Uncertainties and knowledge gaps in the effects of nitrogen fertilisation on tree growth, carbon sequestration, and environmental risks in boreal forest landscapes

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ABSTRACT

Nitrogen fertilisation is a key strategy for enhancing tree growth and increasing carbon sequestration rates in boreal forests. In this review we evaluate the uncertainties of the effects of forest fertilisation for carbon sequestration and highlight important gaps in current knowledge about the efficiency and environmental consequences of nitrogen amendment. Uncertainties in the influence on carbon sequestration rates, along with variation in tree growth effects depending on soil type and climatic conditions, make scaling up of the benefits of increased fertilisation uncertain. Further, the potential benefits of increased forest fertilisation must be weighed against the risks of negative impacts on biodiversity, water quality, and tree physiology. Before expanding forest fertilisation, it is important to consider the balance of benefits, risks, and uncertainties.

1. Introduction

Nitrogen (N) is the nutrient that is considered to limit tree stem growth in most boreal forests (Tamm, 1991). Consequently, N fertilisation is widely perceived as an effective way of enhancing forest production and increasing carbon sequestration (Hyvönen et al., 2008; Jörgensen et al., 2021). In the light of growing ambitions to enhance carbon sequestration to meet EU climate goals, forest fertilisation is once again on the political agenda in Sweden, Finland, and Norway (Laudon et al., 2024; Lindkvist et al., 2011). However, fertiliser-induced tree growth also risks having undesirable side effects such as altered species composition of understorey plants (Olsson and Kellner, 2006; Strengbom and Nordin, 2008) and soil fungi (Jörgensen et al., 2022), reduced functional diversity of ground-living beetles (Rodríguez et al., 2021), and increased risk of N leakage (Ring, 1995; Ring et al., 2013, 2021).

Although N addition can lead to an apparent increased carbon stock, the overall impact results from changes in many complex processes, making it difficult to estimate the net long-term ecosystem effect. Changes include increasing green canopy biomass that enhances total photosynthesis and can contribute to greater carbon capture (Marshall et al., 2023). However, the growth benefit from N addition is associated with altered partitioning of tree biomass, typically increasing investment in aboveground biomass and reducing that to belowground components including the transfer of carbon to mycorrhizal fungi (Marshall et al., 2023). Thus, estimates based solely on aboveground tree responses may overestimate the net effect on overall carbon sequestration (Forsmark et al., 2020; Marshall et al., 2023).

Fertilisation may also increase soil carbon storage by inhibiting decomposition of soil organic matter (Berg and Matzner, 1997; Bonner et al., 2019; Jörgensen et al., 2021). One explanation for this is that changes in the composition of microbial communities hampers decomposition of complex organic compounds (Bonner et al., 2019; Maaroufi et al., 2019; Jörgensen et al., 2022). This could have long-term effects on soil processes, potentially altering soil nutrient availability, and affecting forest growth over time (Kyaschenko et al., 2017; Lindahl et al., 2021; Jörgensen et al., 2022). Therefore, understanding the impact of fertilisation on boreal forest soil carbon stocks is crucial, particularly since a significantly larger portion of carbon is stored belowground than in aboveground biomass (Bradshaw and Warkentin, 2015; Larson et al., 2023). The aim of this critical review is to summarise

current understanding of the effects of N fertilisation on tree growth and carbon sequestration in relation to the risks of changing biodiversity, water quality, and tree physiology in boreal forests. Here we primarily focus on a Fennoscandic perspective, where fertilisation is most commonly applied to enhance forest growth and discussed as a way to enhance carbon storage in the forested landscape.

2. Why does nitrogen limit forest growth?

Boreal forest soils contain large amounts of N, ranging from 100 kg N ha^{-1} to 8 000 kg N ha^{-1} (Björkman et al., 1967). Although these stocks are large relative to annual N tree uptake of 15–50 kg N ha^{-1} (Korhonen et al., 2013), most boreal forests on mineral soils remain N limited. This is because low temperatures and short growing seasons hamper decomposition (Cleve et al., 1981), and N becomes bound into undecomposed soil organic matter and microbial biomass (Högberg et al., 2017; Kyaschenko et al., 2019; Näsholm et al., 2013) where it becomes unavailable for direct uptake by plants (Vitousek et al., 2002). Slow decomposition of complex organic compounds into simpler organic and inorganic N compounds (ammonium, nitrate and free amino acids) is probably the greatest limiting factor for tree N availability (Schimel and Bennett 2004). However, it has become clear that in nutrient poor soils, tree N acquisition is more likely determined by the N uptake by mycorrhizal fungi (Näsholm et al., 2013; Högberg et al., 2017). Within a growing forest stand, rapid N uptake by microbial communities and plants minimises N losses via hydrological leakage and gas fluxes, making these losses small compared with, for example, agricultural areas (Sponseller et al., 2016). This closed N cycle seems to persist until a major disturbance, such as fire, storm, insect infestation, or logging, which involves soil disturbance, stimulates decomposition and increases plant-available N (Tamm, 1991).

