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RESEARCH ARTICLE

Fertilizer-induced soil carbon rapidly disappears after clearcutting in boreal production forests

Margaux Boeraeve[1] | Gustaf Granath[2] | Björn D. Lindahl[3] | Karina E. Clemmensen[4] | Joachim Strengbom[1]

[1]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]Department of Ecology and Genetics, EBC, Uppsala University, Uppsala, Sweden

[3]Department of Soil and Environment, Swedish University of Agricultural Sciences, Uppsala, Sweden

[4]Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence
Margaux Boeraeve
Email: margaux.boeraeve@gmail.com

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Abstract

1. Forests have a substantial potential to contribute to climate change mitigation, depending on how they are managed. Forest fertilization with nitrogen is used to increase tree productivity in Fennoscandian forests, but it can also increase soil carbon stocks. However, such forests are often harvested through clearcutting, a practice known to impact soil carbon stocks, nitrogen mineralization and biodiversity.
2. To test whether fertilizer-induced soil carbon stocks are persistent, we studied post-clearcut soil carbon and nitrogen stocks, soil respiration, tree growth, ground vegetation and soil fungal communities in 48 previously fertilized and unfertilized production forests in central Sweden.
3. In the first year after clearcutting, clearcuts of previously fertilized forests stored 7 t (+30%) more carbon and 210 kg (+32%) more nitrogen per hectare in the soil organic layer than clearcuts of unfertilized forests.
4. Four to 13 years after clearcutting, there was no significant difference in carbon and nitrogen stocks of the organic layer, or in soil CO_2 efflux, between clearcuts of previously fertilized and unfertilized forests.
5. Saprotrophic ascomycetes were more abundant in clearcuts of previously fertilized forests, independent of time since clearcutting. Previous fertilization did neither result in increased growth of regenerating trees nor alter understory vegetation.
6. *Synthesis and applications*. Overall, the carry-over effects on biodiversity from forest fertilization into stands regenerating after clearcutting were limited. We conclude that soil organic carbon stores induced by fertilization are short-lived and do not persist after clearcutting. Consequently, the potential of forest fertilization to mitigate climate change is likely limited to increases in aboveground biomass and the products that can be produced with the harvested biomass. Our study raises questions about where the added nitrogen and the fertilizer-induced increase in soil carbon have ended up—knowledge that is essential for making well-informed decisions about future fertilization strategies.

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KEYWORDS
boreal forests, clearcut harvesting, forest fertilization, soil carbon, soil fungi, soil respiration

1 | INTRODUCTION

Forests have a substantial potential to contribute to climate change mitigation (Grassi et al., 2017). On the one hand, they constitute a large and growing carbon stock, and on the other hand, they provide forestry products that can substitute fossil fuel products or store carbon in long-lasting wood products (Pan et al., 2011; Petersson et al., 2022). Approximately one third of the global forest carbon stock is found in boreal forests (Pan et al., 2011), the majority of which is under some form of management (Burton et al., 2010; Gauthier et al., 2015). The climate mitigation potential of boreal forests depends largely on how they are managed, especially for intensively managed forests in Fennoscandia (Gauthier et al., 2015; Mäkipää et al., 2023). Consequently, forest management practices to increase forest carbon sinks are increasingly adopted into climate policies (European Environment Agency, 2024; Gulbrandsen, 2024). Common forest management practices in boreal forests include thinning, fertilization, harvesting by clearcutting, and site preparation, all of which are known to influence forest carbon stocks (Gundale et al., 2024; Mäkipää et al., 2023; Mayer et al., 2020; Noormets et al., 2015).

Forest fertilization with nitrogen is frequently used to increase tree productivity and boosts both aboveground and belowground carbon stocks (Boeraeve et al., 2025a; Jörgensen et al., 2021; Marshall et al., 2023; Zhao et al., 2022). Increases in belowground carbon stocks are attributed to a combination of increased litter input and decreased decomposition and soil respiration (Forsmark et al., 2020; Janssens & Luyssaert, 2009; Marshall et al., 2021). Nitrogen-induced reductions of soil respiration are often ascribed to shifts in soil microbial communities and activities (Bonner et al., 2019; Kuyper et al., 2024; Maaroufi et al., 2017; Zak et al., 2008). More specifically, increased nitrogen availability has been found to hamper ectomycorrhizal fungi with decomposer capabilities, shifting communities away from nitrogen-mining species, thereby decreasing organic matter degradation (Argiroff et al., 2022; Jörgensen et al., 2022; Jörgensen et al., 2024; Zak et al., 2019). While nitrogen fertilization can increase soil carbon stocks, it also increases nitrogen leaching (Binkley et al., 1999; Lundin & Nilsson, 2021) and has negative effects on biodiversity (Maaroufi et al., 2019; Strengbom et al., 2001; Strengbom & Nordin, 2008). The potential of fertilization to improve tree productivity and belowground carbon storage, as a measure for climate mitigation, should thus be carefully balanced against the negative effects. The potential of fertilization as a climate mitigation measure also depends on the persistence of the induced carbon stores, which are currently unexplored.

Fennoscandian production forests are commonly harvested through clearcutting, which is known to reduce soil carbon stocks (Covington, 1981; Johnson & Curtis, 2001; Nave et al., 2010; Olsson et al., 1996), increase nitrogen mineralization (Binkley, 1984; Prescott, 1997; Smethurst & Nambiar, 1990) and to severely disrupt biodiversity (Lunde et al., 2025; Matveinen-Huju & Koivula, 2008; Vanha-Majamaa et al., 2017), especially in groups that depend on living host trees, such as ectomycorrhizal fungi (Kohout et al., 2018; Sterkenburg et al., 2019). Clearcutting can be expected to release saprotrophic fungi from suppression by ectomycorrhizal fungi (Kyaschenko et al., 2017), thereby increasing decomposition (Bödeker et al., 2016; Fernandez & Kennedy, 2016). Whether increased decomposition after clearcutting annihilates fertilizer-induced soil carbon stocks remains an open question. Previous research found that nitrogen addition not only increases the quantity but also alters the chemical composition of soil organic matter, with potential consequences for its degradability (Berg & Matzner, 1997; Hasegawa et al., 2021; Moorhead & Sinsabaugh, 2006; Neff et al., 2002). If fertilization increases the quality of soil organic matter as a substrate for decomposers, we expect to see higher nutrient release after clearcutting of previously fertilized forests compared to unfertilized forests, which should stimulate tree growth and increase vegetation biomass. However, previous studies in nitrogen addition experiments that were harvested by clearcutting report contradicting results. While some studies found increased tree growth, needle nitrogen concentration, nitrogen mineralization, and soil inorganic nitrogen concentration in forests fertilized during the preceding rotation period (Footen et al., 2009; From et al., 2015; Högbom et al., 2001), others found no difference in seedling mortality, tree growth, needle nitrogen concentration, and understory biomass between clearcuts of fertilized and unfertilized stands (Johansson et al., 2013; Larsson et al., 2024; Sikström, 2005).

