2007)
Höglwald, DE	HW	48°17' N	11°4' E	Norway spruce	Cambisol	850	7.6	Harvest intensity	Wu et al. (2010, 2011)
Klausenleopoldsdorf, AT	KL	48°07' N	16°03' E	Beech	Dystric Cambisol	768	7.6	N addition	Kaiser et al. (2010)
Achenkirch, AT	AK	47°34' N	11°38' E	Norway spruce	Chromic Cambisol	1480	5.7	Soil warming	Schindlbacher et al. (2011)
Alptal, CH	AT	47°03' N	8°43' E	Norway spruce	Gleysol	2300	6	N addition	Hagedorn et al. (2001)
Tolfa Allumiere, IT	TA	42°11' N	11°56' E	<i>Arbutus unedo</i>	Andisol	729	13	Precipitation	Cotrufo et al. (2011)
Herdade da Mitra, PT	HM	38°31' N	8°00' W	Cork oak	Haplic Cambisol	669	15.5	Precipitation	Shvaleyva et al. (2011)

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Table 2. Methods for determination of GHG fluxes.

Site	Method	Chambers per treatment	Frequency	Area ^a m ²	No. of conc. Measurement ^b	Interpolation in flux calculation method ^c	Reference to GHG method details
Falköping (FK)	manual	2–3	weekly– fortnightly	0.5	2	linear	Weslien et al. (2009)
Gårdsjön (GS)	manual	10	fortnightly	2.6	4	linear	Moldan et al., in prep.
Skogaryd (SR)	manual	12	fortnightly	3.1	4	linear	Klemetsson et al. (2010)
Klosterhede (KH)	manual	8	monthly	0.6	4	linear	Christiansen (2010)
Strødam (ST) Vestskoven	manual	6–9	fortnightly	0.4–0.7	4	linear	Christiansen et al. (2012)
Dry–wet (VS1)	manual	9	fortnightly	0.66	4	linear	Christiansen et al. (2012)
Age × species (VS2)	manual	9	monthly	0.66	4	linear	Christiansen and Gundersen (2011)
Höglwald (HW)	automated	5	2-hourly	1.25	4	linear	Wu et al. (2011)
Klausenleopoldsdorf (KL)	manual	3	fortnightly	3.0	4	linear	Kitzler et al. (2006)
Achenkirch (AK)		9	fortnightly	0.28	4	linear	Kitzler et al., in prep.
Alptal (AT)	manual	6	monthly	0.37	3	linear	Schleppi et al., in prep.
Tolfa Allumiere (TA)	manual	9	fortnightly	0.16	3	linear	Castaldi et al. (2004)
Herdade da Mitra (HM)	manual	6	monthly	1.27	3	linear	Shvaleva et al. (2011).

^a Area sampled pr treatment (chamber area × # chambers).

^b In each chamber to estimate the flux.

^c Method used to estimate flux from concentration development, evaluated in Kroon et al. (2008).

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Table 3. N deposition, soil characteristics and GHG exchange for control treatments and the response (ΔN_2O , ΔCH_4) to the forest change treatments (n.d. = not determined; n.s. = not significant).