Increasing tree N uptake efficiency is key to minimising the environmental impact of forest fertilisation and increasing the economic incentives for landowners. In general, less than 20–30 % of applied N fertiliser is taken up by trees, the bulk remaining in the soil (Fig. 1, Björkman et al., 1967; Melin et al., 1983) where it does not appear to become available to trees, even in the long term (Melin et al., 1983; Tamm, 1991). These efficiencies are low in comparison to agricultural systems, in which N uptake efficiency can be up to 50 % (Udvardi et al., 2021). A possible reason for this is that uptake rates of nitrate in Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and most ectomycorrhiza fungal species is low compared to agricultural plants (Näsholm et al., 2009). In addition, N application affects the composition of N compounds in the soil. Boreal forest soils naturally contain more N in organic form (amino acids, peptides, proteins, chitin, etc.) than in inorganic form (nitrate and ammonium) (Inselsbacher and Näsholm, 2012), whereas N fertilisation creates a temporary dominance of inorganic N. Nitrate, in particular, is readily soluble and highly mobile in the soil. By contrast, many organic forms, which are also taken up by plants (Näsholm et al., 2009), are much less mobile because they bind to soil particles. The shift in dominant N form caused by fertilisation affects
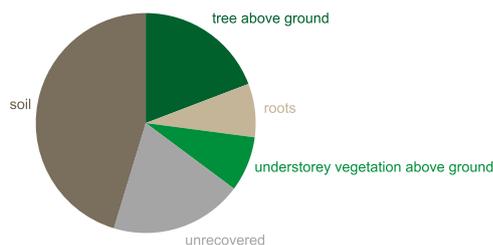
root morphology, uptake capacity, potentially drought tolerance (see section Carbon partitioning in trees following N fertilisation, Wang et al., 2018), and root-associated microbial communities.

3. Effects on stem growth

The goal of N fertilisation is to increase tree stem growth, but the efficiency depends strongly on application intensity and on factors such as region, soil type, tree species, and stand age. To some extent this is taken into consideration in the current recommendations in Sweden which restrict fertilisation to stands where tree stem growth is expected to increase by about 15 % with fertilisation (Jacobson and Hannertz, 2007). The promoted growth corresponds to an increase of between 12 and 20 m^3 ha^{-1} by the end of the 8–10 years period over which fertilisation is expected to have an effect (Jacobson and Hannertz, 2007) (Fig. 2).

This growth response was recently confirmed by a study of 32 498 harvested forest stands across Sweden which were either unfertilised or fertilised according to current recommendations (Boeraeve et al., 2025b). The fertilisation response of 4–9 % (14–20 m^3 ha^{-1}, standing biomass ca 200–375 m^3 ha^{-1}) was, however, highly context-dependent, suggesting that current recommendations do not always accurately identify forest stands that will produce the desired growth response. Fertilisation had no or marginal effect on harvestable tree volumes in Swedish stands in cold regions (temperature sum below 800°C) and on sites in the lower range of the soil fertility spectrum (Boeraeve et al., 2025b). In fact, fertilisation had no effect on 17 % of the 7971 Scots pine-dominated stands or on 6.8 % of the 2724 Norway spruce-dominated stands (Boeraeve et al., 2025b). Thus, even when forest fertilisation is performed according to recommendations, the outcome is still influenced by unknown factors likely related to weather and soil fertility (Bergh et al., 2014; Nilsson et al., 2010). For instance, rainfall after fertiliser application has been found to enhance the fertilisation effect of stem growth (Lim et al., 2015), suggesting a need to include climatic conditions when estimating N fertilisation effects on stem growth and carbon sequestration. Soil moisture is another important factor (see further in the section on N in water).

The fertilisation effect varies with N dose and application intervals. Stem growth is not linearly dependent on total N dose and peaks at lower levels on high fertility soils (150–250 kg N ha^{-1}) than on low fertility soils (300–350 kg N ha^{-1}) (Nohrstedt, 2001). In some studies, repeated applications of lower N doses (20–60 kg N ha^{-1}) had larger effects on stem growth than repeated applications of higher N doses (60–180 kg N ha^{-1}). One hypothesis is that an intermediate N dose may stimulate tree growth without inhibiting soil microbes (Prescott, 2024). Nitrogen deposition studies have shown that doses below 12.5–50 kg N ha^{-1} do not enhance tree stem growth (Binkley and Högberg, 2016; From et al., 2015), while very high N doses can lead to limitation of other nutrients such as phosphorus and potassium (Svensson et al., 2024). In line with this, some studies of young forest stands where repeated fertilisation with N and other nutrients (phosphorus, potassium) were applied, to total applications far higher than current recommendations (800–1500 kg N ha^{-1}) resulted in larger effects on stem growth, than the current recommendations which applies to older stands (Bergh et al., 2008; Svensson et al., 2023). Differences in stem density might partly explain this. In this context, it is both economically and environmentally important to understand the reasons behind the low tree uptake efficiency of applied N, given the large proportion of N that remains in the soil and its unknown destiny after natural disturbances or harvesting (Melin et al., 1983).