Here, we investigated the long-term effects of fertilization on post-harvest tree growth (i.e. the next generation of trees), topsoil carbon and nitrogen stocks, and plant and fungal communities in boreal production forests. As nitrogen limitation is expected to be less severe in clearcuts of fertilized forests, we hypothesized that the biomass, diversity, and activity of saprotrophic fungi would be higher and the re-establishment of ectomycorrhizal fungi delayed in clearcuts of previously fertilized forests. We further hypothesized that this, in combination with a decreased C:N ratio of the organic layer, would lead to increased decomposition after clearcutting in previously fertilized forests compared to unfertilized forests. Finally, we hypothesized that increased decomposition would increase soil respiration, lead to soil carbon losses and nutrient release in clearcuts of previously fertilized forests compared to clearcuts of unfertilized forests, resulting in increased tree growth and altered ground vegetation composition, with a larger dominance of grasses and fewer ericaceous dwarf-shrubs after fertilization.

2 | MATERIALS AND METHODS

2.1 | Study area and design

The research was conducted in central Sweden (59–60° N) in two study areas (Figure S1) in the transition between the hemiboreal and boreal zone (Ahti et al., 1968). In total, 36 clearcuts were selected: 18 clearcuts of previously fertilized forests paired with 18 clearcuts of unfertilized forests with similar characteristics (site index, time since clearcutting, soil type). All forests were the property of Sveaskog AB, who provided the data necessary to select them. No permission was needed for the fieldwork. Before clearcutting, the forests were dominated by coniferous trees, with a composition ranging from 100% *Pinus sylvestris* to 94% *Picea abies*. The share of deciduous trees was very low, with no stand containing more than 4% *Betula pendula*. In the fertilized sites, 150 kg N ha^{-1} had been applied once ($n = 14$) or twice ($n = 4$) between 1973 and 2006 in the form of the commonly used Skog-CAN, which is ammonium nitrate with added dolomite [$CaMg(CO_3)_2$] to reduce the risk of acidification, and 0.2% boron (B). A space-for-time substitution approach was used to determine the change over time in soil conditions, plant and fungal communities after clearcutting. The forests were clearcut between 2009 and 2018 and sampled between May and September 2022, that is, 4–13 years after clearcutting. All clearcuts had undergone mechanical soil preparation and had been planted with tree seedlings (*Pinus sylvestris* and *Picea abies*). On each clearcut, three circular plots with a radius of 10 m were delineated away from any retention trees. In these plots, soil samples were taken, soil respiration was measured, ground vegetation and tree layer were surveyed, and young trees were sampled to estimate tree growth rate. Soil samples and soil respiration measurements were taken in the parts of the plot that were undisturbed during soil preparation, that is, where the soil organic layer was intact.

After analysing the results from this first field campaign, an additional sampling campaign in August 2023 was set up to collect soil samples and measure soil respiration in more recent clearcuts, that is, within a year before sampling (clearcut in 2022 or the beginning of 2023, before the start of the growing season). In this campaign, six clearcuts of previously fertilized forests were selected and paired with six clearcuts of unfertilized stands with similar characteristics (Figure S1). In the fertilized sites, 150 kg N ha^{-1} had been applied once between 2004 and 2012. After clearcutting, the soil was mechanically prepared in two of the six pairs. None of these clearcuts had undergone tree planting yet, which is the common regeneration practice. The soil sampling and soil respiration measurements were conducted in the same way as during the first sampling campaign.

2.2 | Tree and ground vegetation survey

Composition of ground vegetation was determined using a 1 × 1 m frame divided into 25 quadrats. The number of quadrats in which a taxon was present was recorded for each vascular plant species and for mosses, lichens, and vascular plants as a group. For tree species, a distinction was made between individuals belonging to the tree layer (>1.2 m) or the ground vegetation (<1.2 m). This was repeated six times across each 10-m radius plot. In each plot, a circular subplot with radius of 3 m was delineated, in which the species and height of all trees (>1.2 m) were recorded, from which tree density and tree layer composition were later calculated. In the clearcuts from 2009 to 2015, three tree individuals (>1.2 m) of both *Picea abies* and *Pinus sylvestris* were sampled for estimation of tree growth rate. If fewer than three individuals of a species were present in a plot, the species was not sampled. Sampling was done by cutting the tree at the base and collecting a disc of the stem. These cross-sections were taken back to the laboratory where they were sanded and scanned. Tree ring widths were measured using the measuRing R package (Lara et al., 2015), and growth rates (yearly diameter increase, in mm) were extracted from linear regressions of cumulative tree ring width against year, plotted for each individual tree separately.

2.3 | Soil respiration

Soil CO_2 flux was measured on rain-free days in two rounds: one in spring (16 May–9 June 2022) and one in summer (22 August–12 September 2022). During the second sampling campaign in 2023, only one round of soil CO_2 flux measurements was conducted (11–17 August 2023). In each plot, respiration was measured at five locations: one in the middle and four closer to the edge, using a closed chamber constructed from a dark, non-transparent PVC collar (diameter = 23.5 cm, height = 15 cm) equipped with a portable infrared CO_2 gas analyser (Vaisala GMP343) and a humidity and temperature meter (Vaisala HM70). All living ground vegetation was removed before gently pushing the chamber 0–1 cm into the soil, minimizing soil disturbance while making sure that no gaps were present between the collar and the soil surface. CO_2 concentration was then recorded for 3 min at 15 s intervals. A quadratic function was fitted between CO_2 concentration and time, and CO_2 flux was calculated from the linear term on a per area basis (mg C m^{-2} h^{-1}), accounting for chamber temperature and volume according to standard equations (Kutzbach et al., 2007). After each CO_2 measurement, the soil water content and temperature, as well as the depth of the organic layer, were determined. Soil water content was measured four times with a soil moisture sensor (Meter GS3 with a Pro-Check reader) and the mean value was used in further analyses. Soil temperature was measured at a depth of 3 cm depth.

2.4 | Soil sampling and analyses

Twenty-five soil cores (diameter 3 cm) were taken in a grid pattern across each plot; the mineral layer was removed, and the organic layer, including litter, was pooled into one soil sample. Parts of the plot where the soil organic layer was removed during soil preparation

were avoided. Soil samples were stored on ice until frozen at −20°C. After weighing and homogenisation in a freeze-mill, a subsample was freeze-dried, weighed (before and after to determine % dry weight), and assessed for carbon and nitrogen content using a combustion elemental analyser (TruMac CN; LECO, St. Joseph, MI, USA). A 5 g subsample of freshly frozen, homogenised soil was shaken in 25 mL of deionized water for 10 min at 650 rpm and left to equilibrate for 15 min before measuring pH with a PHM93 pH meter (Radiometer, Copenhagen). The carbon and nitrogen stocks of the organic layer were calculated by multiplying the dry weight of the soil sample by the carbon and nitrogen content, respectively, and scaling it up to tonnes ha^{-1} based on the total area of the soil cores.

