~~Reduced microbial respiration sensitivity to soil moisture following long-term N fertilization enhances soil C retention in a boreal Scots pine forest~~Long-term nitrogen fertilization alters microbial respiration sensitivity to temperature and moisture, potentially enhancing soil carbon retention in a boreal Scots pine forest

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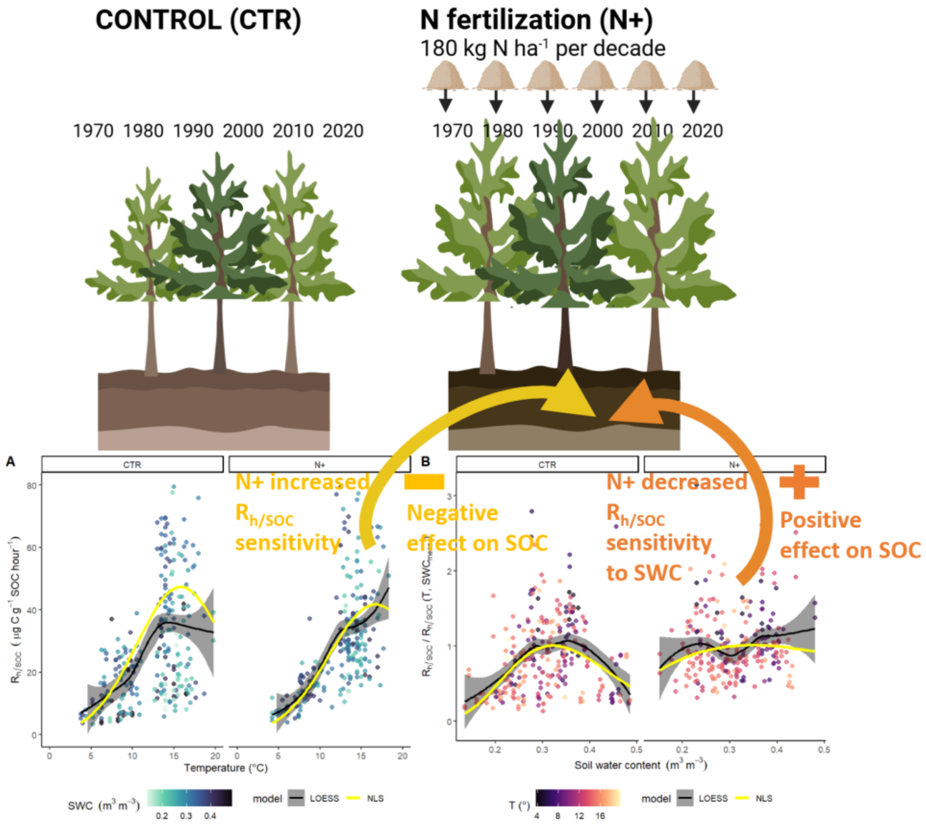
Abstract. Nutrient availability ~~effects~~ affects microbial respiration kinetics and their sensitivities to environmental conditions, thus the soil organic ~~C~~ carbon (SOC) stocks. We examined long-term nitrogen (N) addition effects on soil heterotrophic respiration (R_h), methane (CH_4) oxidation, and nitrous oxide (N_2O) emissions in an N-limited boreal Scots pine (*Pinus sylvestris*) forest. Measurements included long term 1960-2020 tree biomass monitoring, 2023 SOC, 2021-2023 monthly aboveground litterfall, 2021–2023 growing seasons biweekly CO_2, CH_4, and N_2O fluxes, and quarter-hourly soil temperature (T), and soil water content (SWC) in both control and N-fertilized plots. We assessed mean greenhouse gas (GHG) flux differences and R_h dependence on T and SWC using polynomial and parametric non-linear regression models. Tree biomass, litterfall and SOC increased with long-term N fertilization. However, N fertilization significantly increased mean R_h, reduced CH_4 oxidation slightly, and modestly raised N_2O emissions. SOC-normalized R_h ($R_{h/SOC}$) did not significantly differ between treatments, yet relationships between $R_{h/SOC}$ and T and SWC diverged with fertilization. In control plots, $R_{h/SOC}$ peaked at 15.8 °C ~~but increased monotonically with T~~ and at 16.8 °C in N-fertilized plots. Under N fertilization, $R_{h/SOC}$ was weakly SWC-dependent, contrasting with a distinct humped SWC response in control plots, enhancing annual $R_{h/SOC}$. Annually, N-fertilized plots respired 10~~1~~.~~2~~3% ~~%~~ of SOC (± 0.3 standard error (SE)), compared to 12.~~6~~2% (± 0.5 SE) in controls, suggesting N fertilization promoted SOC retention. Consequently, N fertilization reduced average annual net CO_2 emissions by ~~262.5~~345.4 (± 73.6 SE) ~~-~~g CO_2 m^{-2} $year^{-1}$, while combined effects on CH_4 and N_2O fluxes and the production energy of N fertilizer contributed annually a minor CO_2-equivalent increase of ~~15~~17.~~8~~7 (± 0.5 SE) g CO_2-eq m^{-2} $year^{-1}$.

In conclusion, long-term N fertilization in boreal forests could ~~mitigate climate warming by~~reduce global warming potential of ~~reducing~~ soil GHG emissions, mainly by slowing $R_{h/SOC}$, and altering its responses to T and SWC, thereby enhancing SOC sequestration in addition to the increased tree biomass carbon sink.

Graphical abstract.


CONTROL (CTR)
N fertilization (N+)
180 kg N ha-1 per decade
1970 1980 1990 2000 2010 2020
1970 1980 1990 2000 2010 2020
A
CTR
N+
N+ increased
Rh/soc
sensitivity
Negative
effect on SOC
B
CTR
N+
N+ decreased
Rh/soc
sensitivity
to SWC
Positive
effect on SOC
Rh/soc (µg C g-1 SOC hour-1)
0
20
40
60
80
0 5 10 15 20
0 5 10 15 20
Temperature (°C)
Rh/soc / Rh/soc (T, SWCmean)
0
1
2
3
0.2 0.3 0.4 0.5
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Soil water content (m3 m-3)
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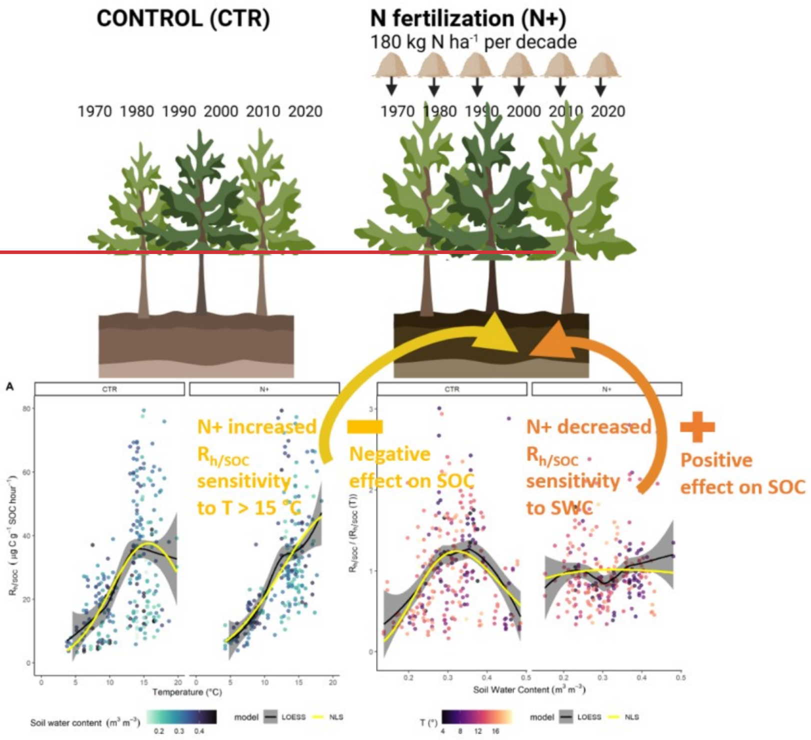