The effect of different intervals of repeated fertilisation may be linked to leaf lifespan. The fertilisation effect lasts longer in Norway spruce stands (7–8 years) than in Scots pine stands (4–5 years) (Björkman et al., 1967). This roughly corresponds to the foliar lifespan of the two species (5–10 years and 3–5 years, respectively), suggesting that the fertilisation effect may be linked to the enhanced photosynthetic

Fig. 1. Recovery of applied ^{15}N 2 years after application of 40–160 kg N ha^{-1} to a 15–140 year Pinus sylvestris stands (based on data from Björkman et al., 1967; Melin et al., 1983; Nõmmik and Larsson, 1989). The bulk of ^{15}N remains in the soil, 20–30 % is taken up by the trees.

Box 1

Forest fertilisation in Fennoscandia.

Historical overview

The first fertilisation experiments in Fennoscandia began in the 1920s (Tamm, 1965), but large-scale N fertilisation started in the 1950s as a strategy to reduce the timber shortage (Fig. 2, Jetsonen et al., 2025; Nilsen, 2001; Swedish Forest Agency, 2025). In Sweden and Finland, commercial use peaked in the 1970s, when up to 250,000 ha was fertilised annually (Swedish Forest Agency, 2011; Swedish Forest Agency, 2013; The Natural Resources Institute Finland). In Norway, fertiliser use peak during the 1960s and then again in 2018 (Svanøe-Hafstad, 2021). Except for the 2018 peak in Norway, the trends over time are similar across Fennoscandia, although the total area of productive forest and thus fertilised area in Norway is lower than in Sweden and Finland. During the 1990s the area decreased to 50–20 000 ha fertilised per year. Reasons for this decline include new guidelines issued in the 1990s following large-scale field experiments testing various fertiliser types, amounts and intervals, and environmental impacts (Nohrstedt, 2001; Swedish Forest Agency, 2011, 2013), which raised concerns about atmospheric N deposition and a restricted fertiliser use was recommended (Pihl Karlsson et al., 2024). Since the early 2000s, the annual area fertilised has not exceeded 83 000 ha in any of the countries and in 2023 the areas were 440–77000 ha, representing < 0.1 % of the productive forest land in each country.

The most used fertilisation practice is to apply 150 kg N ha^{-1} as a single application, approximately ten years prior to the final harvest (Jacobson and Pettersson, 2010; Swedish Forest Agency, 2011; Swedish Forest Agency, 2013; Rekommendationer för skogsvård, 2025; Svanøe-Hafstad, 2021). In some cases, fertilisation is repeated twice, and occasionally three times, during a rotation. The recommended applications rates are lower than most long-term fertilisation experiments. Fertilisation primarily target conifer-dominated stands of intermediate forest productivity, excluding low-productivity sites, such as those with a high cover of ground-living lichens, and highly fertile sites where the relative efficiency in terms of productivity gain is expected to be lower. In Sweden, the southern region of Götaland is exempted from fertilisation due to historically high N deposition. In Finland, also peatlands are fertilised, but mainly with limiting phosphorus and potassium in the form of wood ash (Rekommendationer för skogsvård, 2025).

Composition of fertilisers

The primary fertilisers currently used are based on inorganic N, almost exclusively Skog-CAN (Calcium Ammonium Nitrate; Lindkvist et al., 2011). To compensate for the acidification induced and to avoid growth disorders on tree height and shoot development observed in parts of northern Sweden and eastern Finland, 20 % dolomite and 0.2 % boron are added to the fertiliser (corresponding to 1 kg B ha^{-1}, Sutinen et al., 2006; Vartiainen et al., 2025). Different N compositions of fertilisers have been tested, and ammonium sulphate and urea tend to acidify the soil more than ammonium nitrate (Högberg et al., 2024). In addition, urea has lower growth effects compared to ammonium nitrate, despite the higher N content. There is also a higher risk of ammonia losses to the atmosphere and a risk of understorey vegetation damage due to the basic properties of urea (Kissel et al., 2009). Urea and ammonium sulphate are still in use (Rekommendationer för skogsvård, 2025). Experiments with different types of organic N fertilisers are testing possibilities for affecting the ratio between organic and inorganic N in the soil less (Näsholm et al., 2009).
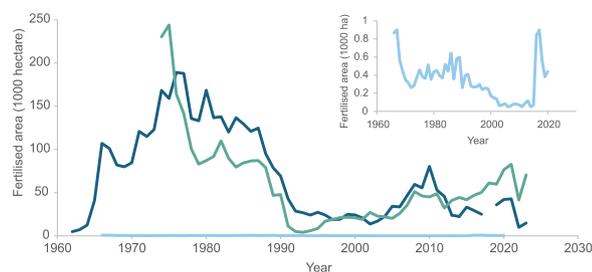

Fig. 2. Fertilised forest area in Fennoscandia over 50–60 years (based on data from Svanøe-Hafstad, 2021; The Natural Resources Institute Finland; Swedish Forest Agency, 2025). *Sweden (Dark blue), Finland (light green) and Norway (light blue).*

capacity of foliage with higher N concentration. The fertilisation effect is greatest when the effect of one application is allowed to fade before the next is carried out (Pettersson and Högbom, 2004). A second fertilisation can be expected to give about the same growth effect as the first, but according to some studies, it is reduced with further applications (Pettersson and Högbom, 2004). The long-term effects of fertilisation, i. e. effects on the next generation of trees, have been measured in some sites and the effects may continue for longer than expected (4–10 years) (From et al., 2015; Larsson et al., 2024) but seem to cease by 17 years after final harvest (Larsson et al., 2024; Boeraeve et al., 2025b, Hjelm et al., 2025).

