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Research article

Temperate grassland conversion to conifer forest destabilises mineral soil carbon stocks

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ABSTRACT

Tree-planting is increasingly presented as a cost-effective strategy to maximise ecosystem carbon (C) storage and thus mitigate climate change. Its success largely depends on the associated response of soil C stocks, where most terrestrial C is stored. Yet, we lack a precise understanding of how soil C stocks develop following tree planting, and particularly how it affects the form in which soil C is stored and its associated stability and resistance to climate change. Here, we present changes in C and nitrogen (N) stored as mineral-associated organic matter (OM), occluded particulate OM, free particulate OM and dissolved OM, from four regional chronosequences of Scots pine (*Pinus sylvestris* L.) forests planted on former grasslands across Scotland. We found that c. 58–68 years after the plantation, bulk soil C and N stocks in the organic layer and the top 20 cm of mineral soil decreased by half relative to unforested grasslands - a decrease roughly equivalent to a third of the simultaneous C gain in the tree biomass. This pattern was driven predominantly by a decrease in the amount of C and N stored as mineral-associated OM, an OM fraction considered as relatively long-lived. Our findings demonstrate the need to estimate C storage in response to tree planting based both on soil C stocks and tree biomass, as the use of the latter alone may significantly over-estimate net C benefits of tree planting on permanent grasslands.

1. Introduction

Climate change poses a paramount threat to the biosphere and humanity, requiring urgent actions to limit its devastating effects (IPCC, 2021). Alongside necessary cuts in carbon dioxide (CO_2) emissions from fossil fuel combustion, management of ecosystems to maximise carbon (C) sequestration aimed at reducing atmospheric CO_2 concentrations could contribute to avoiding extremes in climate change and give more time to reach C neutrality (Paris Agreement, 2015). Tree planting is increasingly presented as a cost-effective strategy for C sequestration in the vegetation (Bastin et al., 2019). However, most of the C in terrestrial ecosystems is found in soils which store more C than the vegetation and atmosphere combined (Schlesinger, 2005). Furthermore, soil C is stored in heterogeneous compartments with distinct primary mechanisms of formation and persistence (Cotrufo and Lavallee, 2022) and vulnerability to climate change (Georgiou et al., 2024; Lugato et al., 2021). Efficacies of afforestation strategies thus depend on changes in soil C stock, and on the form and resilience of the newly created soil C pools.

Afforestation can substantially alter the amount of C stored in soils, but general patterns of the direction and magnitude of such changes are difficult to predict. In intensively managed ecosystems such as croplands, where organic matter (OM) inputs to soils are limited by regular harvests and seasons without vegetation, land-use changes (e.g., to grasslands or plantations) lead to strong increases in soil C stocks (Guo and Gifford, 2002; Mayer et al., 2020; Shi et al., 2013). However, given the pressure on agricultural lands, their availability for tree planting is

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limited. In turn, for extensively managed ecosystems such as grasslands, the picture is less clear (Mayer et al., 2020). Through meta-analyses (Guo and Gifford, 2002) and modelling approaches (Poeplau et al., 2011), several studies pointed towards smaller soil C stocks in planted forests compared to grasslands. This effect, however, seems to depend on whether the C stored in the organic layer is considered (Tew et al., 2021), and on the age of plantations, with initially smaller soil C stocks in young plantations compared to grasslands, but similar or higher in the oldest forests (>30–50 years old) (Bárcena et al., 2014; Li et al., 2012; Poeplau et al., 2011; Ražauskaitė et al., 2020; Speckert et al., 2023). Yet, these findings mostly result from paired-plots, which have limited potential to predict the consequences of land-use change on soil C accrual or changes, given the absence of comparable past levels. In turn, spatially replicated chronosequences of plantations on former grasslands are less common.