1 Introduction

Vegetation growth in boreal forests is primarily constrained by temperature (Jarvis and Linder, 2000) and soil nutrient availability, particularly nitrogen (N) (Näsholm et al., 1998; Högberg et al., 2017). Atmospheric N deposition or fertilization can enhance tree biomass growth (Lupi et al., 2013; Saarsalmi and Mälkönen, 2001; Sponseller et al., 2016) and increase soil carbon (C) sequestration by promoting productivity and litter inputs while reducing decomposition rates (Janssens et al., 2010; Marshall et al., 2021; Smolander et al., 1994). This increased C storage in both tree biomass and soil after N fertilization could be seen as a positive feedback effect on ecosystem C balance in Northern forests (Hyvönen et al., 2008; Mäkipää et al., 2023). However, the effects of N fertilization on organic matter (OM) decomposition and the net balance of greenhouse gas (GHG) emissions (CO_2, CH_4, N_2O) are less well understood and equally critical for assessing the forest C balance and its global warming potential. N fertilization may reduce soil CO_2 emissions (Janssens et al., 2010) due to enhanced microbial carbon use efficiency (CUE) (Manzoni et al., 2012b, 2017) and decreased need for N mineralization. It may also increase N_2O emissions due to greater soil N availability (Högberg et al., 2017; Öquist et al., 2024) and potentially alter CH_4 uptake by either increasing N availability for CH_4 oxidizing microbes or by competing with NH_4 for reduction (Öquist et al., 2024). These processes could offset the enhanced tree C sink, potentially converting the ecosystem into a net C source. Evaluating the feedback of N fertilization on forest climate mitigation potential thus requires consideration of impacts on both tree growth and OM decomposition. Moreover, full accounting of GHG emissions should include emissions associated with N fertilizer production (Osorio-Tejada et al., 2022).

The soil C balance in boreal forests, which is a dynamic balance between C input from litterfall and CO_2 emissions from OM decomposition, is influenced by temperature (T), soil water content (SWC), nutrient status, and vegetation composition (Deluca and Boisvenue, 2012)—factors sensitive to forest management (Mäkipää et al., 2023; Mayer et al., 2020). For example, N fertilization enhances soil N availability, promoting plant growth and litterfall (C input) while potentially reducing OM decomposition due to increased CUE in microbial decomposers (Manzoni et al., 2017). These effects, alongside T and SWC controls, can be integrated into soil C models (Zhang et al., 2018). Consequently, changes in SOC decomposition dynamics related to microbial community structure (e.g., activity, CUE, and biodiversity; Khurana et al., 2023) may influence soil microbial respiration dependencies on T and SWC. Shifts in respiration responses to temperature due to N fertilization may attenuate CO_2 emissions under warming scenarios (Chen et al., 2024; Wei et al., 2017). Although the effects of N addition on moisture dependency remain understudied, interactions between T and SWC are critical for forecasting respiration responses (Pallandt et al., 2022; Sierra et al., 2017, 2015).

Empirically derived relationships between soil respiration and T and SWC are widely used in soil C models to adjust decomposition rate constants (Luo et al., 2016), yet differences in SWC responses (Sierra et al., 2015) contribute to projection uncertainties (Falloon et al., 2011). Boreal forest soils with higher nutrient levels and water availability often have underestimated SOC stocks in model projections (Dalsgaard et al., 2016; Tupek et al., 2016). Moreover, SWC response curves vary with soil properties like porosity, clay content, and OM fraction (Moyano et al., 2013, 2012) and may also be influenced by soil N status. Improving SOC projections would therefore require accounting for these variations. Given the significant spatial variability in SOC within forest sites (Muukkonen et al., 2009) and the measurement uncertainty over time (Ortiz et al., 2013), assessing changes in the T and SWC dependencies of soil CO_2 emissions after long-term N fertilization and applying them over multiple years could clarify the SOC sink/source dynamics.

In southern boreal region's Scots pine forests on well-drained mineral soils, soil CO_2 emissions range from 1 to 3 kg CO_2 m^{-2} $year^{-1}$, accounting for 70–91% of total ecosystem respiration (Tupek et al., 2008; Uri et al., 2022) and its global warming potential (GWP). Although CH_4 and N_2O have higher GWP than CO_2 (~~23~~ 27 and ~~296~~ 273 times over a 100-year horizon, respectively; ~~Ramaswamy et al., 2018~~IPCC (2023)), the soil CH_4 exchange is generally a small sink, and N_2O emissions are negligible in N-limited soils (Machacova et al., 2016; Matson et al., 2009; Pihlatie et al., 2007; Siljanen et al., 2020; Tupek et al., 2015).

In this study, we investigated the effects of long-term N fertilization on soil CO_2, CH_4, and N_2O fluxes and SOC stocks in a boreal Scots pine forest. We hypothesized that (i) increased soil nitrogen availability would enhance soil organic carbon (SOC) accumulation and heterotrophic respiration (R_h) due to greater biomass growth and litter inputs, while SOC-normalized R_h ($R_{h/SOC}$) would decline due to reduced microbial nitrogen demand; and (ii) nitrogen fertilization would alter CH_4 oxidation and increase N_2O emissions compared to N-limited soils, reflecting shifts in microbial activity and substrate availability~~We hypothesized that: (i) increased soil N would enhance both SOC and R_h due to greater biomass growth and litter inputs, while SOC-normalized R_h ($R_{h/SOC}$) would decrease due to reduced microbial N demand; and (ii) N_2O emissions and CH_4 oxidation rates would diverge from those observed in N-limited soils.~~

2 Methods

2.1 Study site and N fertilization

The Karstula forest study site is in central Finland (62°54'43.343"N, 24°34'16.021"E) (Fig. 1) and is dominated by Pinus sylvestris (Scots pine) with an understory comprising *Vaccinium myrtillus*, *V. vitis-idaea*, *Empetrum nigrum*, *Calluna vulgaris*, and various boreal mosses and lichens. Established on a low-fertility sandy podzol, the site corresponds to the Calluna (CT) and Vaccinium vitis-idaea (VT) types in the Finnish classification system (Cajander, 1949). Nitrogen (N) fertilization has been applied here since 1960, with 180 kg N ha^{-1} potassium nitrate applied every decade until 2020. The stand underwent ~~cleaning in 1964 and thinnings~~thinning in ~~1969,~~ 1990 (reducing 16.2% and 26.5% of basal area (BA) for CTR and N+, respectively), and 2015 (reducing 36.7 % and 40.1% of BA for CTR and N+, respectively)~~ following standard silvicultural practices~~.~~.~~

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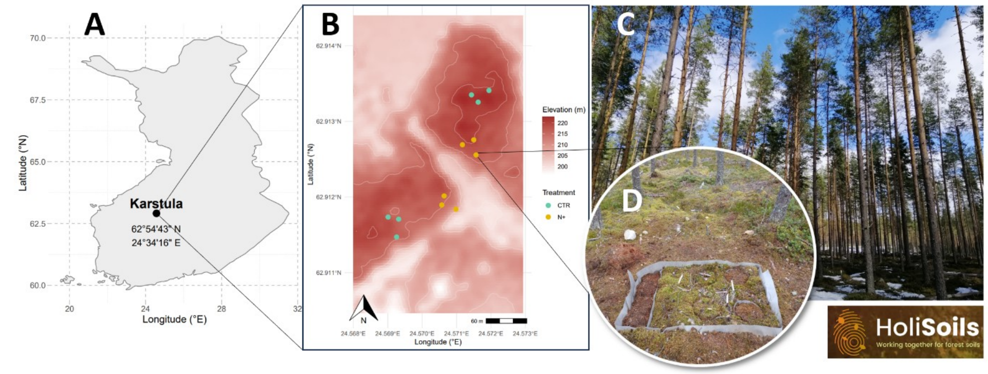

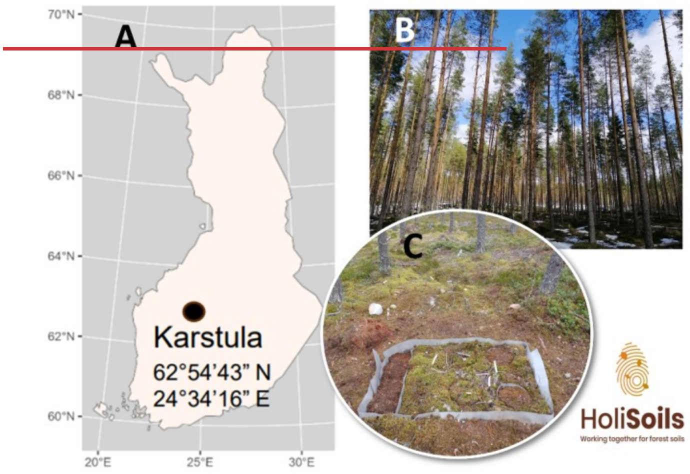

Figure 1: Geographical location of the Karstula forest study site in Finland (A); topographical variation of the study site and the location of treatment (control CTR and N-fertilized N+) plots (B); photograph of the forest stand (~~B~~C); and one of six 2 x 1 m forest floor plot groups, each with four subplots used for measuring soil greenhouse gases, soil organic C, and soil temperature and moisture following the installation of a root-exclusion fabric (~~C~~D).