Translating stem volume into carbon sequestration is complicated. Because fertilisation has been shown to decrease sapwood density (Kalliokoski et al., 2013; Mäkinen and Hynynen, 2014), there is a risk of

overestimating the effect of fertilisation on carbon sequestration based on stem diameter measurements only. The effect of fertilisation as per current recommendations is generally small (0–8 %, Mäkinen and Hynynen, 2014) and less than the effect on stem growth. However, it increases with larger applications of N, and density reductions of up to 20 % have been observed (Mäkinen et al., 2002). With repeated fertiliser applications and increased doses, decreased density could have a large effect on the amount of carbon sequestered in the stem. Long-term experiments have found increases in carbon sequestration in stems of approximately 25 kg of carbon per kg of applied N for Norway spruce and 11 kg for Scots pine (Hyvönen et al., 2009).

4. Effects of nitrogen fertilisation on carbon stocks in forest soils

Soil organic matter comprises the largest carbon pool in boreal forests, 70–100 tonnes of carbon ha^{-1}, and contains an array of organic substances with different degrees of recalcitrance and longevity, including fungal hyphae and fine roots (<2 mm, Bradshaw and Warkentin, 2015). The size of this pool makes it challenging to detect the relatively small changes caused by fertilisation, which is further complicated by large spatial variability (Mayer et al., 2020). Despite these complications, there is seemingly a consensus in the scientific literature that N application, through fertilisation or atmospheric N deposition, increases the forest soil carbon stock, at least in a short-term perspective (i.e. within a rotation). Nitrogen addition in boreal forest ecosystems can affect soil carbon stocks, partly by increasing plant production and thus the supply of litter (dead plant parts above and below ground) to the soil, and partly by inhibiting the decomposition of soil organic matter due to changes in the composition of decomposer

communities (see section Effects of forest fertilisation on biodiversity, Hyvönen et al., 2008; Blaško et al., 2022). Increases in soil carbon stocks following N fertilisation are well documented in many forest ecosystems globally (Jandl et al., 2007; Hyvönen et al., 2008; Mayer et al., 2020). The effect on carbon sequestration in the soil is usually 3–4 times lower (3–20 kg C sequestered per kg^{-1} N applied) than the effect on trees but varies with N dose and site index (Hyvönen et al., 2008). As with the effect on stem growth, lower application rates (20–50 kg N per ha^{-1} year^{-1}) have a larger effect on soil carbon stocks per unit of N applied than higher application rates (50–200 kg N per ha^{-1} year^{-1}). The effect is often up to twice as large on Norway spruce sites as on Scots pine sites (13 and 7 kg C per kg^{-1} N) (Hyvönen et al., 2008). However, there are also indications that in sites with larger soil carbon stocks the fertilisation effect on soil carbon is low, and sometimes there is no effect (Blaško et al., 2022). However, most of these studies are based on high N additions or simulation of N deposition and their findings cannot be directly transferred to current fertilisation recommendations.

Another consideration is how N fertilisation impacts the net production of other soil-generated greenhouse gases which act as agents of atmospheric radiative forcing. It is known that N fertilisation can increase soil N_2O through different transformation processes (cf. Hu et al., 2015) and because N_2O is a powerful greenhouse gas with a global warming potential (GWP-100) 273 times higher than CO_2 (Masson-Delmotte et al., 2021), this may counteract the climate mitigation potential of increased forest biomass production and soil C accumulation (Zaehle et al., 2011). N_2O exchange in boreal forests is generally low and systems range from weak sinks to weak sources due to the low N availability (Kim et al., 2013). But only few studies have explored how N fertilisation affects N_2O dynamics in boreal forest soils, and field trials have reported both increased emissions (e.g. Håkansson et al., 2021) and undetectable responses (Maljanen et al., 2006). Although, two recent studies on N addition to both Norway spruce and Scots pine stands in northern Sweden found N_2O emissions to be negligible compared to increased carbon sequestration in biomass and soils over multi-decadal time scales (Rütting et al., 2021; Öquist et al., 2024).

The longevity of the effect of fertilisation on soil carbon sequestration is another crucial factor. A recent study focused on the effect of current fertilisation recommendations on soil carbon sequestration in 24 previously fertilised versus 24 unfertilised stands found an increase in soil carbon stocks following N fertilisation but noted that the gained carbon decreased rapidly after final felling and reached levels similar to those on unfertilised sites within 4–13 years of harvesting (Boeraeve et al., 2025a). This aligns with previous studies of higher N doses (360–1800 kg N ha^{-1}) in south and central Sweden which found that the initial increase in carbon stocks disappeared 5–13 years after final felling (Högbom et al., 2001; Ring et al., 2013). This indicates that fertiliser-induced increases in soil organic carbon stocks are short-lived, possibly because decomposition rates are higher on clearcuts of fertilised forest stands than of unfertilised stands due to a shifted decomposer community composition after fertilisation (Boeraeve et al., 2025a) (see further in the section Effects of forest fertilisation on biodiversity).