From the frozen homogenised soil samples of the 2023 sampling campaign, potential enzymatic activities of five hydrolytic enzymes (cellobiohydrolase, β-glucosidase, β-xylosidase, β-*N*-acetylglucosaminidase and acid phosphatase) and of manganese peroxidase were determined (Kyaschenko et al., 2017; Saiya-Cork et al., 2002). Soil suspensions were made by shaking a volume of frozen soil equivalent to 2 g dry soil in 200 mL sodium acetate buffer (50 mM, pH 5) for the hydrolytic enzyme assay and equivalent to 5 g dry soil in 50 mL sodium acetate buffer for the manganese peroxidase assay. For the hydrolytic enzymes, the soil suspensions were further diluted 10 times, and 50 μL fluorogenic umbelliferyl substrate was added to 200 μL soil suspensions (0.001 g dry weight soil mL^{-1}). After incubating in the dark for 2 h, 10 μL 0.5 M NaOH was added to stop the reaction, and fluorescence was measured, controlling for background fluorescence (assays without the incubation step). The soil suspensions were also incubated with a standard methylumbelliferone solution as a quenching control. Soil suspensions with too high quenching were further diluted, and the assay was repeated. Net fluorescence was converted to enzyme activity expressed per min and g organic matter. For the manganese peroxidase assay, 50 μL of clear supernatant of soil suspensions (0.1 g dry weight soil mL^{-1}) was added to a buffer solution with 3-dimethylaminobenzoic acid and 3-methyl-2-benzothiazolinone hydrazone hydrochloride and either $MnSO_4$ or EDTA (which chelates Mn). Four combinations were done: one with Mn and H_2O_2 (peroxidase activity including Mn-dependent), one with EDTA and H_2O_2 (Mn-independent peroxidase activity), one with EDTA (negative control) and one with Mn, H_2O_2, and a commercial horseradish peroxidase (Sigma-Aldrich, Burlington, MA, USA) (positive control). Immediately after mixing the reagents, plates were put in the plate reader, and absorbance was measured every 3 min for 30 min. Mn-dependent activity was calculated as total peroxidase activity minus Mn-independent peroxidase activity and expressed as absorbance per minute and g organic matter.

A 0.25 g subsample of freeze-dried and ball-milled soil was used for DNA extractions with the Nucleospin Soil kit (Macherey-Nagel) following the manufacturer's instructions. About 1000 bp long markers, including the ITS2 region together with parts of the large subunit, were amplified from diluted DNA extracts (1 ng $μL^{-1}$), using the forward primer gITS7 and the reverse primer TW13 with unique identification tags attached to both primers (Ihrmark et al., 2012; Tedersoo et al., 2018). Amplification was done in 50 μL reactions consisting of 0.5 μM forward primer, 0.3 μM μL reverse primer, 0.25 μL DreamTaq polymerase, 5 μL dNTPs, 5 μL DreamTaq buffer, 1.5 μL $MgCl_2$, 3.25 μL H_2O, and 25 ng template DNA under the following conditions: 5 min at 94°C, 21–25 cycles of 30 s at 94°C, 30 s at 56°C, and 1 min at 72°C, and finally 8 min at 72°C. PCR products were equimolarly pooled and cleaned with the E.Z.N.A. Cycle Pure Kit (Omega Bio-Tek). After a quality control by Bioanalyzer (Agilent tech), the amplicon pool was sequenced on the PacBio Sequel II platform (Pacific Biosciences) at SciLifeLab NGI (Uppsala, Sweden). Sequence data was submitted to the NCBI Sequence Read Archive under BioProject PRJNA1191207. Quality filtering and OTU clustering were conducted with the SCATA bioinformatics pipeline (https://scata.mykopat.slu.se). Sequences containing both primer and identification tag sequences, with a minimum length of 200 bp, average quality >20, and single base quality >3 were used in single-linkage OTU clustering. Clustering was done at four different similarity thresholds (99.5%, 99%, 98.75% and 98.5%). OTUs were identified using the Species Hypothesis (SH) matching service, based on the UNITE database (Nilsson et al., 2019) and integrated into the PlutoF platform (Abarenkov et al., 2010). Identifications were double-checked against NCBI Genbank.

After comparing the identifications at the various similarity thresholds, the optimal threshold for this dataset, with the greatest correspondence between OTUs and species, was determined to be 98.75%. Only sequences attributed to the fungal kingdom were used in further analyses. The FungalTraits database (Põlme et al., 2020) was used to attribute OTUs to a specific lifestyle. OTUs that were attributed a saprotrophic lifestyle were split up into saprotrophic ascomycetes, saprotrophic agaricomycetes, and other saprotrophs. For ascomycete OTUs with potentially versatile saprotrophic and root-associated lifestyles (e.g. root endophyte, dark septate endophyte and ericoid mycorrhizal fungus) or with an unknown primary lifestyle, the SH to which they were attributed was searched in UNITE to check whether it had been found in root samples before. If so, they were attributed to root-associated ascomycetes and otherwise either to saprotrophic ascomycetes (saprotrophic primary or secondary lifestyle according to FungalTraits) or as unknown (unknown lifestyle according to FungalTraits). Copy numbers of the ITS2 region were quantified from diluted DNA extracts (0.5 ng per reaction) on a CFX Connect Real-Time System (Bio-Rad) using the forward primer gITS7 (Ihrmark et al., 2012) and reverse primers ITS4 and ITS4arch (Sterkenburg et al., 2018; White et al., 1990) in duplicates. The ITS2 copy numbers were converted to ITS2 copy number mg^{-1} organic matter and corrected to fungal ITS2 copy number mg^{-1} organic matter by multiplying total copies with the ratio of fungal sequences in that sample, based on the metabarcoding data (to correct for non-target amplification, e.g. of plant DNA). ITS2 copy numbers of the four dominant ecological groups (root-associated ascomycetes, saprotrophic ascomycetes, ectomycorrhizal fungi and saprotrophic agaricomycetes) and of individual OTUs were estimated by dividing the number of sequences from each group or OTU by the total number of fungal sequences (both from metabarcoding data) and then multiplying by the fungal ITS2 copy numbers for that sample to end

Variable	Unfertilized ($n=54$)	Fertilized ($n=54$)	$F_{1,15}$	p-Value
Organic layer depth (cm)	5.9 ± 2.1	5.6 ± 2.1	0.9	0.35
Organic layer pH	4.1 ± 0.3	4.1 ± 0.3	0.2	0.52
C:N organic layer	29.9 ± 3.2	30.0 ± 3.6	0.0	0.94
C stock (t ha^{-1}) organic layer	35.7 ± 20.3	35.2 ± 19.5	0.0	0.99
N stock (t ha^{-1}) organic layer	1.2 ± 0.6	1.1 ± 0.6	0.0	0.94
Soil CO_2 efflux spring (mg C m^{-2} h^{-1})	318.6 ± 166.2	320.5 ± 157.8	0.0[a]	0.96
Soil CO_2 efflux summer (mg C m^{-2} h^{-1})	454.2 ± 335.0	446.9 ± 291.9		

TABLE 1 Mean ± standard deviation of the depth, pH, carbon stock, nitrogen stock, and C:N ratio of the soil organic layer and of the spring and summer soil CO_2 efflux in clearcuts of fertilized and unfertilized forests, sampled 4–13 years after clearcutting.

Note: Previous fertilization, age of the clearcut, and their interaction did not have a significant effect on any of the variables according to the linear mixed models. *F* and *p* values for the variable fertilization are given.

[a]For soil CO_2 efflux, the denominator degrees of freedom was 17.

up with a copy number-corrected OTU table, which was used in further analyses.