2.2 Field measurements

2.2.1 Tree inventory and litterfall

Measurements of tree diameter (at 1.3 m height), total height, and crown base height have been conducted at 10-year intervals from 1960 to 2010 and every 5 years thereafter. The breast-height diameter (d1.3) of all trees has been measured using a caliper (±1 mm precision) once per decade since 1960, as well as after the 2015 thinning. Additionally, in a permanent subset of trees representing various size categories, tree height and crown base height have been recorded using a hypsometer (precision ~0.5–1 m). Mortality and thinning-related removals were recorded, and tree biomass was calculated using biomass expansion models (Repola, 2009). Litterfall rates were estimated using compartment-specific turnover rates (Lehtonen et al., 2016). From May 2021 to October 2023, litter (needles, twigs, cones) was collected monthly during the growing season using 0.8 m mesh collectors and subsequently sorted and weighed.

2.2.2 Soil organic carbon stock (SOC)

Soil sampling was performed in June 2023 in control and N-fertilized plots (n=6 each) using a 58 mm diameter corer. Samples were stratified by layer, separating humus from mineral soil, which was sampled in 10 cm increments to a depth of 30 cm. Samples from each layer were composited across two subsites with differing rock content. Samples were dried, weighed, and sieved, and C and N contents were analyzed using dry combustion (LECO TruMac CN, LECO Corporation, St. Joseph, MI, USA). Stoniness was assessed in the field using rod penetration (Eriksson and Holmgren, 1996) and corrected for rock fragment content following Poeplau et al. (2017).

2.2.2 Soil greenhouse gas (GHG) fluxes, temperature, and moisture

Soil GHG fluxes (CO_2, CH_4, and N_2O) were measured biweekly during the growing seasons of 2021-2023 (spanning from 20th May to 16th August in 2021, 5th May to 3rd November in 2022, and 10th May to 10th October in 2023). Measurements were taken from 12 plots (6 plots or 3 pairs per treatment). Plots in each pair were located 30 cm apart (Fig. 1c) and CTR and N pairs were on average 122 m apart (Fig. 1b). As the single plot area was relatively large (706 cm^2), we considered 2 plots pair to be representative of the trenched area (Fig. 1c) and 3 pairs to be representative of the spatial variation of the treatment. ~~12 plot groups (two 30 cm diameter plots per group; n=6 per treatment).~~ In May 2021, each plot was trenched (1 x 2 m) and fitted with water-permeable geotextile to prevent root ingrowth, isolating heterotrophic respiration (Rh) from autotrophic sources (Tupek et al., 2019).

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Gas fluxes were measured using a non-transparent 21.7 L dynamic chamber (30 cm in diameter and height) equipped with a fan and connected to a LI-COR LI-7810 $CH_4/CO_2/H_2O$ or LI-7820 N_2O/H_2O trace gas analyzer (LICOR, Lincoln, NE, USA). ~~LI-7810 or LI-7820 trace gas analyzer.~~ Gas concentrations were recorded every second for 3 minutes, and linearity was monitored visually during the measurements to accept only fluxes with increasing trends in CO_2 concentration

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evolution.~~,~~ Fluxes were calculated from the stable portion of the data (Zhao, 2019). R_h values (g CO_2 m^{-2} h^{-1}) were normalized to SOC content and expressed as a C fraction of SOC per hour (µg C g^{-1} SOC h^{-1}). The CH_4 and N_2O concentrations were also measured during 3 min intervals with 5 second averaging at the 0.25 ppb precision for CH_4 and 0.20 ppb precision for N_2O. The minimum detectable flux of measurements estimated using the formula by Parkin et al., (2012) was 0.0238 µg m^{-2} h^{-1} for CH_4 and 0.0524 µg m^{-2} h^{-1} for N_2O.

~~The non-transparent dynamic chamber (21.7 L) equipped with a small fan for air mixing was connected via Teflon tubing to the LI-COR LI-7810 $CH_4/CO_2/H_2O$ or LI-7820 N_2O/H_2O trace gas analyzer and manually placed air tightly on the soil (inside the pre-cut 2 cm deep ridge along the circumference of the chamber). The gas concentration measurements were conducted every second for 3 min. periods. The linearity of the concentration evolution inside the chamber headspace in time was monitored during each measurement. Only stable concentration data were accepted for the flux calculation. The gas flux was calculated (Zhao, 2019) from the period after 30 s of recorded measurement started and 15 s before the recorded measurement end. To evaluate relative differences in R_h between CTR and N+, the Rh values for each plot, initially expressed in g CO_2 m^{-2} h^{-1}, were normalized by the nearest measurement of soil organic C stock (in kg C m^{-2} of 1 m soil depth). The normalized R_h was thus expressed as C fraction of SOC per hour ($R_{h/SOC}$, µg C g^{-1} SOC h^{-1}).~~

Continuous monitoring of soil temperature (T) and volumetric soil moisture (SWC) at 5 cm depth was achieved with Soil Scout Oy sensors, recording data at 15 min intervals since June 2021. T and SWC were matched with flux data by timestamp.

2.3 Data analysis

All data analyses and visualizations were conducted using R software (R Core Team, 2023). A one-way ANOVA was employed to test the effect of N fertilization on greenhouse gas (GHG) fluxes.

Annual CO_2 emissions were estimated using functional dependencies of observed $R_{h/SOC}$ on soil temperature (T) and soil water content (SWC), extrapolated to continuous hourly T and SWC data. Two regression approaches were used to characterize the dependency of $R_{h/SOC}$ on T and SWC: (i) local polynomial regression (LOESS) to assess the functional form of Rh/SOC dependencies ~~on T ($R_{h/SOC}$(T)) and~~ on combined T and SWC ($R_{h/SOC}$(T, SWC)) separately for the N-fertilized (N+) and control (CTR) plots; and (ii) nonlinear least squares (NLS) regression, guided by LOESS to identify suitable mathematical forms. The LOESS and NLS models for $R_{h/SOC}$ dependency on SWC alone were compared using $R_{h/SOC}$ ratios normalized by $R_{h/SOC}(T, SWC_{mean})$.

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NLS regression was used to extrapolate $R_{h/SOC}$ to continuous hourly data and to upscale $R_{h/SOC}$ to the annual level. ~~Temperature dependency of $R_{h/SOC}$ was fitted with a Gaussian function as described in Tuomi et al. (2008) (Eq. 1):~~

~~$R_{h/SOC}(T) = r_a\, e^{(\beta_1 T + \beta_2 T^2)}$, (1)~~

~~where r_a represents basal respiration, and β_1 and β_2 are parameters controlling the exponential temperature response.~~ The combined T and SWC dependency of $R_{h/SOC}$ was modeled by multiplying ~~the~~ a Gaussian T function as described in Tuomi et al. (2008) ~~temperature function (Eq. 1)~~ with a Ricker function for SWC (Bolker, 2008) (Eq. ~~2~~1):

$$R_{h/SOC}(T, SWC) = \cancel{r_a}\, e^{(\beta_1 T + \beta_2 T^2)} (a\, SWC\, e^{(-b\, SWC)})^c \,, \qquad (1\cancel{2})$$

where β_1 and β_2 are parameters controlling the exponential T response, and parameter~~s~~ a determine~~s~~ the initial slope, b the post-optimal decline, and c the peak height of SWC ~~,~~response.

Model performance was assessed using proportion of explained variance (R^2), root mean square error (RMSE), mean bias error (MBE), and mean absolute error (MAE) derived from model residuals. ~~, as well as Akaike Information Criterion (AIC) (Eq. 3) and Bayesian Information Criterion (BIC) (Eq. 4), which balance model fit with complexity (Wang and Liu, 2006):~~

~~$AIC = -2 \log L + 2\, DF$, (3)~~

~~$BIC = -2 \log L + \log(n)\, DF$, (4)~~

~~where L is model likelihood, DF is the the number of parameters, and n is the sample size. The model deviance for NLS regression is represented by -2logL. for NLS regression is the model deviance. Lower AIC and BIC values indicate better model fit.~~ Model robustness was further evaluated with 10-fold cross-validation (Kuhn, 2008).