The change in the form in which soil C is stored following afforestation, and its associated stability, is even less clear. Soil C can be found in various soil organic matter (SOM) forms that differ in biochemical composition and degree of physical protection, resulting in contrasting degrees of stabilisation (Lavallee et al., 2020). This can range from bioavailable free particulate OM (fPOM), to occluded particulate OM (oPOM) which is less bioavailable due to entrapment within aggregates, and to mineral-associated OM (MAOM) which may persist longer than POM due to mineral binding making the OM less bioavailable. Recent advances in SOM formation (Angst et al., 2021; Cotrufo et al., 2015) and the role of mycorrhizal associations in this process (Craig et al., 2018; Talbot et al., 2008; Zak et al., 2019) provide insights into the response of SOM stocks and distribution across fractions to afforestation of grasslands. Particularly, grassland afforestation results in two changes. First, plant litter input typically changes towards higher C/N ratio and lignin content (Osono et al., 2014), thus reducing the efficiency of microbial degradation and MAOM formation (Cotrufo et al., 2015) while fostering POM accumulation (Fulton-Smith and Cotrufo, 2019). Second, grassland afforestation in temperate regions leads to important changes in soil microbial communities, with often a switch from vegetation associating with arbuscular mycorrhizal (AM) to ectomycorrhizal (ECM) fungi. This results in fundamental shifts in the way OM is turned over and transformed into more persistent SOM forms over time. There is growing evidence that ECM fungi may reduce the efficiency of saprotrophic decomposition (Mayer et al., 2021), leading to less efficient SOM formation. Changes in litter quality and in dominant mycorrhizal type hence both point towards less efficient saprotrophic decomposition, leading to greater C losses through respiration, and a reduced formation of the more stable MAOM stock. In line with this idea, Cotrufo et al. (2019) found that across European soils, more soil C was stored as MAOM in grassland and AM-dominated forests, while soil C in ECM-dominated forests was predominantly stored as POM. Similarly, Craig et al. (2018) reported a higher POM formation from ECM-tree litter and a higher MAOM formation from AM-tree litter. This suggests that a transition from AM-dominated to ECM-dominated vegetation can result in reduced soil C storage, and particularly less stable SOM. Yet, this evidence derives from comparisons of contrasting ecosystems rather than from studies on transition from one ecosystem type to another, limiting our understanding of the actual changes that occur after tree planting.

Here, we determine the responses of soil C and N stocks to the conversion of permanent grasslands to Scots pine (*Pinus sylvestris* L.) forests, and the changes in the relative distribution of these stocks across SOM fractions. To do so, we established four chronosequences of grasslands to Scots pine forest conversion (‘grassland-to-pine forest conversion’ hereafter) at regional scale across Scotland (Fig. 1), ranging from long-term grasslands as control to 58-68 year-old forests planted on former grasslands. We focussed on Scots pine given its Eurasian distribution, its historical importance, and current economical relevance in European forestry. Additionally, it is an ideal candidate species to test our hypotheses given its ECM-association and its relatively slow-decomposing litter. We used chronosequences as they provide a space-for-time substitution approach to estimate changes in soil C over time after afforestation of sites with comparable past soil characteristics and land-use. In turn, we used four separate chronosequences to add spatial replication and avoid any chance of spatial autocorrelation and non-independence for each age category. We hypothesised that grassland-to-pine forest conversion reduces SOM stocks, and results in a reduction of more stable forms of OM (MAOM), alongside higher accumulation of C in the organic layer, and increased pools of shorter-lived C stocks (fPOM). We tested these hypotheses by measuring soil C and N stocks in the organic layer, and, at depths of 0–5 and 5–20 cm of the mineral soil, in the bulk soil, water-extactable OM (WEOM), fPOM,