5. Carbon partitioning in trees following nitrogen fertilisation

In addition to its effects on tree stem biomass production, N fertilisation causes shifts in tree carbon partitioning (Fig. 3). A large part of its reported effect on forest production relates to redistributed growth, with more carbon being used for above-ground growth, in stems, branches, and foliage, and less for roots and mycorrhizal fungi (Fig. 3, Haynes and Gower, 1995; Albaugh et al., 1998; Lim et al., 2015). These data come from studies under experimental conditions, with long term, repeated annual N applications, with the exception of Haynes and Gower (1995) which is based on a North American *Pinus ponderosa* stand which received four additions of 150 kg N ha^{-1}, during a 4-year period.

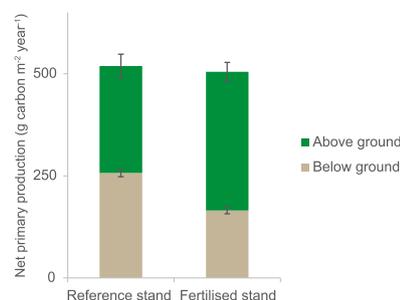If the goal of forest fertilisation is to increase carbon sequestration, it

Fig. 3. Carbon storage (NPP: net primary production) and growth distribution in tree biomass for two 100-year-old Scots pine (Pinus sylvestris) stands in northern Sweden, 2012. One stand is an untreated reference stand and the other has been fertilised annually with inorganic N (ammonium nitrate) to a total N of 700 kg N ha^{-1}. In the figure, carbon storage is divided into aboveground biomass (stem, branches, needles, cones) and belowground biomass (roots only - tree carbon investment in mycorrhizal fungi is not included in this figure). Figure redrawn from Lim et al., (2015).

is critical to account for shifting partitioning patterns in tree growth. This requires measuring the production and turnover of fine roots in relation to stem growth. The amount of carbon partitioned to roots (and mycorrhizal fungi) decreases with N application (Högberg et al., 2010; Law et al., 2022). However, it remains unclear how N affects root growth. There are some indications that root biomass decreases because the turnover of fine roots (< 2 mm diameter) increases more than the production of new roots, resulting in lower root biomass than on equivalent unfertilised land (Hyvönen et al., 2008) and less root biomass for a given stem biomass. Because stem wood is more long-lived than fine roots, allocation to the stem can increase the carbon stock in trees even if the difference in biomass is not large (Vicca et al., 2012).

The anatomy of tree roots is also affected by N fertilisation, mainly because elevated soil nitrate levels result in thicker roots (Wang et al., 2018) and/or because the proportion of coarse roots increases relative to fine roots (Lim et al., 2015). According to an isotopic study in northern Sweden, tree N uptake becomes concentrated closer to the stem in annually fertilised Scots pines (5 m radius) than in trees in a nearby reference stand (5.9 m radius) (Henriksson et al., 2021).

Fertilisation may lead to increased drought sensitivity, because of greater transpiring leaf area and reduced carbon partitioning to belowground structures including water absorbing roots (Lim et al., 2015). This together with the decreased stem wood density, which is the result of increased tracheid lumen stem vessel diameter, due to increased proportion of early wood, which has lower density, increases the risk of cavitation during warmer and drier summers, decreasing tree water uptake capacity (Gessler et al., 2017; Renström et al., 2024). Adding to this, the leaves of fertilised trees may be more susceptible to humidity-based stress (Betson et al., 2007). In addition, wet soils can improve the delivery of dissolved mineral N toward roots (Oyewole et al., 2017), suggesting that a specific soil moisture level may be required to realise the potential fertilisation effect (Fig. 4).

6. Effects of forest fertilisation on biodiversity

In N limited ecosystems, fertilisation generally leads to reduced species richness (Bobbink et al., 2011; Gilliam, 2006). Most studies address effects on plant communities, but increased N availability also affects other organism groups (Sullivan and Sullivan, 2018). In general, both magnitude and longevity of the effects increase with the N dose applied (Strengbom and Nordin, 2008), and even greater effects, such as population decline in disfavoured species, can be expected with more intensive fertilisation regimes than those currently in use (Strengbom et al., 2011).