Annual CH_4 and N_2O fluxes were estimated by scaling the treatment-specific mean hourly flux values. The global warming potential (GWP) was calculated using the AR6 GWP-100 values (27 for CH_4 and 273 for N_2O) (IPCC, 2023). As flux data were unavailable for the November–March period, the CH_4 and N_2O annual estimates are limited to the extrapolating the conditions of Apr–Oct, during which fluxes are generally higher.

The associated emissions with fertilizers productions were accounted for according to Osorio-Tejada et al. (2022). We estimated the CO_2 emissions associated with six nitrogen fertilization events, which occurred once per decade between 1960 and 2020. The applied nitrogen fertilization rate was 180 kg N ha^{-1} per event. Converting this to ammonia (NH_3) using the molecular weight ratio of NH_3 to N (17.031/14.007) resulted in an estimated 218.86 kg NH_3 ha^{-1} per fertilization event. Given an emission factor of 2.96 kg CO_2 per kg NH_3, this corresponds to 647.93 kg CO_2 ha^{-1} per event. Over six fertilization events spanning 60 years, the annualized CO_2 emission was calculated as 64.79 kg CO_2 ha^{-1} yr^{-1}, equivalent to approximately 6.5 g CO_2 m^{-2} yr^{-1}.

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3 Results

3.1 N fertilization enhanced tree biomass, litterfall, and SOC

N fertilization led to increased tree stand biomass and litterfall in N+ compared to CTR plots, based on tree inventory and biomass and litter models. Despite reductions following thinning events, tree biomass was highest in 2014 for both treatments (9 kg C m^{-2} in N+ and 7 kg C m^{-2} in CTR), decreasing to 6 and 5 kg C m^{-2}, respectively, by 2020 due to thinning in 2015 (Fig. 2a). This thinning led to peak litter input in 2015 (1.5 kg C m^{-2} in N+ and 1 kg C m^{-2} in CTR), which then stabilized around 0.6 and 0.5 kg C m^{-2} due to fewer trees (Fig. 2a). Litter fraction accounted for 16% of N+ and 14% of CTR biomass in 2015, falling to 10% for both by 2020. Monthly litterfall, including needles, branches, and cones, was significantly higher in N+ (25.1 g m^{-2} month^{-1}) than in CTR (14.3 g m^{-2} month^{-1}) plots from 2021 to 2023 (Fig. 2b). SOC also increased under N fertilization, from 4.9 kg C m^{-2} in CTR to 5.6 kg C m^{-2} in N+ (Fig. 2c).

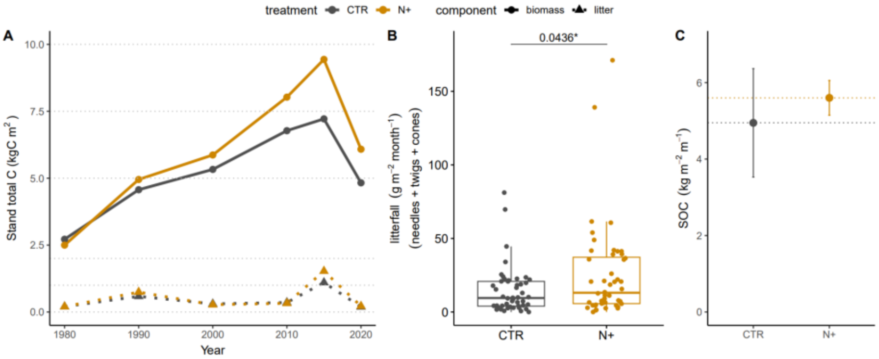

Figure 2: Biomass, litterfall, and SOC in control (CTR) and N-fertilized (N^{+}) stands. (A) Estimated ~~T~~ tree biomass and litterfall from 1980 to 2020~~, estimated from inventory and models (Lehtonen et al., 2016).~~ forest tree stands inventory measurements. (B) Monthly litterfall from July 2021 to October 2023 (box plot shows median, quartiles, and outliers). (C) SOC at 1 m depth in 2023 (error bars indicate minimum and maximum values across replicates).

3.2 N fertilization effects in mean CO_2, CH_4, and N_2O fluxes but not in SOC-normalized CO_2

Pairwise ANOVA showed that mean annual soil microbial R_h (g CO_2 m^{-2} h^{-1}) was significantly higher in N+ (0.58 ± 0.01 SE) than in CTR plots (0.46 ± 0.01 SE) (F-value 15.96, degrees of freedom 449, p-value 8.92e-05) (Fig. 3a). However, R_h normalized by SOC (µg C g^{-1} SOC h^{-1}) did not differ significantly between N+ (28.3 ± 1.1 SE) and CTR plots (28.6 ± 1.1 SE) (Fig. 3b).

CH_4 oxidation was slower in N+ (-0.14 ± 0.002 SE mg CH_4 m^{-2} h^{-1}) than in CTR (-0.18 ± 0.002 SE mg CH_4 m^{-2} h^{-1}) (Fig. 3c), with annual CH_4 oxidation rates of -1.58 g CH_4 m^{-2} y^{-1} in CTR and -1.~~23~~21 g CH_4 m^{-2} y^{-1} in N^+ plots. Mean net N_2O exchange was significantly lower than zero in CTR (-0.25 ± 0.09 SE µg N_2O m^{-2} h^{-1}), while in N+ it was positive (0.22 ± 0.06 SE µg N_2O m^{-2} h^{-1}), resulting in a mean annual difference of 4.17 mg N_2O m^{-2} y^{-1} between treatments (Fig. 3d). The method detection limits were smaller than SE of mean CH_4 and N_2O fluxes.

Average T at 5 cm depth was higher in CTR (12.6 ± 0.17 SE °C) than in N+ (12.0 ± 0.16 SE °C) (Fig. 3e), while SWC at 5 cm depth (0.31 m^3 m^{-3}) did not differ significantly between treatments (Fig. 3f).

Mean annual T was 5.92 ± 0.18 SE °C in CTR and 5.83 ± 0.17 SE °C in N^+, with an annual SWC of 0.31 ± 0.002 SE m^3 m^{-3} for both (Fig. S1). Soil T increased rapidly after snowmelt in April, with cooler summer conditions in 2022 than in 2021 and 2023. SWC ranged from 0.07 to 0.42 m^3 m^{-3}, dropping below 0.2 m^3 m^{-3} during drought conditions in summer 2021 (Fig. S1, S2). Rh showed sensitivity to T and SWC, rising with warmer conditions and declining in dry periods, then recovering after rewetting events (Fig. S2). However, this pattern was more pronounced in CTR than in N+ plots. Part of the variation in soil moisture between CTR and N+ plots (located on average 122 m apart) could be attributed to the measured topsoil humus layer being affected by microscale variations of vertical and lateral water flows due to variable microtopography (Fig. 1b).

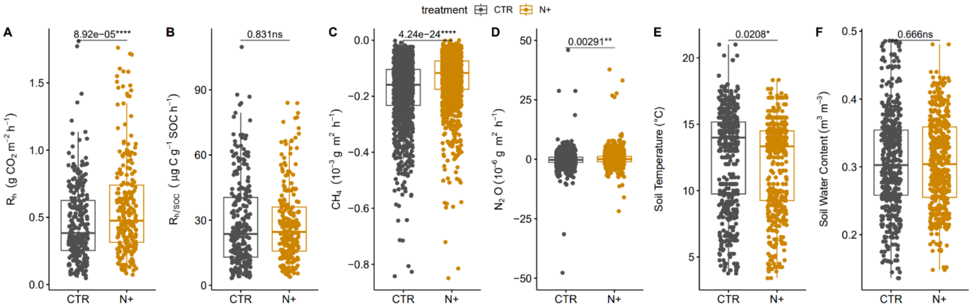

Figure 3: Soil (A) heterotrophic respiration (Rh, g CO_2 m^{-2} h^{-1}), (B) Rh normalized by SOC (µg C g^{-1} SOC h^{-1}), (C) net CH_4 flux (mg CH_4 m^{-2} h^{-1}), (D) net N_2O flux (µg N_2O m^{-2} h^{-1}), (E) soil temperature (T, °C), and (F) soil volumetric water content (SWC, m^3 m^{-3}) for N^+ and CTR plots in 2021, 2022, and 2023 field campaigns.