Treatment/Site	N deposition g N m ⁻² yr ⁻¹	SOC ^a kg C m ⁻²	Soil T ^b °C	Soil moisture v/v %	Bulk density g cm ⁻³	pH- org	pH- ms ^c	C/N- org	C/N- ms ^c	N ₂ O ^d μg N m ⁻² h ⁻¹	ΔN ₂ O	Significance ^e	CH ₄ ^d μg C m ⁻² h ⁻¹	ΔCH ₄	Significance ^e
N addition															
Klosterhede (KH)	1.5	13.2	8.8	25	1.29	3.9	4	33	30	0.1	0.5	1, 2, 16	-5.8	0.6	16
Alptal (AT)	1.7	8.9	7.8	24	0.42	3.3	5.5	21	18	0.3	0.8	14 [*] –16 [*] , all [*]	3.1	8.9	14–16
Klausenleopoldsdorf (KL)	1.4	18.5	9.7	36	0.83	5	4.6	43	16	8.2	5.8	1–2 [*] , 3 ^{**}	-21	4	1–3, 2 [*]
Gårdsjön (GS), dry	0.8	19.0	8.5	31	0.78	3.6	4.3	42	34	0.3	2.1	1–2, 16 ^{**}	-27	13	16 ^{**}
Gårdsjön (GS), wet	0.8	17.6	8.5	n.d.	0.78	3.8	4.5	36	23	-0.5	2.6	1–2, 16 ^{**}	-5.4	11	16 ^{**}
Climate change															
Achenkirch (AK) soil +4 °C	1.1	28.3	6.4	45	1.26	n.d.	6.5	n.d.	17	4.9	2.7	1–4 ^{***}	-15	1.5	1–4 ^{**}
Tolfa Allumiere (TA), +rain	0.6	17.4	13.5	14	0.91	4.3	4.0	36	25	≈ 0	0	3–4	-28	1.5	3–4
Tolfa Allumiere (TA), -rain											0	3–4		7	3–4
Herdade da Mitra (HM), +rain	0.5		19	12	1.18	n.d.	5.5	n.d.	19	0.04	0.5	5–6	-22	-2.4	5–6
Herdade da Mitra (HM), -rain											-0.07	5–6		1.5	5–6
Land use change															
Strödam (ST) dry vs wet	1.5	3.9	9.8	30	0.90	n.d.	3.5	29	18	4.2	3.4	*	-7	86	***
Strödam (ST) dry vs wet when pH < 4	1.5	3.9	9.8	30	0.90	n.d.	3.5	29	18	4.6	6.0	*	-11	2	n.s.
Vestskoven (VS1) dry vs wet	1.2	8.0	9.3	39	1.28	n.d.	5.3	34	11	7.1	30	*	-2.4	44	*
Vestskoven (VS2) tree species stand age	1.0	3.1	8.4	32	1.46	5.2	5.1	34	11	3.8	0.6	n.s. ***	-10.3	5.6	n.s.
Vestskoven (VS2) stand age											-2.5			4.8	n.s.
Forest management															
Höglwald (HW) clear-cut	2.6	7.4	7.2	30	0.99	3.3	3.7	23	16	6.3	39	1–5 ^{**} , 6 [*] , 7–8	-11	7.7	1–8 ^{**}
Höglwald (HW) selective cutting											3.0	1–5 [*] , 6–8		-1.3	1–8
Skogaryd (SR) 3.3 t ash	0.8	27.7	8.3	n.d.	0.19	4.5	-	23	-	30	-12	1–2 [*]	-38	-2.6	1, 2 [*]
Falköping (FK) pH 5.8 vs 4.6	0.8	9.2	6.2	47	0.24	5.8	-	51	-	77	85	*	-20	10	*
Falköping (FK) pH 5.8 vs 3.7											290	*		23	*

^a Soil organic carbon pool: organic horizon + 0–30 cm in mineral soil.
^b Soil temperature (°C) at 5 cm below the surface.
^c Mean over the depth 0–20 cm of the mineral soil.
^d Annual mean fluxes of N₂O and CH₄ soil exchange measured during the NitroEurope project.
^e Treatment years where GHG exchange was measured and the significance of the response:
^o $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.
 For the studies over gradient the significance of the gradient factor is displayed.

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Table 4. The results of the stepwise regression analyses for control plots ($n = 13$) only and all plots (treatments+controls, $n = 30$). Only significant ($p < 0.05$; bold) and marginal significant effects ($p < 0.1$) are shown.