The effects of N fertilisation on understorey vegetation are relatively well-documented and generally involve increased dominance by
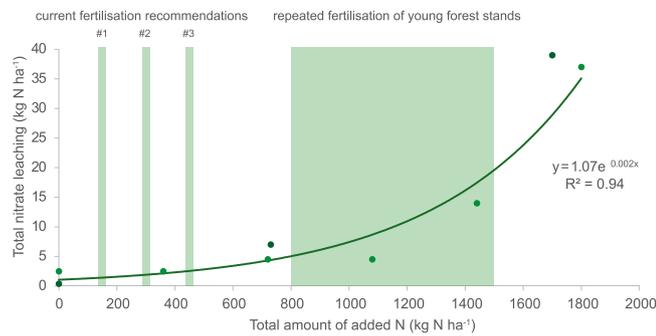
Fig. 4. Nitrogen leakage after clear-felling and different doses of fertiliser. Common fertilisation rates are illustrated with green fields in the figure, including current fertilisation recommendations with up to three applications of 150 kg N ha^{-1} yr^{-1}, and repeated fertilisation of young forest stands with a recommended total application of 800–1500 kg N ha^{-1} yr^{-1} spread over many years (based on Berden et al., 1997; Ring, 1995).

nitrophilous and shade-tolerant vascular plants and declines in light-demanding and N-conservative species (Olsson and Kellner, 2006; Strengbom and Nordin, 2008; 2012; Strengbom et al., 2018; Hedwall et al., 2021). In addition, coverage by common forest mosses is reduced, and ground-dwelling lichens may completely disappear (Olsson and Kellner, 2006; Strengbom et al., 2018). In stands with more intensive fertilisation regimes, understorey vegetation is often limited to mosses or is absent (Strengbom et al., 2011), although current fertilisation recommendations incur smaller changes in understorey vegetation (Strengbom and Nordin, 2008). Effects on other organism groups are less well-studied, but the evidence that exists suggests that the effects of current fertilisation recommendations on soil fauna are small (Sullivan and Sullivan, 2018), but intensive fertilisation can reduce functional species composition among ground-living beetles (Rodríguez et al., 2021). Higher species richness of birds has been reported following intensive fertilisation (Edenius et al., 2011). The reason for this is unclear but may relate to increased supply of food such as invertebrates (Edenius et al., 2012).

It is not clear how transient the impacts of N fertilisation are on biota, but effects on understorey vegetation, such as reduced cover of dwarf-shrubs, ground-living bryophytes, and lichens, often vanish 10–15 years after fertilisation (Strengbom et al., 2011) and then reappear after final felling (Olsson and Kellner, 2006; Strengbom and Nordin, 2008, 2012). The exact mechanism behind this is unclear, but increased N mineralisation indicates that fertiliser N is immobilised in roots and microbial biomass, and becomes released after final felling (From et al., 2015). The longevity of the effects on biodiversity after final felling is not well-studied, but recent studies suggest that they depending on region be rather short-lived in the hemiboreal region (Boeraeve et al., 2025b) to more long-lived (>15–20 years) in the boreal region (Larsson et al., 2024).

Since some of the negative impacts of fertilisation on biodiversity can be linked to forest stands becoming denser, some of the unwanted effects on understorey vegetation can be reduced if fertilisation is combined with thinning (Strengbom et al., 2018). This has mainly been studied in the context of more intensive and frequent fertilisation. From a production perspective, thinning fertilised stands may not be rational as it entails sacrificing a relatively large proportion of the increased production and therefore one of the seven criteria for fertilisation is that no thinnings are planned during the effect period (Strengbom et al., 2018). It is possible that fertilisation could increase the profitability of continuous cover forestry, but this might impact the intended effects on biodiversity by continuous cover forestry so hence, further research is required before such a recommendation can be made. Another knowledge gap related to this is the effect of fertilisation on mixed-species stands. Differences in below ground site occupancy, indicates that

uptake efficiency might differ compared to single species stands for pine and spruce (Lutter et al., 2021). Most likely the effect on stands including deciduous trees will be smaller due to the shorter foliar life span compared to pine and spruce and hence need more frequent fertilisation.

It is well-documented that increased N availability changes the species composition of soil microbial communities, particularly among mycorrhiza-forming fungi (Högberg et al., 2014a, 2014b; Maaroufi et al., 2019; Lilleskov et al., 2019; Jörgensen et al., 2022; Law et al., 2022). Although fungal biomass and the trees-fungal mycorrhizal associations *per se* seem to recover quickly after the cessation of N application (Hasselquist and Högberg, 2014; Högberg et al., 2014b), effects on species composition may persist for longer periods (Strengbom et al., 2001; Lilleskov et al., 2019). Older studies on the effects of N fertilisation are based on surveys of fungal fruiting bodies and morphological types of ectomycorrhizal tree roots (e.g. Kårén, 1997; Brandrud and Timmermann, 1998), but there are still only few studies based on modern (DNA-based) methods of how soil microbial community composition is affected by current fertilisation recommendations. However, a recent study indicates that effects on soil fungi in stands that re-established after clear-felling are transient if fertilisation of the previous stand is carried out according to current recommendations (Boeraeve et al., 2025a), but more profound after higher and more frequent N additions (Jörgensen et al., 2022).