2.5 | Statistical analyses

Linear mixed models (LMMs) were used to test for differences between clearcuts from fertilized and unfertilized forests, with clearcuts nested in pairs as a random factor. The response variables were soil characteristics (organic soil depth, pH, C stock, N stock and C:N of the organic layer and CO_2 efflux), vegetation characteristics (vascular plant, moss and lichen cover, vascular plant and tree diversity, tree density, average height and average growth rate), enzymatic activities, and abundance and diversity metrics of the total fungal communities, ectomycorrhizal fungi, saprotrophic agaricomycetes, saprotrophic ascomycetes, and root-associated ascomycetes. Diversity metrics were calculated using the R package *vegan* (Oksanen et al., 2022) and were square-root transformed when necessary to meet model assumptions. Explanatory variables were pre-clearcutting fertilization, time since clearcutting, and their interaction. In the analyses of tree height, tree species was also included as an explanatory variable, as well as its interactions with fertilization and time since clearcutting (to account for differences in vertical growth rate and reaction to fertilization among species). Models were fitted using the R package *nlme* (Pinheiro & Bates, 2024), estimated marginal means were extracted using the R package *emmeans* (Lenth, 2022) and data was visualized using the R packages *ggplot2* and *ggpubr* (Kassambara, 2020; Wickham, 2016).

Community composition of the studied taxonomic and ecological groups (ground vegetation, tree layer, total fungi, ectomycorrhizal fungi, root-associated ascomycetes, saprotrophic agaricomycetes, saprotrophic ascomycetes) was visually examined using non-metric multidimensional scaling (NMDS) and subjected to permutational analysis of variance (PERMANOVA) to test for differences between clearcuts from fertilized and unfertilized forests and along the time since clearcutting gradient. This was done using the functions *metaMDS* and *adonis2*, respectively, from the vegan R package v2.6-4 (Oksanen et al., 2022). Bray–Curtis dissimilarity matrices were used as input for the PERMANOVA, and permutations were constrained to within the clearcut pairs to account for the paired sampling design.

3 | RESULTS

The soil organic layer of the clearcuts sampled in 2022 (4–13 years after clearcutting) was 6 ± 2 cm deep (mean ± standard deviation), acidic (pH 3.4–5.0) and had a C:N ratio ranging from 22 to 37. There were no significant differences in pH, nitrogen stock, carbon stock, C:N, or depth of the organic layer between clearcuts of fertilized forests and unfertilized forests (Table 1; Figure 1). Neither did time since clearcutting, nor its interaction with previous fertilization have a significant effect on these variables. After accounting for the effect of soil temperature, soil CO_2 efflux was significantly higher in summer than in the spring season ($F_{1,168}=48.2$, $p<0.001$), increased with time since clearcutting ($F_{1,17}=7.3$, $p=0.02$), which almost significantly interacted with season ($F_{1,168}=3.8$, $p=0.05$). There was no significant difference between clearcuts of previously fertilized and unfertilized forests ($F_{1,17}=0.0$, $p=0.96$) (Table 1).

The ground vegetation (<1.2 m high) was dominated by ericoids (*Vaccinium myrtillus*, *V. vitis-idaea* and *Calluna vulgaris*) and grasses (mainly *Deschampsia flexuosa*), while the tree layer (>1.2 m high), if present, predominantly consisted of planted *Pinus sylvestris* and *Picea abies* intermixed with spontaneously regenerated *Betula pendula*, *B. pubescens*, *Sorbus aucuparia*, *Salix caprea*, and *Populus tremula*. There was no significant difference in the cover of vascular plants, mosses, or lichens between clearcuts of fertilized and unfertilized forests (Table S1; Figure S2). There was also no significant difference in the cover of the most dominant ericaceous and grass species (Table S1). Species richness, Shannon diversity, Pielou's evenness, and community composition of vascular plants did not differ between clearcuts of fertilized and unfertilized forests (Table S1; Figure S2; Figure 2, PERMANOVA: $F_{1,104}=0.5$, $p=0.41$).

There was no significant difference in tree species richness, tree density, or tree species composition between clearcuts from fertilized and unfertilized forests (Table S1, PERMANOVA: $F_{1,103}=0.8$,

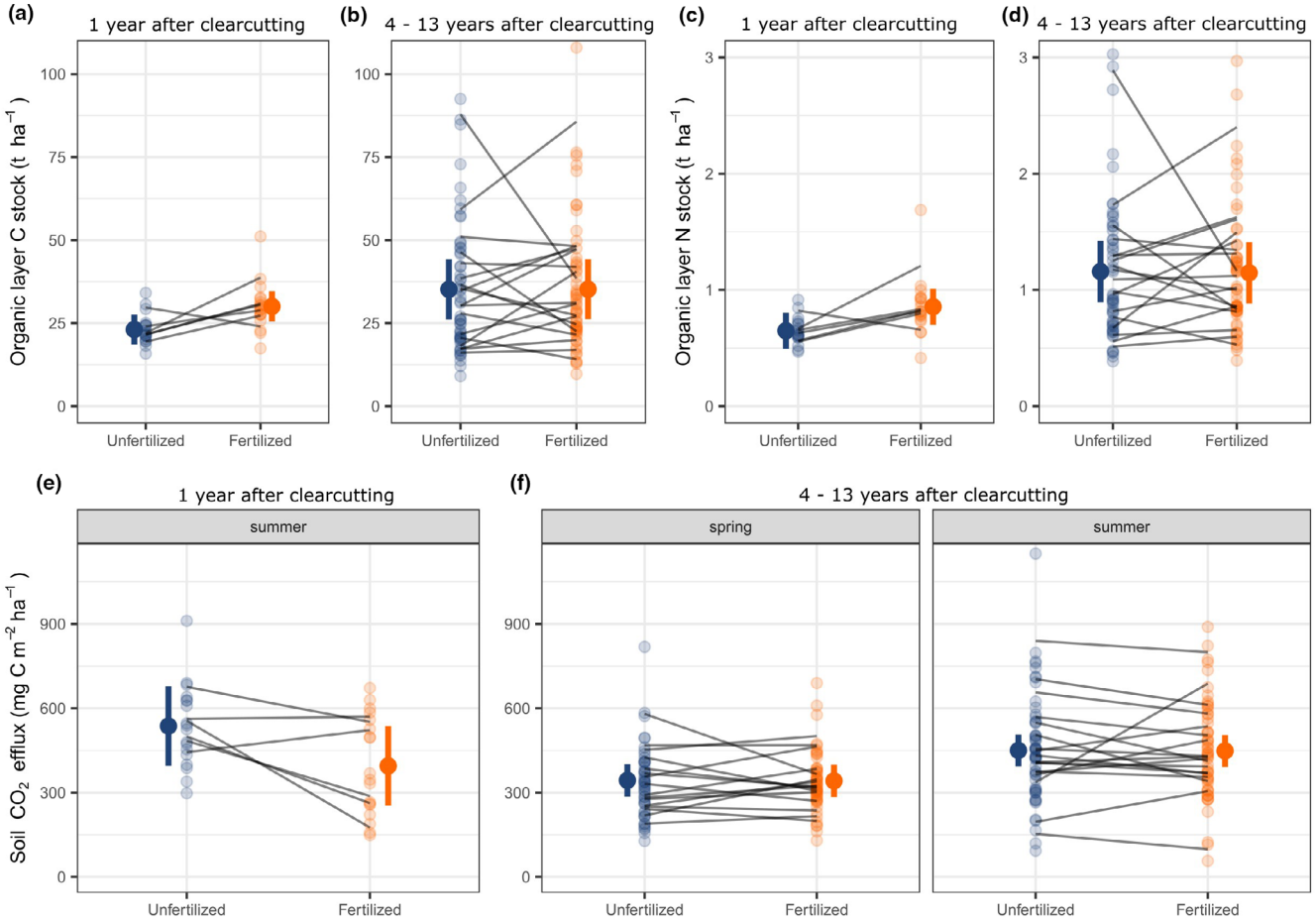

FIGURE 1 Carbon (a, b) and nitrogen (c, d) stocks of the soil organic layer and soil CO_2 efflux (e, f) 1 year (a, c, e) and 4–13 years (b, d, f) after clearcutting of previously fertilized and unfertilized forests. The soil organic layer in clearcuts of previously fertilized forests stored significantly more carbon (a) and marginally significantly more nitrogen (c) in the first year after clearcutting (Table 2), but there were no significant differences 4–13 years after clearcutting (b, d) (Table 1). Soil CO_2 efflux tended to be higher in clearcuts of unfertilized forests in the first year after clearcutting (e) (Table 2), but did not differ between clearcuts of previously fertilized and unfertilized forests 4–13 years after clearcutting (f) (Table 1). Transparent dots indicate data points per plot, lines connect the averages per clearcut (three plots per clearcut) in each pair, and the opaque dots indicate the overall estimated marginal means with the vertical lines indicating the 95% confidence intervals.