Factor	N ₂ O		CH ₄					
	Control	All	Control	All	Control	All		
	<i>R</i> ² ^a	<i>p</i> ^b	<i>R</i> ²	<i>p</i>	<i>R</i> ²	<i>p</i>	<i>R</i> ² ^a	<i>p</i>
Soil moisture	–	–	0.44	< 0.0001	0.31	0.059	0.23	0.007
C/N ^c	0.40	0.027	0.11	0.017	–	–	0.14	0.021
Soil pH	–	–	0.08	0.025	–	–	–	–
Throughfall amount	–	–	–	–	–	–	0.07	0.082
Overall model ^d	0.40	0.027	0.63	< 0.0001	–	–	0.37	0.0020

^a The partial *R*² value in the stepwise regression.

^b The partial *p*-value for the specific factor.

^c The significant effects were based on the reciprocal C/N ratio (N/C ratio) of the mineral soil (0–30 cm).

^d The statistics for the regression model combining all factors that were significant at $p < 0.05$.

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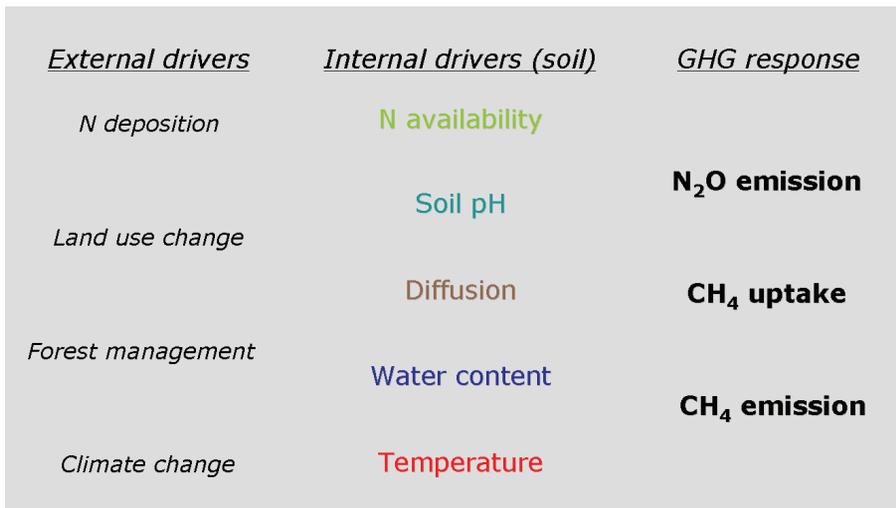


Fig. 1. The conceptual frame of the study. Environmental changes (external drivers) affect gas exchange (GHG response) at annual or longer timescales through changes in soil conditions (internal drivers).

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Fig. 2. Forest change sites in the NitroEurope project.

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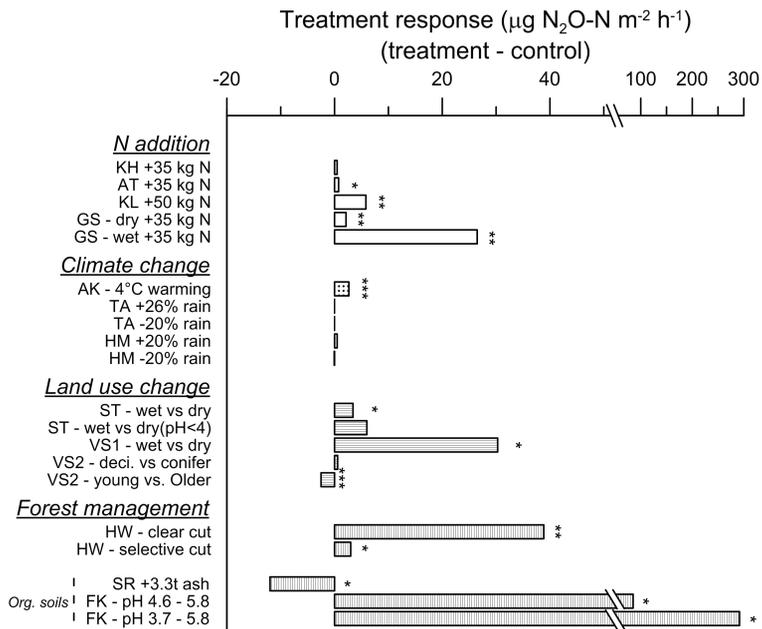