Landscape effects of fertilisation on biodiversity are difficult to assess, and we found no studies that investigate such effects. Those assessments that have been made are all based on scaling up the effects of fertilisation from individual stands or individual fertilisation experiments to landscape scale. Although the fertilisation effect in an individual stand may seem marginal, fertilisation leads to reduced variation in plant and insect communities across sites (Strengbom et al., 2011; Rodríguez et al., 2021). If fertilisation is widespread, this could lead to more homogeneous communities across stands at the landscape level (>1000 km^2). The distribution of understorey vegetation types in Swedish forests has undergone a dramatic change since the 1950s with increased cover of shade-adapted and nutrient-demanding species (such as herbs with high specific leaf area) at the expense of light-demanding and nutrient-conservative (low specific leaf area) species such as ericaceous dwarf shrubs (Hedwall et al., 2021). Increased forest fertilisation is likely to amplify such changes.

7. Nitrogen in water

The concentration of inorganic N in most of Sweden's lakes and streams is a result of nutrient leakage of N that is not taken up by plants, stored in the soil, or released in gaseous form in surrounding land. In general, the more nutrient-rich the contributing landscape is, the higher the N concentrations will be in runoff water. Leakage therefore differs markedly in different parts of Sweden with low levels in the north and higher levels in the south due to much larger agricultural areas and higher deposition (Sponseller et al., 2016). The proportion of agricultural areas in a catchment is particularly critical to N leakage in surface waters (Sponseller et al., 2016).

Forested areas contribute some natural background N leakage, particularly in late autumn, winter, and early spring when vegetation uptake is at its lowest and substantially increased export during clear-felling or extensive storm and insect damage when the N cycle opens up and small organic and inorganic N compounds are produced. Conventional forestry therefore leads to significant N leakage through clear-felling, but this effect is both local and time-limited, subsiding after 5–10 years (Löfgren et al., 2009; Futter et al., 2010). From a forest landscape perspective, the N effect of clear-felling is limited, partly because many lakes (Bergström et al., 2008) and running waters (Burrows et al., 2015) are strongly N-limited. This means that pulses of inorganic N have limited downstream consequences because it is rapidly taken up by microorganisms once it reaches surface waters (Schelker et al., 2016). In

addition, the rate of N uptake has probably increased in the last decade as inorganic N concentrations in forest soil waters have gradually decreased across the country (Lucas et al., 2016; Mosquera et al., 2022), despite continuously intensive forestry.

From a coastal and marine perspective, current forestry has a marginal impact on the anthropogenic N load. Official statistics suggest that forestry-related export currently contributes 8 % of the total estimated anthropogenic load of N reaching the Bothnian Bay and Bothnian Sea (Havs- och Vattemyndigheten, 2019). In other parts of the Baltic Sea, forestry's share is about 1 %. The main contributors apart from deposition and agriculture are coastal industry and private and municipal sewage plants (Havs- och Vattenmyndigheten, 2019).

Increased use of fertilisers does, however, risk increasing the load on aquatic systems, although the effect is likely to be local and time limited. In two fertilisation experiments in southern Sweden, involving N applications of between zero and 1800 kg N ha^{-1} (four times the current recommended dose), increasing dose was associated with increased leakage, measured 0.5 m into the soil on clear-felled sites (Ring et al., 2013; Berden et al., 1997) (Fig. 5). The proportion of N reaching nearby watercourses was not measured but would probably depend on numerous factors including where and how the fertiliser was applied and the structure of the landscape.

8. Optimisation in a landscape perspective

It is important that fertiliser is applied where the growth effect can clearly be enhanced while its environmental impact can be minimised. One approach to achieving this would be to increase the specificity of the current recommendations regarding the type of stands that it is most efficient to fertilise, taking into consideration the natural structure of the forest landscape, topography, and the historical human transformation of wetter soils. Forest land with medium to high conservation value should be avoided. Stand selection should also minimise the risk of further fragmentation of the landscape, and the quantity and quality of key structures (e.g. standing and lying dead wood, and high-value trees) should be maintained at the landscape level. It has recently been shown that commercially applied fertilisers resulted in increased growth after c. 10 years of, on average, 9 % in Norway spruce and 4 % for Scots pine across 36,000 stands in Sweden (Boeraeve et al., 2025b). It has also been shown that the effects of fertilisation on forest growth are particularly limited under dry conditions, despite nutrient limitation, due to soil water scarcity (Lim et al., 2015). Hence, in a warmer and drier future climate, the growth effect may be further hampered by water scarcity, suggesting that areas that will experience increasingly dry and water-limited conditions should not be recommended for fertilisation in the future.

As discussed, misplaced N fertilisation can lead to either no growth effect and/or unnecessary negative impacts on soil and water environments. As in the drier parts of the forest landscape, growth in wetter areas may also not be positively affected by extra nutrients. Wetter areas are also limited by having high hydrological connectivity to surface water, which greatly increases the potential for leakage (Ploum et al., 2021). Wet areas, which often occur in topographic hollows, also tend to be species-rich and may contain endangered species (Gustafsson et al., 2005; Kuglerová et al., 2014). If measures are taken to exempt such environments from fertilisation, i.e. to ensure that no fertiliser ends up in these micro- environments, its negative impacts can be minimised (Gustafsson et al., 2005). The soils that are best suited for N fertilisation, in terms of achieving the desired and avoiding the undesired effects, are those with intermediate moisture levels and relatively low hydrological connectivity to surrounding surface water.