3.3 N fertilization altered $R_{h/SOC}$ dependencies on T and SWC

LOESS and NLS regression models showed similar $R_{h/SOC}$ dependencies on T and SWC (Fig. 4a, 4b). In CTR and N+, NLS models indicated a T optimum at 15.8 °C and 16.8 °C, respectively, above which decomposition was limited by dry soil conditions. ~~In contrast, $R_{h/SOC}$ in N+ increased continuously with T up to 20 °C (Fig. 4a). At T below 9 °C,~~Thus $R_{h/SOC}$~~(T)~~ in CTR at T below the optimum ~~had lower basal values and~~ rose more steeply compared to N+ plots (Fig. 4a)~~, whereas at T above 15 °C, $R_{h/SOC}$ in CTR began to decline.~~.

~~Incorporating SWC into the model (~~The $R_{h/SOC}$ ~~/($R_{h/SOC}$(T)) ratios)~~ revealed an SWC optimum in CTR, ~~but no clear~~while ~~SWC dependency~~ in N+ plots the $R_{h/SOC}$ - SWC dependency was less pronounced (Fig. 4b).~~.~~ The ~~In CTR,~~ $R_{h/SOC}$ ~~/($R_{h/SOC}$(T))~~ was maximized at SWC = 0.~~33~~ 32 m³ m⁻³ in CTR and at SWC = 0.35 m³ m⁻³ in N+, and in CTR it ~~declining~~ declined more steeply under both drier and wetter conditions than in N+ ~~. Conversely, $R_{h/SOC}$/($R_{h/SOC}$(T)) in N+ plots showed no SWC dependency across measured values (0.07–0.47 m³ m⁻³) (Fig. 4b).~~.

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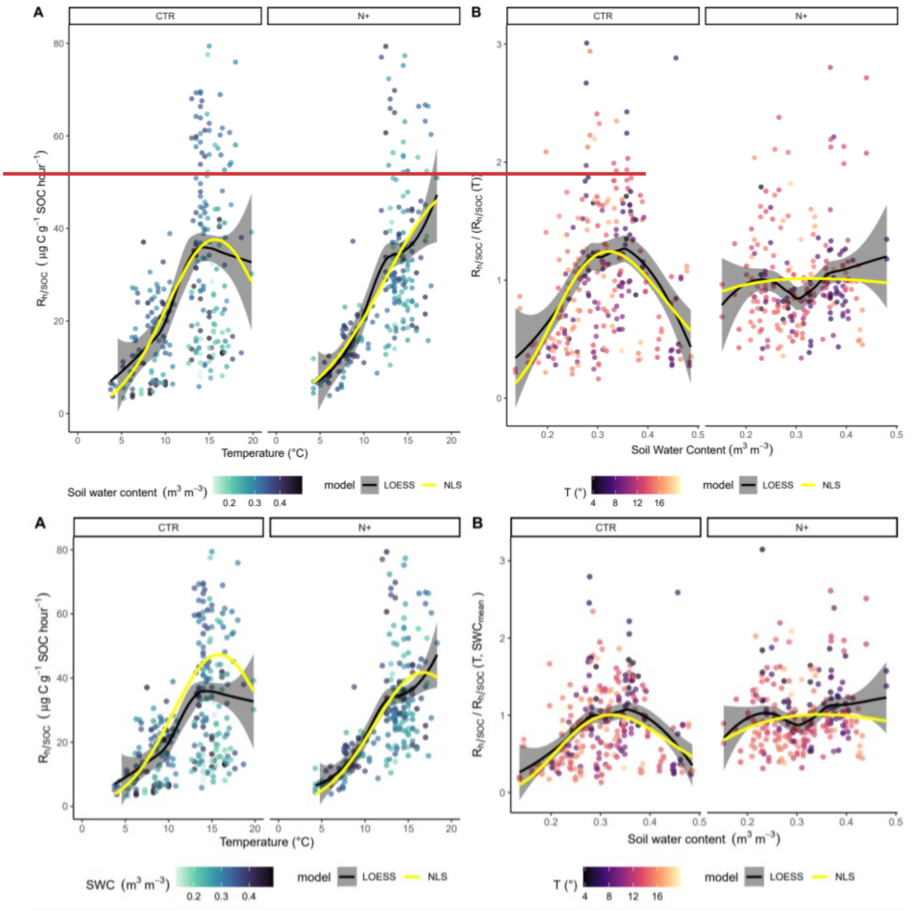

Figure 4: (A) Dependence of soil microbial respiration normalized by soil organic carbon ($R_{h/SOC}$, µg C g^{-1} SOC h^{-1}) on soil temperature at 5 cm depth (T, °C). (B) Ratio of measured $R_{h/SOC}$ to modeled $R_{h/SOC}$(T, SWC_{mean}) as a function of volumetric water content (SWC, m³ m^{-3}) at 5 cm depth. Panels display results separately for control (CTR) and N-fertilized (N+) plots. Shading of turquoise points in (A) reflects varying SWC, while shading of red points in (B) corresponds to variation in T. Black lines indicate local polynomial regression (LOESS) fits with gray ribbons showing 95% confidence intervals; yellow lines represent nonlinear least square (NLS) regression model fits. The NLS lines in (A) are modeled as $R_{h/SOC}$(T, SWC_{mean}) and in (B) as $R_{h/SOC}$(T, SWC)/ $R_{h/SOC}$(T, SWC_{mean}).

Model parameters and fit statistics are provided in Table 1 and Table 2. In CTR, the Ricker power parameter *c* significantly differed from one, indicating suppressed respiration in non-optimal SWC conditions. The model parameters describing functional dependencies on soil moisture were statistically significant for CTR but not for N+. ~~NLS model fit metrics (AIC, BIC) showed that adding SWC was statistically beneficial only for CTR plots, with reduced RMSE, MBE, and MAE values in CTR when using $R_{h/SOC}$(T, SWC), supporting the inclusion of SWC as a predictive variable in CTR only (Table 2).~~ However, neither the CTR nor N+ models showed bias (Table 2 and S1). NLS model fit metrics showed that R^2, RMSE, MBE, and MAE values were comparable between CTR and N+ models (Table 2). RMSE and MAE for NLS ~~$R_{h/SOC}$(T) and $R_{h/SOC}$(T, SWC)~~ models fell within the range of standard deviations from 10-fold cross-validation (Table S1).

Table 1: Parameter estimates with standard errors and p-values for ~~temperature-only (T) models (Eq.1: r_a, β_1, and β_2) and~~ combined temperature and SWC models (Eq. 1~~2~~: ~~r_a,~~ β_1, β_2, a, b, and c).

Treatment	Parameter	Estimate	Std. Error	p-value
CTR ~~CTR~~	β_1~~r_a~~	0.545~~0.733~~	0.101~~0.542~~	<0.001~~0.178~~
-	β_2~~β_1~~	-0.017~~0.502~~	0.004~~0.113~~	<0.001~~<0.001~~
-	a~~β_2~~	7.967~~-0.016~~	0.703~~0.004~~	<0.001~~<0.001~~
-	b~~a~~	3.101~~8.681~~	0.073~~0.196~~	<0.001~~<0.001~~
-	c~~b~~	8.045~~3.108~~	1.347~~0.072~~	<0.001~~<0.001~~
N+-	β_1~~c~~	0.515~~7.984~~	0.105~~1.341~~	<0.001~~<0.001~~
~~N+~~	β_2~~r_a~~	-0.015~~2.101~~	0.004~~1.183~~	<0.001~~0.077~~
-	a~~β_1~~	5.317~~0.301~~	3.250~~0.087~~	0.103~~0.001~~
-	b~~β_2~~	2.871~~-0.007~~	0.432~~0.003~~	<0.001~~0.030~~
-	c~~a~~	1.500~~8.399~~	1.063~~2.980~~	0.160~~0.005~~
-	~~b~~	~~3.000~~	~~1.158~~	~~0.010~~
-	~~c~~	~~0.468~~	~~0.968~~	~~0.629~~

Table 2: Goodness-of-fit statistics for NLS models based on ~~on temperature-only (T) (Eq. 1) and~~ combined temperature and ~~SWC~~ moisture ~~models~~ (Eq. ~~2~~1): ~~Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC),~~ proportion of explained variance (R^2), root mean square error (RMSE), mean bias error (MBE), and mean absolute error (MAE). RMSE, MBE and MAE in µg C g^{-1} SOC h^{-1}.