$p = 0.35$). Average tree growth rate differed significantly between tree species, with *P. sylvestris* growing faster than *P. abies* (4.92 ± 1.61 vs. 3.61 ± 2.04 mm diameter increase year^{-1}, $F_{1,72} = 28.6$, $p < 0.001$), but did not differ between clearcuts of fertilized and unfertilized forests ($F_{1,8} = 1.3$, $p = 0.29$, Figure S3). Average tree height significantly differed among tree species ($F_{3,271} = 16.5$, $p < 0.001$), increased with time since clearcutting ($F_{1,15} = 127.3$, $p < 0.001$), and there was a significant interaction between species and time since clearcutting ($F_{3,271} = 3.9$, $p = 0.01$). Tree height increased most strongly with increasing time since clearcutting in *P. sylvestris*, followed by *P. abies*, *B. pendula*, and *B. pubescens* (Figure S4). Average tree height did not differ between clearcuts of previously fertilized and unfertilized forests ($F_{1,15} = 0.4$, $p = 0.52$).

After consideration of results from the first sampling campaign, we hypothesized that the absence of clear differences in soil characteristics, soil CO_2 efflux, and vegetation characteristics between clearcuts from fertilized and unfertilized forests could be due to the long timespan between clearcutting and sampling (4–13 years). More specifically, we hypothesized that, relative to recent (up to 1 year) clearcuts of unfertilized forests, recent clearcuts of fertilized forests would have (H1) a larger soil carbon stock but also (H2) higher soil CO_2 efflux rates and increased decomposition (measured through potential enzyme activities), which gradually would reduce the soil carbon stock and explain the lack of difference in older clearcuts. In accordance with this first hypothesis, recent clearcuts of fertilized forests had on average an additional 7 ± 2 t C ha^{-1} (+30.2 ± 8.7%; estimated marginal mean ± SE) and 0.21 ± 0.06 t N ha^{-1} (+31.9 ± 9.8%; estimated marginal mean ± SE) stored in the soil organic layer (Table 2; Figure 1), relative to recent clearcuts of unfertilized forests. The soil CO_2 efflux, however, tended to be higher in clearcuts from unfertilized forests than from fertilized forests (Table 2; Figure 1), so our second hypothesis was not supported. While the measured potential enzyme activities of the cellulose-degrading enzymes cellobiohydrolase, β-xylosidase, and β-glucosidase seemed to be higher in

clearcuts of previously fertilized forests in the first year after clearcutting (Figure 3), none of the measured potential enzyme activities differed significantly (Table 2).

The two sequencing runs resulted in 3.4 and 4.3 million reads from the first and second sampling campaigns, respectively. After quality filtering, merging of the two datasets and singleton removal, 3,935,643 sequences were clustered into 12,570 OTUs, the large majority of which (7476 OTUs, 85.9% of the sequences) belonged to the fungal kingdom. Three samples were omitted from further analyses due to low sequencing depth (<40 fungal sequences while the other 141 samples had at least 946 fungal sequences; 23,471 on average). Approximately 60% of the sequences could be assigned to ecological groups, predominantly saprotrophic ascomycetes, root-associated ascomycetes, ectomycorrhizal fungi, and saprotrophic agaricomycetes (Figure 4a). The fungal communities were dominated by the orders Agaricomycetes, Leotiomycetes, Eurotiomycetes, and Archaeorhizomycetes, which together made up approximately three-quarters of the sequences (Figure 4b). Total fungal ITS2 copy numbers, as an indicator of fungal abundance, were significantly higher in fertilized plots than in unfertilized plots (Figure S5) and increased with time since clearcutting, but there was no significant interaction between fertilization and time since clearcutting (Table S2). ITS2 copy numbers of saprotrophic ascomycetes were significantly higher in clearcuts of fertilized stands, saprotrophic agaricomycetes tended to have higher ITS2 copy numbers in clearcuts of fertilized stands (Figure S5) and ectomycorrhizal ITS2 copy numbers increased significantly with time since clearcutting (Table S2). No other significant effects of fertilization, time since clearcutting, or their interaction were found (Table S2).

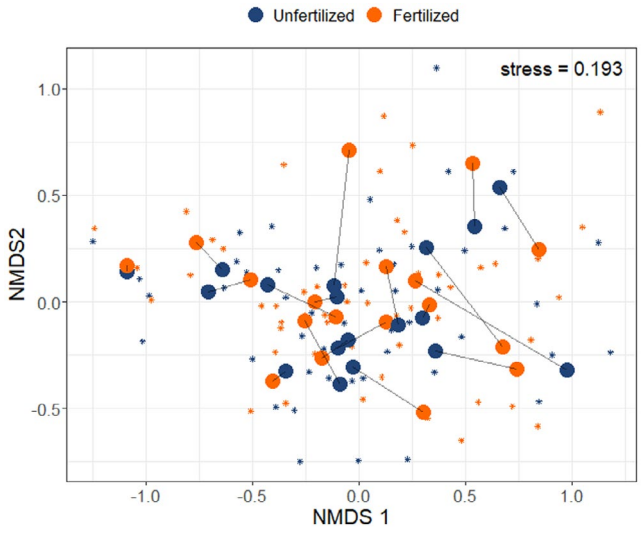

FIGURE 2 NMDS ordination showing the vascular plant community composition (<1.2 m high), which did not differ significantly between plots in clearcuts from fertilized ($n=54$) and unfertilized forests ($n=54$) (PERMANOVA: $F_{1,104}=0.5$, $p=0.41$). Smaller stars indicate individual plots, while the larger circles are clearcut centroids. Lines connect the centroids of two paired clearcuts. NMDS, non-metric multidimensional scaling; PERMANOVA, permutational analyses of variance.

There were no significant differences in OTU richness, Shannon diversity, Pielou's evenness (Figure S5; Table S2) or community composition (Figure 5, PERMANOVA: $F_{1,137}=0.9$, $p=0.523$) of total fungal communities between clearcuts from fertilized and unfertilized forests, but Shannon diversity tended to be lower in previously fertilized clearcuts (Table S2). Fungal communities differed with time since clearcutting (PERMANOVA: $F_{1,137}=7.9$, $p<0.001$). A separate PERMANOVA for the 1 year old clearcuts was also conducted, but did not indicate a difference between clearcuts of fertilized and unfertilized forests ($F_{1,34}=1.2$, $p=0.124$). When ectomycorrhizal fungi, saprotrophic agaricomycetes, saprotrophic ascomycetes and

TABLE 2 Mean ± standard deviation of the carbon stock, nitrogen stock, depth, C:N ratio, and potential enzymatic activities of the soil organic layer and soil CO_2 efflux (after accounting for variation due to soil temperature) in clearcuts from fertilized and unfertilized forests, sampled within the first year after clearcutting.