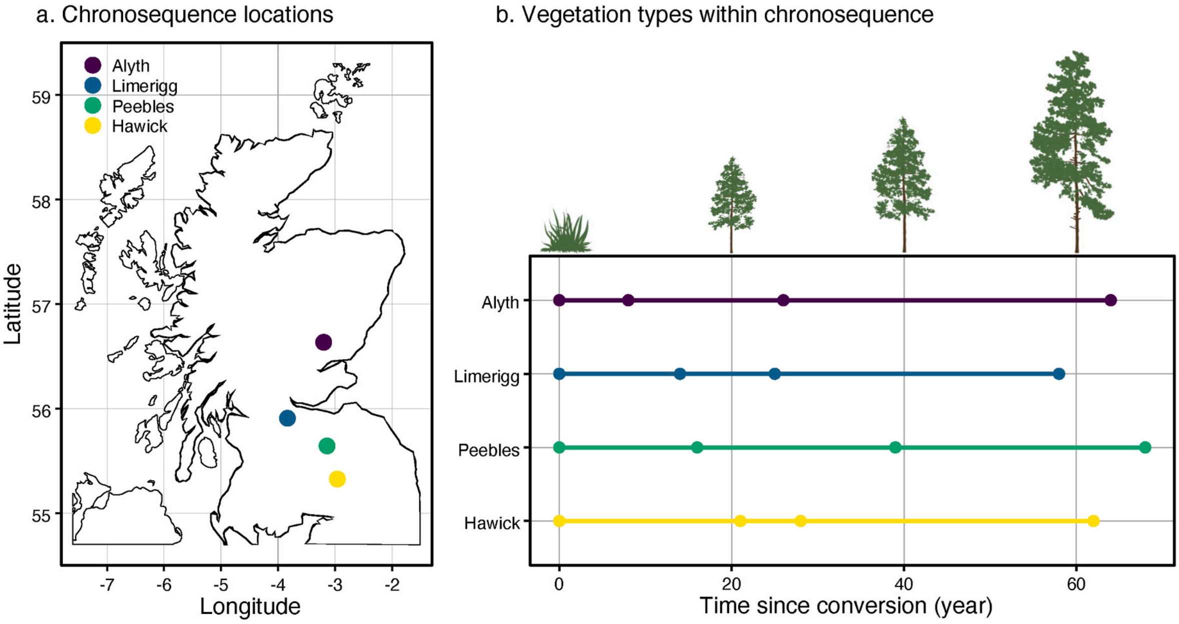

Fig. 1. Study design overview. Four chronosequences were established in Scotland. Coloured dots show the study locations (a), each containing four local plots to form a chronosequence of Scots pine forest planted on permanent grassland, ranging from permanent grassland to mature Scots pine forest (b).

oPOM and MAOM along the four chronosequences.

2. Methods

2.1. Study design

To evaluate the consequences of land conversion from grasslands (AM-dominated) to coniferous forests (ECM-dominated) on soil C and N stocks and their distribution across contrasting SOM fractions, we established four chronosequences, consisting of Scots pine (*Pinus sylvestris* L.) forests planted on former grasslands, in the Scottish Central Lowlands and Southern Uplands (Fig. 1). Each chronosequence contained four plots located within a radius of 2–13 km. Plots consisted of long-term grasslands as controls, and three Scots pine forests planted on former long-term grasslands either 8–21, 26–39, or 58–68 years prior to sampling, respectively (Fig. 1). We selected these categories to obtain a gradient of time since grassland-to-pine forest conversion, which allows analysing the effect of time since conversion using linear regressions. The exact age range for each category was determined by the availability of sites with comparable characteristics (except for the planting year) within a given radius for each chronosequence. Soils were sandy loams or sandy silt loams showing Brown Earth characteristic of continuous soil C distributions across superficial soil horizons (visual determination during field visits). Soils were shallow, with high skeletal content or bedrock encountered between 15 and 30 cm at most sites. Plots were selected based on past land-use (verified with aerial photographs, historical maps and archives from Forestry Commission), and similarity in soil characteristics within chronosequence (Fig. S1, Table S1).

2.2. Soil collection and bulk density determination

In each plot, we established three subplots randomly within a 10 m radius. In September and October 2018, we collected in each subplot the organic layer within a 25 × 25 cm quadrat, and the mineral soil (0–20 cm) using a soil corer (5 cm diameter). In the field, we separated the mineral soil cores into 0–5 cm and 5–20 cm soil layers. We placed all samples in plastic bags and kept them in coolers until we returned to the laboratory. We oven-dried organic layer samples at 60 °C until constant mass and weighed them to determine organic layer density. We sieved the mineral soils to 2 mm and air-dried them prior to analyses.