Fig. 3. Response of N_2O gas exchange to forest change (treatment minus control). Site codes and treatments are explained in Table 1. Stars indicate the level of significance for the treatment effect (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

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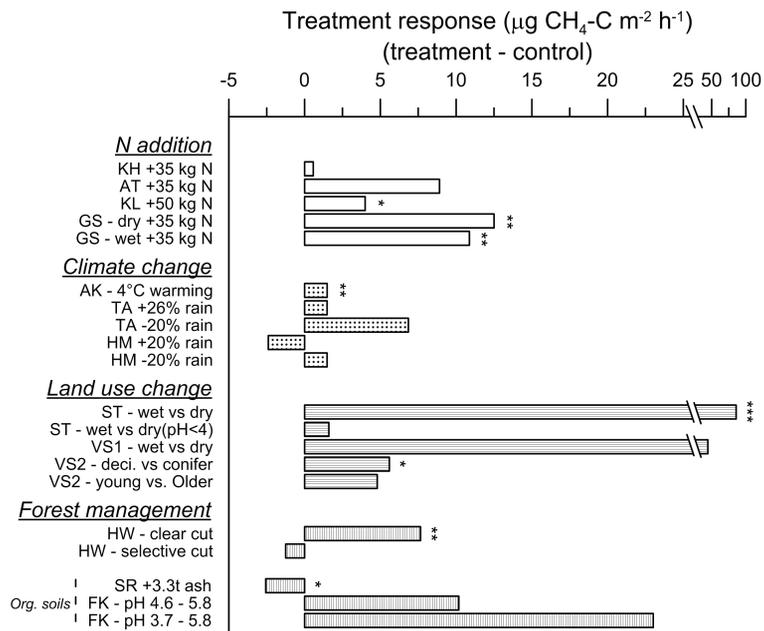


Fig. 4. Response of CH_4 gas exchange to forest change (treatment minus control). Site codes and treatments are explained in Table 1. Stars indicate the level of significance for the treatment effect (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

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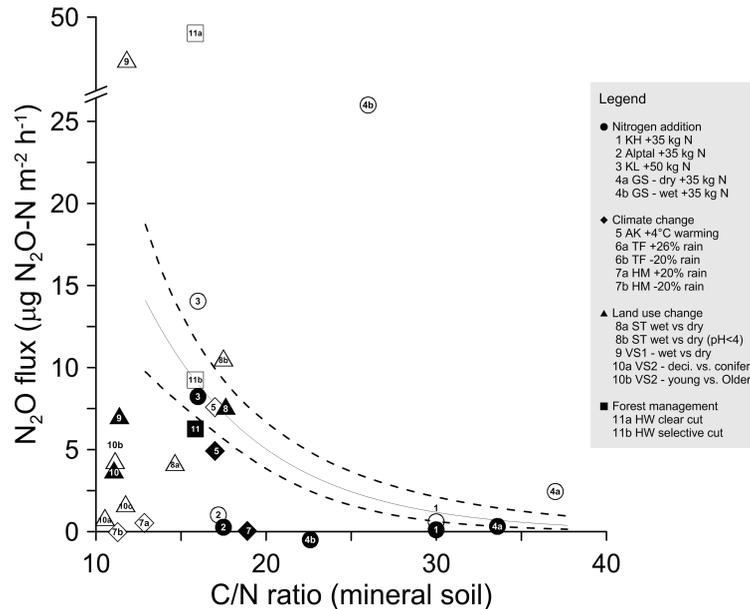


Fig. 5. N_2O emission versus mineral soil C/N ratio (0–20 cm) for control (filled symbols) and treatments (open symbols). Numbers in the symbols refer to sites and letters to treatments within site. Lines show the relationship (and its 95 % confidence interval) found by Pilegaard et al. (2006). The types of forest change treatments are represented by different symbol shapes (circle: N addition; diamond: climate change; triangle: land use change; square: forest management).