Treatment	~~BIC~~R^2	RMSE	MBE	MAE
			µg C g^{-1} SOC h^{-1}	
CTR ~~CTR~~	0.412~~245.21~~	15.55~~17.49~~	-0.33~~-0.11~~	11.42~~13.4~~
-	~~2204.48~~	~~15.66~~	~~-0.07~~	~~11.45~~
N+~~N+~~	0.401~~918.14~~	13.36~~13.3~~	-0.48~~0.05~~	9.28~~8.99~~
-	~~1934.13~~	~~13.29~~	~~0.05~~	~~9.01~~

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3.4 N addition moderates the impact of soil moisture on modeled respiration

The model accuracy was generally higher in N+ than in CTR plots (Table 2). However, ~~S~~the soil moisture effects on $R_{h/SOC}$(T, SWC) ~~$R_{h/SOC}$~~ were ~~only observed in control (~~more pronounced in CTR and N+~~)~~ plots, as evidenced by larger decline and increase of ~~d~~ respiration rates ~~when soil water content (SWC) was included as a variable~~during year 2021 with severe drought (Fig. 5). ~~In contrast, incorporating SWC into N-fertilized (N+) plots did not enhance model performance (Fig. 4), and model accuracy was generally higher in N+ than in CTR plots (Table 2). For CTR plots, models that combined temperature and SWC ($R_{h/SOC}$(T, SWC), Eq. 2) aligned more closely with measured $R_{h/SOC}$ values compared to temperature-only models ($R_{h/SOC}$(T), Eq. 1), as shown in Fig. 5. The addition of SWC to models for N+ plots was not statistically warranted based on Akaike (AIC) and Bayesian Information Criterion (BIC) values.~~

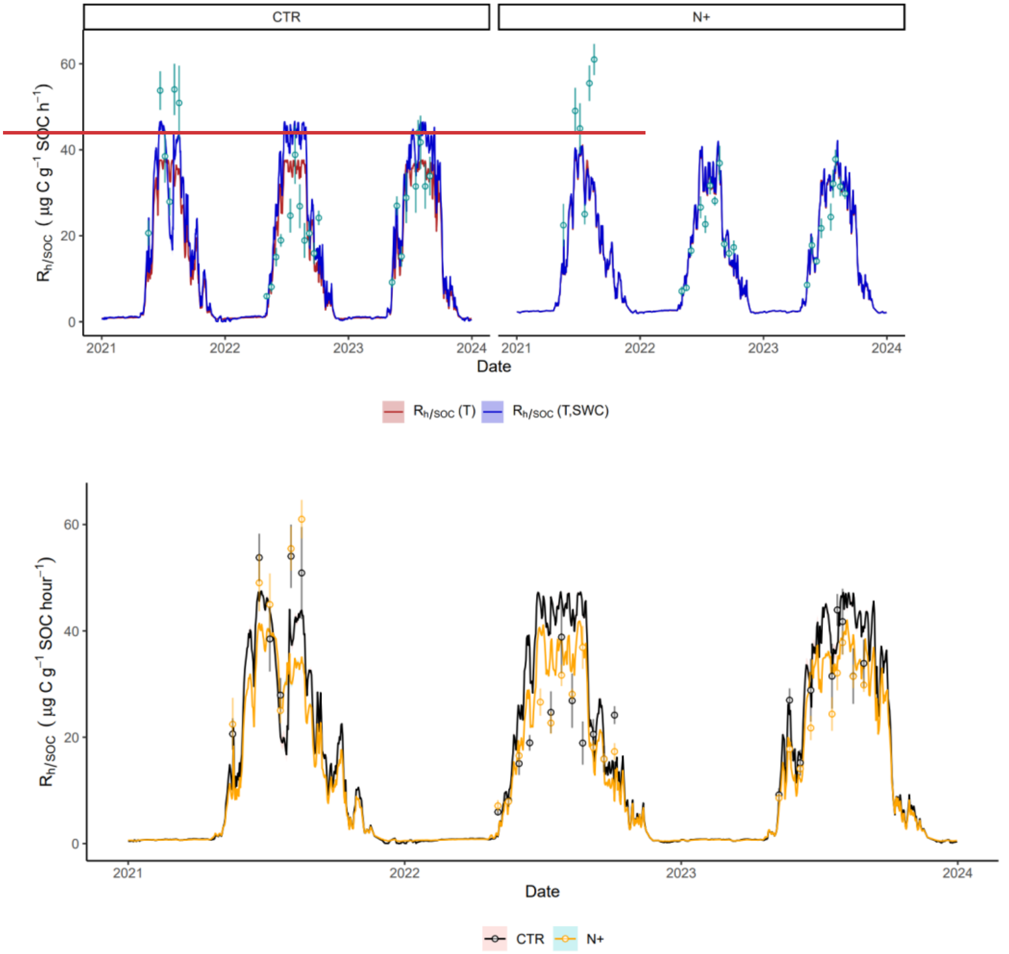

Figure 5: Time series of daily mean $R_{h/SOC}$ (µg C g^{-1} SOC h^{-1}) in CTR and N+ plots, with measurements shown as points (error bars indicate SE) and model estimates as lines (ribbons indicate SE). ~~**Simulations used NLS models driven by temperature alone ($R_{h/SOC}$(T), Eq. 1) or by combined temperature and moisture ($R_{h/SOC}$(T, SWC), Eq. 2), based on hourly T and SWC data (Fig. S1).**~~

3.5 Seasonal and annual differences in $R_{h/SOC}$ between CTR and N+ plots

During the winter, daily model predictions of $R_{h/SOC}$ remained consistent across CTR and N+ treatments, with little variation due to low soil temperatures (Fig. 5). However, in the summer, with temperatures above 5°C, $R_{h/SOC}$ modeled with combined $R_{h/SOC}$(T, SWC) ~~versus $R_{h/SOC}$(T) alone~~ displayed marked differences between ~~in~~ CTR plots ~~but remained similar in~~and N+ plots. In CTR plots, the modeled $R_{h/SOC}$ values ~~modeled with $R_{h/SOC}$(T, SWC)~~ were generally higher, except during a brief drought period in 2021, when modeled $R_{h/SOC}$ values ~~from $R_{h/SOC}$(T, SWC)~~ decreased. The $R_{h/SOC}$(T, SWC) values of N+ plots in drought 2021 period also decreased. However, the daily $R_{h/SOC}$ modeled values of N+ were generally lower and showed less variation then in CTR plots, ~~almost no variation between $R_{h/SOC}$(T) and $R_{h/SOC}$(T, SWC) models from 2021 to 2023,~~ resulting in consistently lower annual $R_{h/SOC}$ ~~regardless of model choice (~~in N+ than in CTR (Fig. 6).

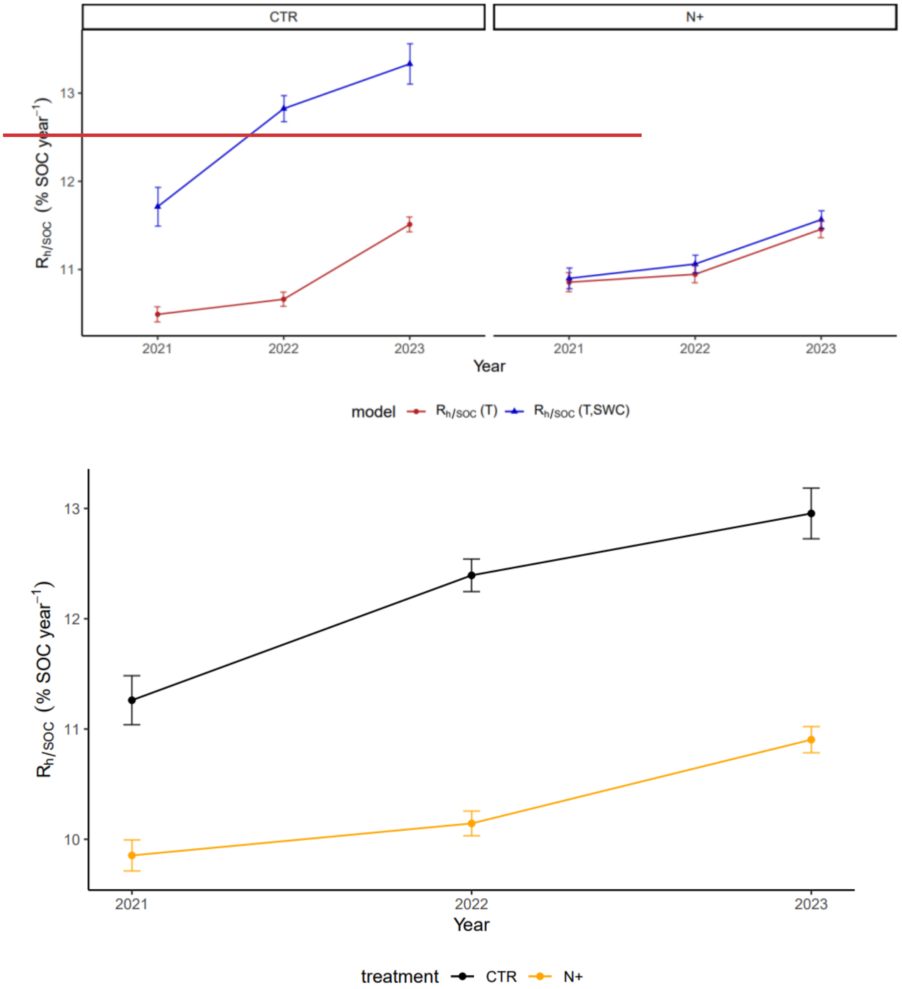

Figure 6: Annual $R_{h/SOC}$ (% SOC per year) estimated with NLS models driven by ~~soil temperature alone ($R_{h/SOC}$(T), Eq. 1) or~~ combined temperature and moisture ($R_{h/SOC}$(T, SWC), Eq. ~~2~~1) in CTR and N+ plots, using hourly T and SWC data for model inputs (Fig. S1).