In each subplot, we measured bulk density of the mineral soil by placing a 25 × 25 cm quadrat on the soil surface (after removing the organic layer) and excavating the 0–5 cm and 5–20 cm layers. The volume of excavated soil was measured by filling excavations with millet seeds and measuring the volume of added seeds (Boot et al., 2015). Excavated soil samples were sieved in the field at 8 mm to remove rocks. Sieved soil samples and rocks (>8 mm) from the 0–5 cm and 5–20 cm layers were weighed at field moisture, and subsamples taken to the laboratory in sealed plastic bags for moisture and rock density measurement. In the laboratory, soil subsamples were further sieved at 2 mm to remove small rocks. Rock subsamples from the field, 2-mm sieved soil, and rocks between 2 and 8 mm from the soil subsamples were dried at 60 °C. We used rock mass, moisture and density to estimate the rock volume in each layer. We used excavated soil volume (V_E [cm^3]), sieved soil mass (M_S [g]), soil water content (SWC [g/g]) and rock volume (V_R [cm^3]) to determine bulk density (BD [g cm^{-3}]) in the rock-free space for each layer:

$$BD = \frac{M_S}{SWC\,(V_E - V_R)}$$

2.3. Soil property determination and C and N stock estimation

To evaluate the effect of grassland-to-pine forest conversion on soil C and N stocks, we measured C and N concentrations in the organic layer, the bulk mineral soil and in SOM fractions for the 0–5 and 5–20 cm layers. For each plot, organic layer and soil samples collected from the three sub-plots were pooled by depth layer and all analyses were performed on composite samples. We determined soil pH in a 2:1 water (ml) to soil (g) solution and soil texture with a hydrometer. Due to insufficient sample mass for the 0–5 cm layer, we measured soil texture on the 5–20 cm layer only, and assumed that the texture was the same in both layers. We fractionated bulk soil samples into water-extractable OM (WEOM), free light particulate OM (fPOM), sand-sized and occluded particulate OM (oPOM) and silt and clay sized, mineral-associated OM (MAOM), following Haddix et al. (2020). To isolate WEOM, 5 g of 2-mm sieved, oven-dried soil were mixed with 30 ml of deionised water, agitated on an orbital shaker for 15 min, and centrifuged for 15 min at 3400 rpm to isolate the <0.45 μm WEOM fraction. The supernatant was filtered over a 20 μm nylon filter, weighed, and its dissolved organic C and total dissolved nitrogen concentrations measured with a TOC analyser (Shimadzu, Kyoto, Japan) equipped with a supplementary module for N. To isolate fPOM, the remaining soil following centrifugation was mixed with 45 ml of sodium polytungstate (SPT) at 1.85 g/cm^3 and centrifuged for 30 min at 3400 rpm. The supernatant with floating fPOM was aspirated and filtered over a 20 μm nylon filter. The fPOM was rinsed with deionised water and dried at 60 °C until total evaporation. To separate oPOM from MAOM, the remaining soil following centrifugation was mixed with 30 ml of sodium hexametaphosphate (0.5%), agitated on an orbital shaker for 18 h to disperse the aggregates, and sieved over a 53 μm sieve. The fraction on the sieve (>53 μm) was taken as oPOM, and the fraction below the sieve (<53 μm) was taken as MAOM. All solid fractions (fPOM, oPOM and MAOM) were oven-dried and weighed. For all organic layer samples, bulk soil samples, and solid fraction samples, subsamples were ground with a ball mill (TissueLyser II, Qiagen). Total C and N concentrations of these subsamples were measured with a flash CHN elemental analyser (Flash Smart, ThermoScientific). We estimated C and N stocks for each soil layer by multiplying the C and N concentrations with the estimated mass of rock-free soil per unit of surface for each soil layer, and with the estimated mass for the organic layer. The data were stored at the NERC EIDC (Joly and Subke, 2022).

2.4. Tree carbon stock modelling

To estimate the increase in tree C stock following afforestation, we assigned a representative yield class to each site using the Yield Index function of the Ecological Site Classification tool (ESC; Pyatt et al. (2001)), and derived the timber volume using the ForestYield model (Edwards and Christie, 1981). This model (Matthews et al., 2016) has been validated against an extensive UK permanent sample plot network, has been reviewed against a stand level dynamic growth model (Lonsdale et al., 2014), and shown to perform well for Scots pine (Lonsdale et al., 2015). We used these values to estimate the C stored in the tree stem, crown, and roots biomass (Morison et al., 2012). The standing volume model output was scaled using robust allometric relationships (Levy et al., 2004) and modified by wood density (Lavers and Moore, 1983) to convert wood volumes to dry weight, 50% of which is assumed to be C (Matthews, 1993).