Variable	Unfertilized ($n=18$)	Fertilized ($n=18$)	$F_{1,5}$	p-Value
C stock (t ha^{-1}) organic layer	**23.1 ± 4.5.**	**30.1 ± 7.1**	**8.7**	**0.03**
N stock (t ha^{-1}) organic layer	0.65 ± 0.12	0.86 ± 0.25	5.9	0.06
Organic layer depth (cm)	6.83 ± 3.01	6.78 ± 3.63	0.0	0.94
C:N organic layer	35.5 ± 2.6	35.6 ± 2.9	0.0	0.91
Soil CO_2 efflux (mg C m^{-2} h^{-1})	521.8 ± 315.1	422.5 ± 262.8	4.3	0.09
Cellobiohydrolase (μmol g^{-1} SOM min^{-1})	36.3 ± 33.7	53.8 ± 55.6	2.1	0.20
β-Xylosidase (μmol g^{-1} SOM min^{-1})	28.4 ± 19.6	47.0 ± 42.8	2.6	0.17
β-Glucosidase (μmol g^{-1} SOM min^{-1})	352.9 ± 258.2	486.3 ± 395.8	1.7	0.25
N-acetyl-β-D-glucosaminidase (μmol g^{-1} SOM min^{-1})	174.1 ± 105.7	209.3 ± 120.4	1.0	0.35
Acid phosphatase (μmol g^{-1} SOM min^{-1})	773.8 ± 630.6	760.3 ± 379.0	0.1	0.82
Mn-peroxidase (absorbance g^{-1} SOM)	0.41 ± 0.34	0.60 ± 0.78	1.2	0.33

Note: *F*- and *p*-values indicate the statistical significance of the fertilization effects, extracted from linear mixed models with clearcut nested within clearcut pair as a random term. Values that were significantly different ($p<0.05$) between clearcuts of fertilized and unfertilized forests are indicated in bold.

Abbreviation: SOM, soil organic matter.

root-associated ascomycetes were analysed separately, we did not find differences in OTU richness, Shannon diversity, Pielou's evenness, or community composition between clearcuts from fertilized and unfertilized forests, except for the community composition of saprotrophic ascomycetes (Tables S2 and S3).

4 | DISCUSSION

Overall, 4–13 years after clearcutting, there were no differences in soil carbon and nitrogen stocks, soil CO_2 efflux, tree growth and density, and understory community composition between unfertilized stands and stands that had been fertilized during the previous rotation period. However, the 1-year-old clearcuts that had been fertilized in the previous rotation period had larger carbon and nitrogen stocks in the organic soil layer than recent clearcuts that had not been fertilized. The difference in carbon stock in these 1-year-old clearcuts ($7 \pm 2\,t\,ha^{-1}$) is similar to the fertilization effect reported in mature forests, i.e. prior to clearcutting (Jörgensen et al., 2021; Olsson et al., 2005). In a similar study conducted 21–24 years after clearcutting, Larsson et al. (2024) found that forests that had been fertilized once during the previous rotation period had lower carbon stocks in the organic soil layer, while forests that had been fertilized twice did not differ. Together, our results indicate that although fertilization can increase soil carbon stocks, the effect appears to diminish over the first few years after clearcutting and become insignificant after 4 to 13 years. Consequently, forest fertilization, as it is currently practiced in the Fennoscandian countries, has limited potential to increase long-term carbon sequestration below ground when combined with clearcutting, and its associated potential to mitigate climate change therefore depends on its effect on aboveground biomass production.

The rapid decline in the difference in organic soil layer carbon stocks between clearcuts of fertilized and unfertilized forests suggests higher decomposition rates in the former. This is supported by the significantly higher abundance (ITS2 copy numbers) of saprotrophic ascomycetes in clearcuts of previously fertilized forests. While not statistically significant, saprotrophic agaricomycetes also tended to be slightly more abundant in clearcuts of previously fertilized forests. Previous fertilization thus seems to favour saprotrophic