3.6 Annual ~~$R_{h/SOC}$~~GWP reduc~~ed~~tion in relation to N addition~~ and low soil moisture sensitivity~~

Annual $R_{h/SOC}$ rates (expressed as % per unit SOC per year) based on daily model estimates ranged from 9~~10~~.85 (±0.14 SE) %~~5~~ to ~~13~~12.~~3~~95 (±0.23 SE) % and increased over 2021–2023 (Fig. 6). In CTR plots, $R_{h/SOC}$(T, SWC) models yielded on average 1.90 (±0.41 SE) ~~7~~% higher rates than ~~$R_{h/SOC}$(T) models, with means of 12.6% and 10.9%, respectively. I~~in N+ plots~~,~~ ~~$R_{h/SOC}$ averaged 11.2%, with only a 0.2% difference between $R_{h/SOC}$(T, SWC) and $R_{h/SOC}$(T) models.~~. These results suggest that ~~reduced~~ changes in sensitivity of annual $R_{h/SOC}$ to soil temperature and moisture in N+ plots contributes to SOC retention. The R_h rate ($R_{h/SOC}$(T, SWC) * SOC_{N+}) difference between CTR and N+ showed potential reduction of CO_2 emissions by -345.4 (±73.6 SE) g CO_2 m^{-2} y^{-1} (Table 3). The GWP of reduced CH_4 oxidation rates after N fertilization equaled to 10.1 (±0.5 SE) g CO_2-eq m^{-2} y^{-1}, and the increase in N_2O emissions to 1.1 (±0.1 SE) g CO_2-eq m^{-2} y^{-1} (Table 3). Thus, when considering the sum of these processes and the associated emissions with fertilizers productions 6.5 g CO_2 m^{-2} yr^{-1}, the total GWP annual reduction in relation to N addition was -327.6 (±73.6 SE) g CO_2 m^{-2} yr^{-1}.

Table 3: Annual global warming potential (GWP) reduction by long-term N fertilization in boreal Scots pine forest with contribution of individual greenhouse gas (GHG) fluxes (microbial respiration normalized by soil organic carbon stock $R_{h/SOC}$, CH_4 net oxidation, and N_2O flux net exchange) evaluated as a difference between control (CTR) and N fertilized plots (N+). Minus values indicate net GWP reduction. The AR6 GWP-100 values 27 for CH_4 and 273 for N_2O were used for calculation of CO_2-equivalents (ICCP, 2023).

Treatment	R_h/SOC (%)		**GWP-CO_2 (g CO_2 m^{-2} y^{-1})**		CH_4 (g CH_4 m^{-2} y^{-1})		**GWP-CH_4 (g CO_2-eq m^{-2} y^{-1})**		N_2O (mg N_2O m^{-2} y^{-1})		**GWP-N_2O (g CO_2-eq m^{-2} y^{-1})**		**GWP-GHG (g CO_2-eq m^{-2} y^{-1})**	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
CTR	12.2	0.5	2214.9	90.4	-1.6	0.0	-42.9	0.5	-2.2	0.8	-0.6	0.2	2171.4	90.4
N+	10.3	0.3	1869.5	56.8	-1.2	0.0	-32.8	0.5	1.9	0.6	0.5	0.2	1837.3	56.8
Difference	-1.9	0.4	**-345.4**	**73.6**	0.4	0.0	**10.1**	**0.5**	4.2	0.7	**1.1**	**0.2**	**-334.1**	**73.6**

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4 Discussion

Our results show that nitrogen (N) fertilization significantly increased tree stand biomass and litterfall in N+ plots compared to control (CTR) plots (Fig. 2a), aligning with previous studies demonstrating enhanced forest productivity with N addition (Hyvönen et al., 2008). Biomass reduction from 2014 to 2020, highlighted the strong impact of thinning in 2015 on aboveground carbon stocks and organic inputs to soil. Thinning corresponded to a litter input peak, with N+ plots showing higher litterfall than CTR. This was further supported also with the above ground litterfall measurements during 2021-2023 (25.1 g m^{-2} $month^{-1}$ in N+ vs. 14.3 g m^{-2} $month^{-1}$ in CTR) (Fig. 2b). Consistently with biomass and litterfall, soil organic carbon (SOC) increased under N fertilization, reaching 5.6 kg C m^{-2} in N+ compared to 4.9 kg C m^{-2} in CTR by 2023 (Fig. 2c), indicating enhanced SOC retention alongside aboveground carbon storage due to reduced microbial respiration (Janssens et al., 2010).

~~In our study,~~ Differences in carbon stocks between treatments, prevented drawing conclusions on soil organic matter decomposition rates solely based on the observed increase in heterotrophic respiration (R_h) under N fertilization (Fig. 3), and required normalizing respiration by SOC ($R_{h/SOC}$). Although, the mean $R_{h/SOC}$ values were not statistically different between CTR and N+. The $R_{h/SOC}$ ~~soil microbial respiration~~ responded to N fertilization with ~~a~~ reduced sensitivity to soil moisture (Fig. 4~~b~~), suggesting a potential mechanism (e.g., microbial adaptation, substrate shifts) for enhanced carbon retention in fertilized plots. ~~However~~However, the slightly increased sensitivity of microbial respiration to temperature at higher values in N fertilized plots (Fig. 4a) may ~~indicates~~ indicate a risk of accelerated carbon loss under warming conditions in these soils compared to controls. This dual response to long-term N fertilization, which are discussed in detail in following chapters, ~~highlights~~ highlights the need to consider both moisture and temperature responses in models predicting boreal forest soil carbon dynamics in the context of long-term atmospheric N depositions and climate change.

4.1 Response of soil heterotrophic respiration to N fertilization

The meta-analysis of R_h responses to N fertilization in temperate and boreal forests, reported a 15% average decrease in heterotrophic CO_2 emissions (Janssens et al., 2010). However, the wide range of responses of heterotrophic CO_2 emissions following N fertilization (Janssens et al., 2010), spanning from a 57% decrease to a 63% increase, encompasses 26% increase in mean soil heterotrophic respiration (R_h) from 2021–2023, observed here (Fig. 3a). Limiting R_h by N fertilization in low-productivity forests (Janssens et al., 2010) may relate to low litter quality, as observed in our study's *Calluna*- and *Vaccinium vitis idaea*-type Scots pine forest.

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~~Limiting R_h by N fertilization in low-productivity forests (Janssens et al., 2010) may relate to low litter quality, as observed in our study's *Calluna*- and *Vaccinium vitis idaea*-type Scots pine forest.~~ Yet, higher litter amount due to higher biomass production and thinning ~~and more pronounced~~ in fertilized (N+) than in control (CTR) plots (Fig. 2a and Fig. 2b) may support increased R_h in N+. Although thinning effects on boreal Scots pine R_h are generally modest (Aun et al., 2021), larger inputs of higher-quality litter from harvest residues in N+ plots, including fine roots, needles, and branches, likely stimulated R_h (Liski et al., 2006; Zhang et al., 2018). This enhanced carbon availability, along with increased soil nitrogen concentrations, and stimulated microbial activity and biopolymers degradation capabilities explains the observed increase in heterotrophic respiration (R_h) under N fertilization (Fig. 3). Additionally, we observed a decline in phosphorus concentrations in N-fertilized plots compared to unfertilized plots, probably due to microorganisms mining for phosphorus to sustain their increased activity (Richy et al., 2024).