2.5. Data analyses

To evaluate the effect of grassland-to-pine forest conversion on soil parameters, we analysed all parameters as a function of time since grassland-to-pine forest conversion with linear regressions. To account for the non-independence of plots within chronosequences, we used mixed-effect models with chronosequence as a random variable. We checked data for normal distribution and homoscedasticity of residuals. To visualise the distribution of basic soil properties (texture, pH, bulk density, rock content) between plots of varying vegetations and chronosequences, we performed principal component analyses (PCAs) on properties from the 0–5 and 5–20 cm layer separately. To visualise the effect of time since grassland-to-pine forest conversion, correlations between time since grassland-to-pine forest conversion and plot co-ordinates on the two main PCA axes were represented on the PCAs. We used the R software, version 4.3.2, for all statistical analyses (R Development Core Team, 2013), the *lme4* package (Bates et al., 2015) to fit mixed-effects models, and the *MuMin* package (Barton and Barton, 2015) to derive model adjusted r-squared.

3. Results

3.1. Changes in basic mineral soil properties

Across the chronosequences of grassland-to-pine forest conversion that we established throughout central and southern Scotland (Fig. 1), basic mineral soil properties (texture, pH, rock content, and bulk density) somewhat differed amongst and within chronosequences (Table S1). However, soil properties were overall more similar between plots of the same chronosequence (Fig. 2c and f) than between plots of the same vegetation category (Fig. 2b and e), allowing meaningful comparisons of soil C and N contents within chronosequence. Additionally, the positions of the 16 plots along PCA axes were not significantly related to time since grassland-to-pine forest conversion (Fig. 2a and d). Furthermore, none of the basic properties significantly varied with time since grassland-to-pine forest conversion, with no significant variation in soil texture and pH and only a marginally significant decrease in bulk density for the 0–5 cm layer ($p\text{-value} = 0.0811$), and a marginally significant increase in rock content in for the 5–20 cm layer ($p\text{-value} = 0.0935$). This indicates that any significant response of soil C and N stocks to time since grassland-to-pine forest conversion cannot be solely attributed to covariation with soil properties.

3.2. Changes in C and N stocks in bulk soil

We observed significant increases in C and N stocks in the organic layer following grassland-to-pine forest conversion, from 0.27 kg C m^{-2} and 8.15 g N m^{-2} in grasslands to 0.51 kg C m^{-2} and 15.83 g N m^{-2} for the oldest Scots pine forests (average of 58–68 year-old forests), representing increases of 94.2% and 88.8% for C and N on average, respectively (Fig. 3a and b). In the 0–5 cm layer, C stocks were unchanged along chronosequences (Fig. 3c), while N stocks decreased (Fig. 3d), from 0.18 kg N m^{-2} in grasslands to 0.10 kg N m^{-2} for the oldest Scots pine forests by 44.3% on average. In the 5–20 cm layer, both C and N stocks declined, from 7.12 kg C m^{-2} and 0.51 kg N m^{-2} in grasslands to 2.47 kg C m^{-2} and 0.14 kg N m^{-2} for the oldest Scots pine forests, representing reductions of 65.3 and 72.3% on average, respectively (Fig. 3e and f). Overall, these reductions in soil C and N stocks in the 5–20 cm layer outweighed the moderate increases in the organic layer, leading to significant declines in total soil C and N stocks, from the organic layer to 20 cm soil depth (Fig. 3g and h). On average, these total soil C and N stocks changed from 9.83 kg C m^{-2} and 0.70 kg N m^{-2} in grasslands to 5.01 kg C m^{-2} and 0.26 kg N m^{-2} for the oldest Scots pine forests (average of 58–68 year-old Scot pine forests), representing reductions of 49.1% and 63.1% for C and N, respectively.