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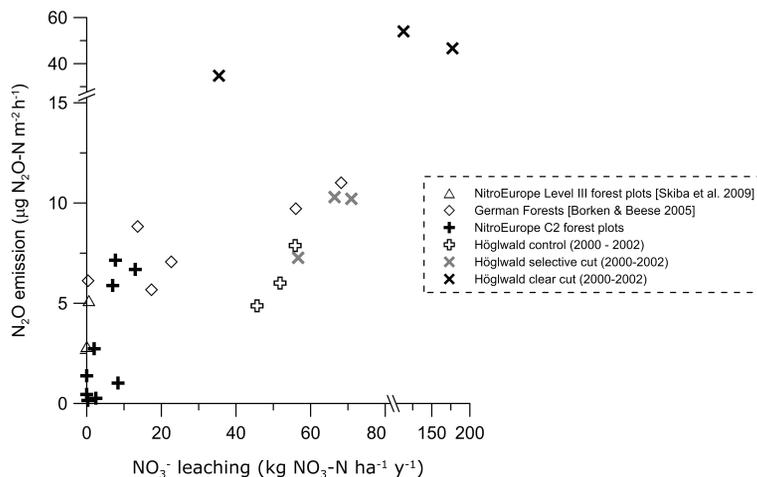


Fig. 6. Nitrogen losses from forest soils plotted as N_2O emission versus NO_3^- leaching below the root zone for forest change sites (crosses) and other European forests (see legend). Höglwald (HW) treatments are represented with data from 3 individual years, where nitrate leaching data were taken from Huber et al. (2004; 2010). Note the breaks on both axes.

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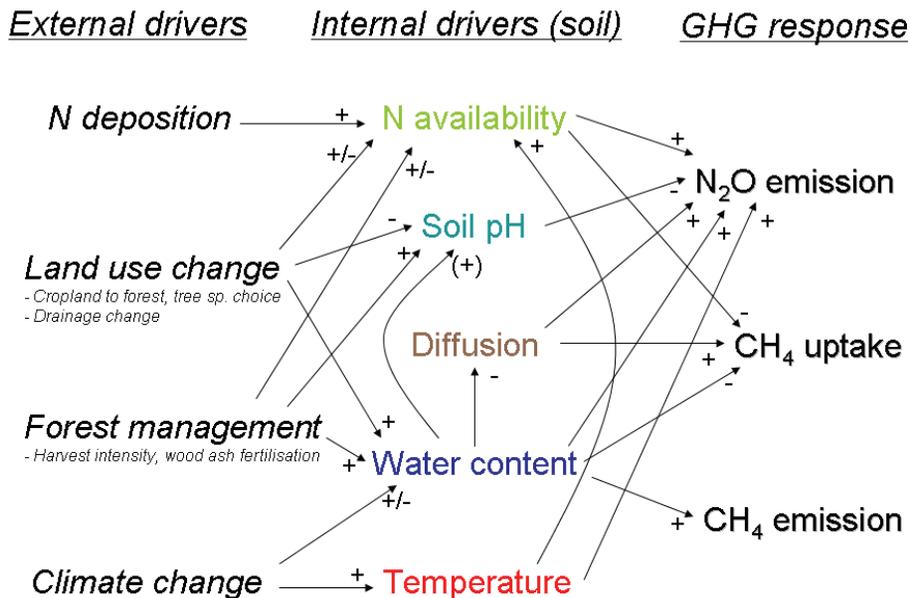


Fig. 7. Synthesis of the effects and interactions of forest change on GHG exchange observed in this study (based on the conceptual framework in Fig. 1). Arrows starting from the external drivers denote those positive or negative impacts on internal drivers comprised in our study. The + or – signs at the arrows starting from an internal driver indicate the observed direction (increase or decrease) of the effect on GHG exchange (or the interaction on another internal driver) when the internal driver in question increases.

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