Despite the significant increase in R_h, SOC-normalized heterotrophic respiration ($R_{h/SOC}$) did not differ significantly between CTR and N+ plots. This suggests that increased R_h with N addition originated more from higher litter input and SOC rather than an enhanced microbial decomposition rates (Fig. 3b). The R_h responses to N in Sweden's Rosinedalsheden Scots pine forest also showed variability, with differing results based on plot size and SOC pool similarity (Hasselquist et al., 2012; Marshall et al., 2021). Using hourly $R_{h/SOC}$ (Curiel Yuste et al., 2007; Shahbaz et al., 2022) may better capture decomposition rate differences than R_h alone, yet hourly-scale $R_{h/SOC}$ responses to N fertilization may still be obscured by fine-scale spatial and temporal variations in soil temperature and moisture (Fig. 3, Fig. S2), primary drivers of $R_{h/SOC}$ (Curiel Yuste et al., 2007; Shahbaz et al., 2022). For example, our biweekly measurements of $R_{h/SOC}$ showed similar means for CTR and N+ plots, but annual $R_{h/SOC}$ means differed (Fig. 6), reflecting differences in temperature and moisture distribution and differences in functional $R_{h/SOC}$ dependencies to temperature and moisture between treatments (Fig. S1 and Fig. S2; Fig. 4).

4.2 Shifts in R_h dependency on soil environmental conditions with N addition

The functional relationships between R_h and environmental variables such as soil temperature (T) and volumetric soil water content (SWC), used in Earth system and soil C models (Falloon et al., 2011; Sierra et al., 2015), often overlook soil N status. Here, we observed that N fertilization modified the $R_{h/SOC}$ dependency on both T and SWC, with a sharper increase in $R_{h/SOC}$ with temperature in N+ plots relative to CTR plots. Unlike CTR plots, where $R_{h/SOC}$ declined at temperatures above 15 °C, N+ plots maintained elevated $R_{h/SOC}$ values under high temperatures (Fig. 4a) which is in line with Chen et al. (2024) and may in warming climates indicate higher risk of increased CO_2 emissions from accumulated SOC. This increased $R_{h/SOC}$ in response to N addition could be attributed to shifts in substrate composition, where N fertilization enhances the decomposition of labile, C-rich litter and suppresses N-rich organic matter with high lignin content (Berg and Matzner, 1997; Bonner et al., 2019; Janssens et al., 2010; Wu et al., 2023). Furthermore, our study site exhibited increased Mn peroxidase activity following long-term N addition, indicating enhanced microbial degradation of polyphenolic compounds (Richy et al., 2024). Thus, shifts in litter quality, specifically C and N ratios, likely contribute to divergent R_h responses to temperature (Robinson et al., 2020).

Moisture also plays a pivotal role in R_h sensitivity to temperature (Robinson et al., 2020), and in modifying soil respiration rates especially under N fertilization and drought conditions (Nair et al., 2024). In our N-fertilized plots, $R_{h/SOC}$ was largely independent of soil moisture, and contrasted with the expected humped response of $R_{h/SOC}$ to SWC in CTR plots (Fig. 4b). This variation in SWC response suggests potential microbial adaptation to moisture availability (Lennon et al., 2012; Manzoni et al., 2021) and changes in soil physical properties influencing O_2 and solute diffusivity (Huang et al., 2023; Moyano et al., 2013). The observed differences between CTR and N+ plots imply that N status or fertilization-induced changes in soil properties influence the sensitivity of organic matter decomposition to moisture. Soil moisture influences microbial carbon use efficiency (CUE) by affecting substrate accessibility and physiological stress, with lower CUE observed in dry soils (Butcher et al., 2020; Ullah et al., 2021). Additionally, accelerated decomposition following soil rewetting, commonly referred to as the “Birch effect,” has been linked to increased short term N availability (Jarvis et al., 2007). However, prolonged N addition may impose a phosphorus limitation on decomposition due to N imbalance (Richy et al., 2024).

Simulating $R_{h/SOC}$ based on both temperature and moisture inputs showed that models relying solely on temperature underestimate $R_{h/SOC}$ for initially N-limited boreal forest soils (Fig. 5 and Fig. 6). Thus, current soil C models should integrate both temperature and moisture dependencies in their environmental modifiers of decomposition rates, as well as consider variations in SWC response under differing N statuses to improve SOC accuracy in fertile soils (Tupek et al., 2016). For example, the CENTURY model, which considers topsoil N content and its effect on the fine-litter C ratio, offers a slight increase in simulated SOC stocks (Tupek et al., 2016), whereas e.g. Yasso model does not account for soil N. However, by restricting topsoil N effects solely to linear scaling of carbon use efficiency (CUE) or decomposition rates (Zhang et al., 2018), current models lack the ability to capture the influence of N-driven variations in temperature and moisture modifiers. This limitation highlights the need to re-evaluate the linear scaling of decomposition with N to better account for the differential respiration sensitivities observed in this study (Fig. 4). Incorporating nonlinear nitrogen effects on temperature and soil moisture modifiers depends on the model's structure. In soil carbon-only models like Yasso, updating these modifiers with a larger dataset that includes nitrogen deposition gradients and soil organic carbon stocks could improve performance. Conversely, in soil carbon-nitrogen models that already account for SOC-N interactions, existing functional relationships should be re-evaluated, considering their interactions with environmental modifiers.

4.3 Implications for climate change mitigation

Annually, N-fertilized plots respired ~~11~~10.3~~2~~% of SOC (± 0.3 SE), compared to 12.2% (± 0.5 SE) ~~12.6%~~ in CTR plots, indicating that N fertilization increased microbial C use efficiency, leading to SOC accumulation. This 1.90 (±0.41 SE) % ~~1.4%~~ reduction in annual SOC loss due to N addition corresponds to an average of 345.4 (±73.6 SE) g CO_2 m^{-2} y^{-1}. ~~262.5 g CO_2 m^{-2} $year^{-1}$.~~ The combined effect of reduced methane (CH_4) oxidation and a slight shift in nitrous oxide (N_2O) from a sink to an emitter comparable to Maljanen et al., (2006), and equivalent to 8.7 g CO_2eq. m^{-2} $year^{-1}$ did not negate this positive mitigation potential and agreed with Öquist et al., (2024). The Haber-Bosch process required for N_2 to NH_3 conversion has an associated emission cost of approximately 2.96 kg CO_2eq. per kg NH_3 (Osorio-Tejada et al., 2022), which would reduce our calculated mitigation potential by about 6.5 g CO_2 m^{-2} $year^{-1}$. Consequently, the average mitigation potential for N fertilization in our forest soil study is estimated at -327.6 ±73.6 SE g CO_2 m^{-2} yr^{-1} ~~at 246.7 g CO_2 m^{-2} $year^{-1}$~~ (equivalent to 0.~~67~~ 89 ±0.2 SE t C ha^{-1} $year^{-1}$). While these findings likely apply to nutrient-poor boreal ecosystems, extrapolation should be done for similar stands with similar climate with caution for other ecosystems. For example, Saarsalmi et al. (2014) showed that N fertilization stimulated growth in relation to mean annual production (more in nutrient poor pine stands and less in spruce stands with higher nutrient status). Schulte-Uebbing et al. (2021) demonstrated that N addition enhance biomass carbon sequestration primarily in boreal regions, while having negative effects in tropical forests.

5 Conclusions

This study reveals that increased soil N status after long-term N fertilization in boreal Scots pine ecosystems can alter the dependency of C decomposition on temperature and moisture. Although the models showed relatively large mean residuals when evaluated against individual measurements, their mean bias errors were close to zero. Incorporating these findings into soil C models suggests global implications for reducing uncertainty of boreal soil CO_2 emission estimates and soil C stock projections under N deposition and climate warming. Our results also suggest a net reduction in soil GHG emissions with long-term N fertilization, indicating that N fertilization in boreal Scots pine ecosystems not only enhances tree biomass but may also serve as a viable forest management strategy for climate change mitigation.

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Data and code availability

Complete data set on GHG fluxes, soil temperature and moisture, tree biomass and litter production, and soil carbon stocks are archived and available on ZENODO (https://doi.org/10.5281/zenodo.13889762). The R scripts supporting results replication is also openly available on ZENODO (https://doi.org/10.5281/zenodo.14101488).

Author contribution

BT, AL, RM designed the hypothesis and experimental design. RM and AL arranged research funding and oversaw project management. BT contributed to data collection and carried out the analysis. BT prepared the manuscript with contributions from all co-authors.

Competing interests

We have no competing interests.