Current recommendations require that fertilisation should only take place at a relatively large distance from all surface waters. New AI-based technology has revealed that Sweden has significantly more water bodies than previously available maps have shown (Laudon et al., 2022). With modern knowledge and new tools based on a mechanistic understanding of ecosystem functions, landscape heterogeneity, and water transport pathways, we can go much further in avoiding the negative impacts of forest fertilisation and identifying places in the landscape where its application is likely to have minimal negative impacts on biodiversity or water quality. In developing such tools, it is also important to evaluate the impact on biodiversity. This involves working with an understanding of landscape heterogeneity and how fertilisation at a large scale risks homogenising biodiversity.

9. Conclusion and outlook

Historically, the rationale for forest fertilisation has been to increase the economic profit by boosting tree stem growth. Today, given the need to sequester more carbon to achieve EU climate goals, the interest has broadened to the consequences for the whole forest ecosystem. Therefore, belowground effects must also be considered, as well as the duration of fertilisation responses. Forest fertilisation mainly affects tree carbon sequestration by temporary increased stem growth but can also lead to increased build-up of organic matter in the soil. Although this increased soil carbon is generally not retained after clear-felling, it is worthwhile to investigate the carbon retention of fertilised soils in alternative forestry systems. This could include management options where tree cover is relatively constant over time, i.e. continuous cover forestry, although fertilisation effects on carbon sequestration and biodiversity in continuous cover forests requires further investigation.

Forest fertilisation has been conducted across large areas in Sweden following current recommendations without any major negative consequences on tree health. However, because nitrogen additions affect
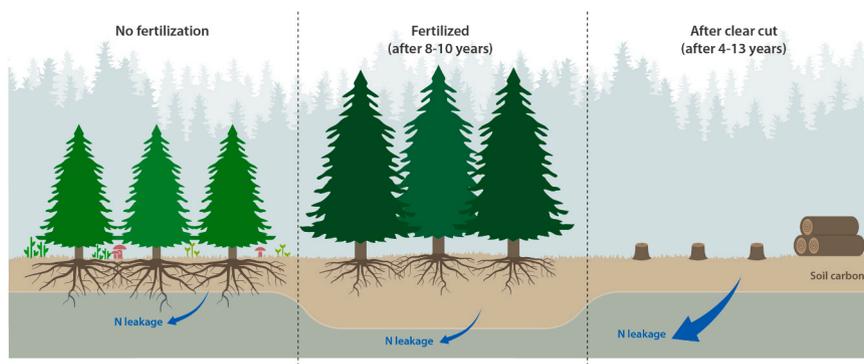

Fig. 5. Conceptual illustration of effects of forest N fertilisation on carbon sequestration, biodiversity above and below ground in boreal forests over time. Within 8–10 years after N fertilisation, tree carbon partitioning is shifted resulting in increased tree stem biomass and decreased root biomass. Due to increased litter input and decreased decomposition caused by shifts in microbial community composition, soil carbon is increased. Biodiversity above and below ground is decreased. Four to thirteen years after clear cutting the increase in soil carbon is lost.

tree growth partitioning and tree anatomy it is advisable to investigate potential connections between fertilisation and forest damage, root physiology, understorey vegetation and soil biology, which can affect the resilience of forest stands in a future climate. Landscape scale planning becomes important in maintaining heterogenous biodiversity since large-scale application of forest fertilisation leads to homogenisation of biodiversity, even though the effect seems to be reversible at the stand-level after clear-felling following fertilisation at moderate doses. Increased fertilisation dose both enhances the growth response and aggravates the environmental impact. Another key knowledge gap is the potential environmental implications of the high amounts of fertiliser nitrogen left in the soil due to the low tree uptake capacities. A further alternative is to explore management options to enhance the use of the large amounts of nitrogen that occur naturally in boreal forest soils.

The potential climate mitigation benefits must be weighed carefully against the risk of exacerbating existing threats to biodiversity, such as those posed by climate change and intensive forestry. In this context, it is particularly important that the expansion of forest fertilisation is concentrated to areas where it can be most effective in delivering climate benefits, while being least harmful to biodiversity. Such spatial restrictions are likely to limit the total area suitable for fertilisation and constrain its overall potential for climate change mitigation.

Author information

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Hjalmar Laudon: Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Karina E Clemmensen:** Writing – review & editing, Conceptualization. **Sandra Jämtgård:** Writing – review & editing, Visualization, Project administration, Funding acquisition, Conceptualization. **Nils Henriksson:** Writing – review & editing, Conceptualization. **Joachim Strengbom:** Writing – review & editing, Conceptualization. **Lars Högbom:** Writing – review & editing, Conceptualization. **Mats Öquist:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

This is a declaration that there is no competing interest in the manuscript Identifying gaps in existing knowledge about the effects of fertilisation on tree growth, carbon sequestration, and environmental risks in boreal forest landscapes.

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Data availability

This is a perspective paper and figures are based on previously published data.

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