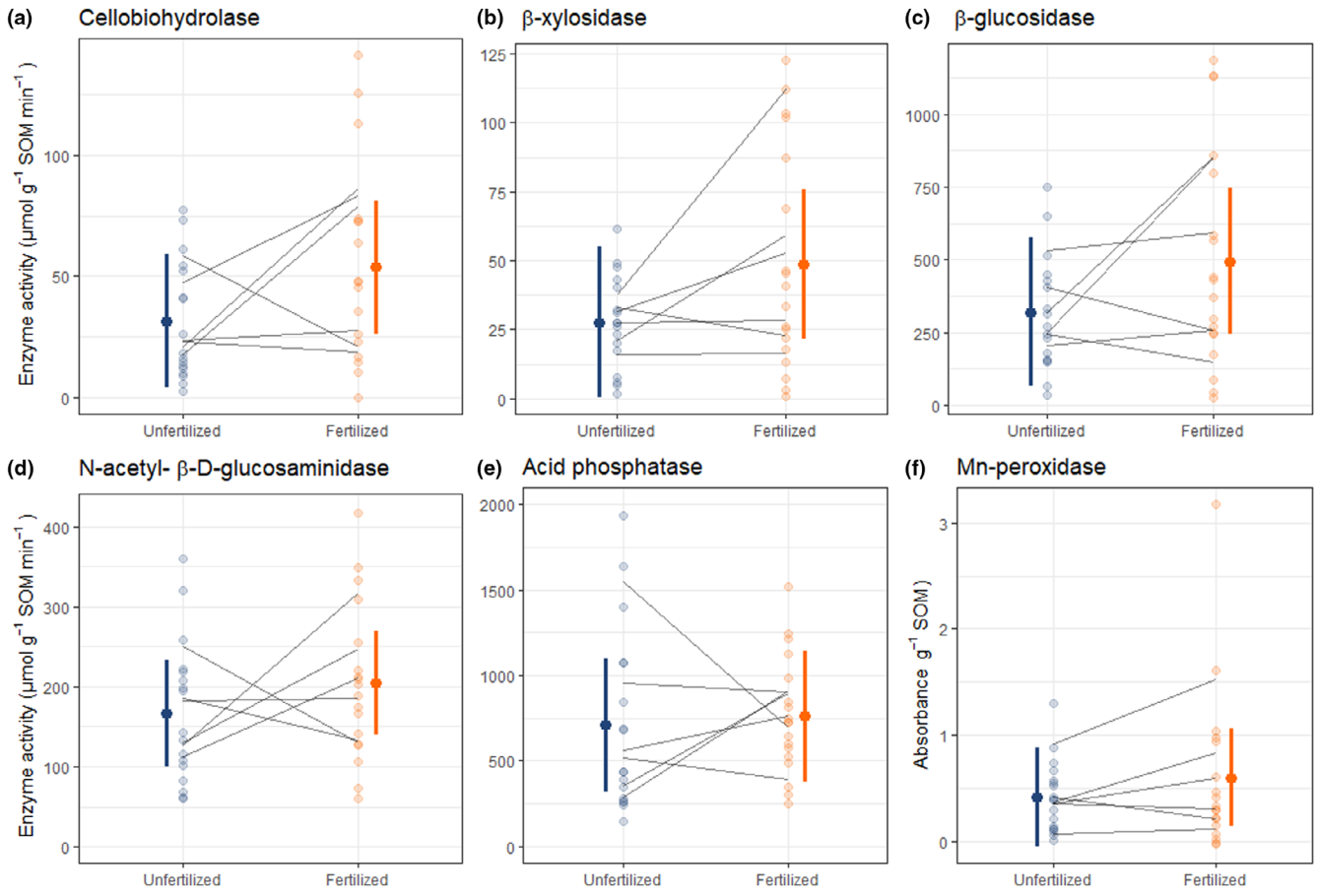

FIGURE 3 Potential enzymatic activities of (a) cellobiohydrolase, (b) β-xylosidase, (c) β-glucosidase, (d) *N*-acetyl-β-D-glucosaminidase, (e) acid phosphatase, and (f) Mn-peroxidase in 1-year-old clearcuts from fertilized and unfertilized forest forests. Transparent dots indicate data points per plot (Unfertilized: $N = 18$, Fertilized: $N = 18$), lines connect the averages per clearcut in each pair, and the opaque dots indicate the overall estimated marginal means with the vertical lines indicating the 95% confidence intervals.

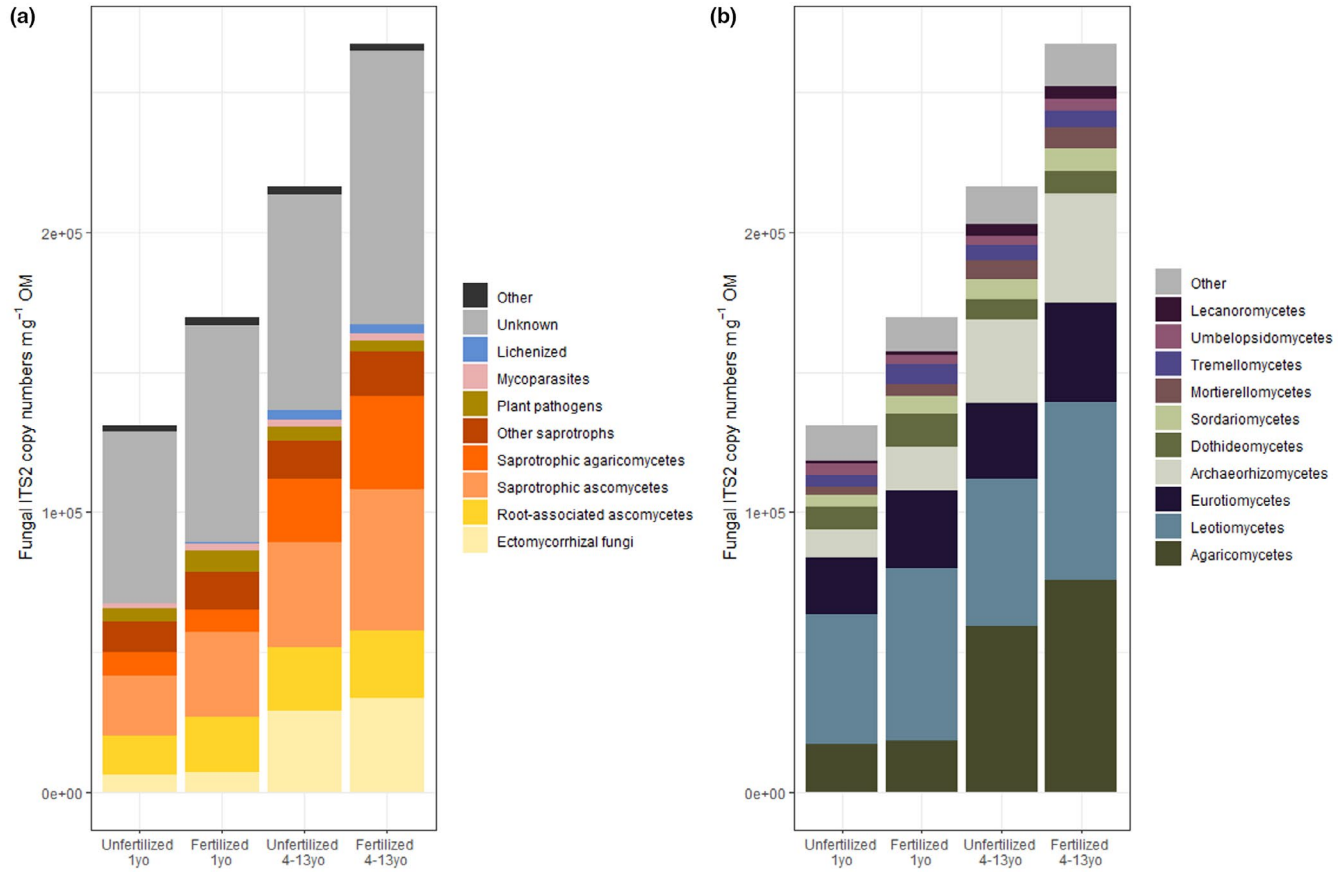

FIGURE 4 Fungal ITS2 copy numbers, averaged over all samples from unfertilized, 1-year-old clearcut plots ($n = 18$), previously fertilized, 1-year-old clearcut plots ($n = 18$), unfertilized 4–13-year-old clearcut plots ($n = 51$) and previously fertilized 4–13-year-old clearcut plots ($n = 51$), attributed to (a) lifestyles and (b) classes.

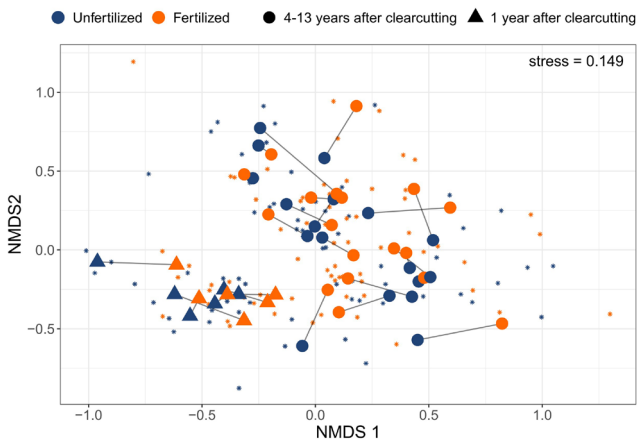

FIGURE 5 NMDS ordination of the soil fungal community composition, which did not differ significantly between plots in clearcuts of fertilized ($n = 69$) and unfertilized forests ($n = 69$) (PERMANOVA: $F_{1,137} = 0.9$, $p = 0.523$). Small stars indicate the three plots, while the larger symbols indicate the centroid per clearcut. Lines connect the centroids of paired clearcuts. NMDS, non-metric multidimensional scaling; PERMANOVA, permutational analyses of variance.

ascomycetes more than saprotrophic agaricomycetes. This is in accordance with previous studies, which also found increases in the relative abundance of saprotrophic fungi and especially saprotrophic ascomycetes in response to nitrogen addition (Moore et al., 2021; Morrison et al., 2016, 2018). This differential response to nitrogen addition has been linked to the differences in decomposition potential, with species with primarily hydrolytic decomposer capacities, that is, saprotrophic ascomycetes (Boberg et al., 2011; Eichlerová et al., 2015; Osono, 2007), reacting positively to nitrogen addition. Nitrogen addition has often been found to negatively impact oxidative enzymes and positively impact hydrolytic enzymes (Jian et al., 2016; Jörgensen et al., 2022; Moore et al., 2021). Although not statistically significant, cellobiohydrolase and β-xylosidase activities seemed to be higher in the previously fertilized forests in three of the six pairs of 1-year-old clearcuts. Previous studies have shown that potential activities of these cellulolytic enzymes can increase both after clearcutting and after nitrogen addition (Danielson et al., 2017; Hasby, 2022; Jian et al., 2016; Stone et al., 2012).

Still, total soil CO_2 efflux was lower in clearcuts of previously fertilized forests compared to clearcuts of unfertilized forests in the first year after clearcutting. Since this contradicts the patterns in

fungal communities and potential enzymatic activities of the soil organic layer, it is possible that potentially higher heterotrophic respiration in clearcuts of previously fertilized forests was obscured by lower autotrophic respiration due to increased fine root growth efficiency (Forsmark et al., 2020, 2021). Another possibility is that the measured total soil CO_2 efflux was mainly coming from other soil compartments than the organic layer, for example, dead tree roots. Kohout et al. (2018) found increased enzymatic activities in the remaining roots of cut *Picea abies* trees within the first two to 19 months after clearcutting, while in the bulk soil, activities remained the same and even decreased 19–25 months after clearcutting. However, this does not explain how and when the fertilizer-induced difference in soil carbon stocks disappeared. It is possible that the carbon was lost as CO_2 during the time period not covered by this study (2–3 years after clearcutting) or that it was lost from the soil organic layer in other forms, for example, as dissolved organic carbon (DOC). Clearcut harvesting has been found to increase DOC export in the first years after clearcutting (Laudon et al., 2009; Smolander et al., 2001), as has fertilization (Fröberg et al., 2013). Given the divergent environmental effects of the different forms of carbon, with CO_2 contributing to climate change and DOC to the browning of freshwater ecosystems (Solomon et al., 2015), more research is needed to determine in which form the fertilizer-induced soil carbon disappears from the organic layer and where it ends up.

While 1-year-old clearcuts of previously fertilized forest stored significantly more nitrogen in the soil organic layer than clearcuts of unfertilized forests, there was no difference in nitrogen stocks in the 4- to 13-year-old clearcuts. Similarly to the soil carbon, this raises the question of where this nitrogen ends up. While a small part might have been lost to the atmosphere through denitrification (Öquist et al., 2024), most of the nitrogen has likely moved to other pools through mineralization, plant uptake, leaching, etc. Previous fertilization experiments have resulted in increased nitrogen mineralization and elevated concentrations of inorganic nitrogen in soil water after clearcutting of previously fertilized plots compared to unfertilized controls (From et al., 2015; Högbom et al., 2001; Ring, 1995). Contrary to our expectations, previous fertilization did not promote tree growth or alter vegetation composition, indicating a limited effect on plant uptake of inorganic nitrogen after clearcutting. While Högbom et al. (2001) also did not find a lasting effect of fertilization on plant growth and establishment or pine needle nitrogen concentration in clearcuts, other similar studies in the middle boreal zone found lasting effects of previous fertilization on understorey vegetation 8–11 years after clearcutting (Strengbom & Nordin, 2008) and on tree growth 10–13 and 21–24 years after clearcutting (From et al., 2015; Larsson et al., 2024). These effects were, however, only observed in forests that had been fertilized twice, and not in forests that had been fertilized only once during the previous rotation period. The majority of the forests in this study were fertilized only once, and we did not find a difference between forests that were fertilized once or twice. To minimize the long-term environmental consequences of forest fertilization, a better understanding of where the added nitrogen ends up after clearcutting is urgently needed.

In conclusion, our results suggest that fertilizer-induced soil carbon stocks disappear rapidly from the organic soil layer after clearcutting, but this is seemingly not linked to increased total soil CO_2 efflux in the first year. The increased abundance of saprotrophic ascomycetes, independent of time since clearcutting, suggests that fungal decomposition in the organic layer after clearcutting is higher in previously fertilized forests compared to unfertilized forests. Correspondingly, the fertilizer-induced difference in organic soil nitrogen disappeared within the first few years. Hence, the legacy effects of forest fertilization on the organic soil layer after clearcutting seem to be small and probably too short-lived to significantly enhance soil carbon storage in the long-term. Consequently, the potential of forest fertilization to mitigate climate change, under current forestry practices, is likely limited to increases in aboveground biomass. Our study raises questions about where and in which form the fertilizer-induced soil carbon and the added nitrogen end up after clearcutting. This study furthermore raises the question whether continuous cover forestry [or "continuous root forestry" (Prescott & Grayston, 2023)] could avoid the loss of soil carbon by avoiding the release of saprotrophic fungi from suppression by ectomycorrhizal fungi (Gadgil & Gadgil, 1971).

AUTHOR CONTRIBUTIONS

Joachim Strengbom, Gustaf Granath, Björn D. Lindahl, and Karina E. Clemmensen conceived the ideas, and all authors contributed to designing the methodology; Margaux Boeraeve collected the data, analysed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

Raw sequence data was submitted to the NCBI Sequence Read Archive under BioProject PRJNA1191207. Data used in the statistical analyses were submitted to the Swedish National Data service (snd.se) and are available under https://doi.org/10.5878/vfre-f585 (Boeraeve et al., 2025b).

ORCID

Margaux Boeraeve https://orcid.org/0000-0003-2835-9798
Gustaf Granath https://orcid.org/0000-0002-3632-9102
Björn D. Lindahl https://orcid.org/0000-0002-3384-4547
Karina E. Clemmensen https://orcid.org/0000-0002-9627-6428
Joachim Strengbom https://orcid.org/0000-0002-1720-5016

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Overview of the sampling locations, coloured according to the year they were sampled.

Figure S2. Clearcuts from fertilized forests had a slightly lower vascular plant cover than unfertilized forest forests, but did not significantly differ in moss or lichen cover, 4–13 years after clearcutting.

Figure S3. Average yearly diameter increase (mm) significantly differed between tree species but not between clearcuts from fertilized and unfertilized forests.

Figure S4. Average tree height in a plot was significantly affected by tree species, time since clearcutting and the two-way interactions between species and time since clearcutting.

Figure S5. Fungal abundance (as measured by ITS2 copy numbers) was significantly higher in clearcuts of previously fertilized forests (a), as was the abundance of saprotrophic ascomycetes (b).

Table S1. Mean ± standard deviation of the variables describing the ground vegetation and tree layer (>1.2 m high) for 4–13-year-old clearcuts from fertilized and from unfertilized forests and *F*- and *p*-values from the linear mixed models on these variables with fertilization, time since clearcutting and their interaction as fixed factors and clearcut nested in clearcut pair as random factors.

Table S2. Mean ± standard deviation of the variables describing diversity of the fungal communities for clearcuts from fertilized and from unfertilized forests and *F*- and *p*-values from the linear mixed models on these variables with fertilization, time since clearcutting and their interaction as fixed factors and clearcut nested within clearcut pair as random factors.

Table S3. Outcomes of the permutational analyses of variance (PERMANOVA), testing for the effect of fertilization, time since clearcutting and their interaction on the community composition for the four most abundant ecological groups of fungi.

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