3.3. Drivers of changes in C and N stocks in bulk soil

The observed increases in C and N stocks in the organic layer by 94.2% and 88.8%, respectively, were driven by a strong increase in the organic layer mass ($p\text{-value} < 0.001$, $r^2 = 0.69$) by 69.9% on average, between grassland and the oldest Scots pine forests, while the organic layer C and N concentrations did not significantly vary with time since grassland-to-pine forest conversion (Figs. S1a and b). In contrast, the reduction in soil C and N stocks in the 5–20 cm layers by 65.3 and 72.3%, respectively, were largely driven by significant decreases in soil

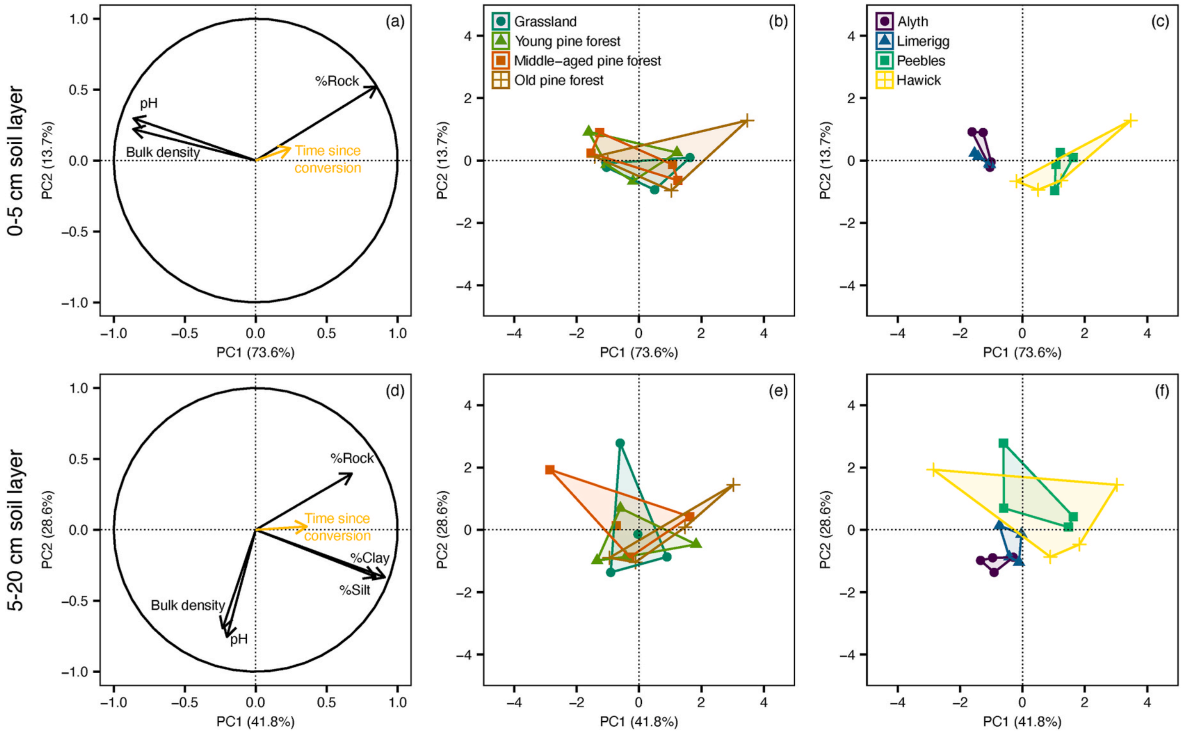

Fig. 2. Soil properties as a function of vegetation and chronosequence. Principal component analyses of soil properties for all 16 plots (4 vegetation types from 4 chronosequences, Fig. 1). (a) and (d) display, for the 0–5 and 5–20 cm mineral soil layers, respectively, the variable loadings (black arrows), and the correlation between time since grassland-to-pine forest conversion and the PCA axes (yellow arrows). The following panels display, for the 0–5 ((b), and (c)) and 5–20 cm ((e), and (f)) soil layers, the scores for all plots with coloured convex hulls containing all plots from each vegetation type ((b) and (e)), or from each chronosequence ((c), and (f)).

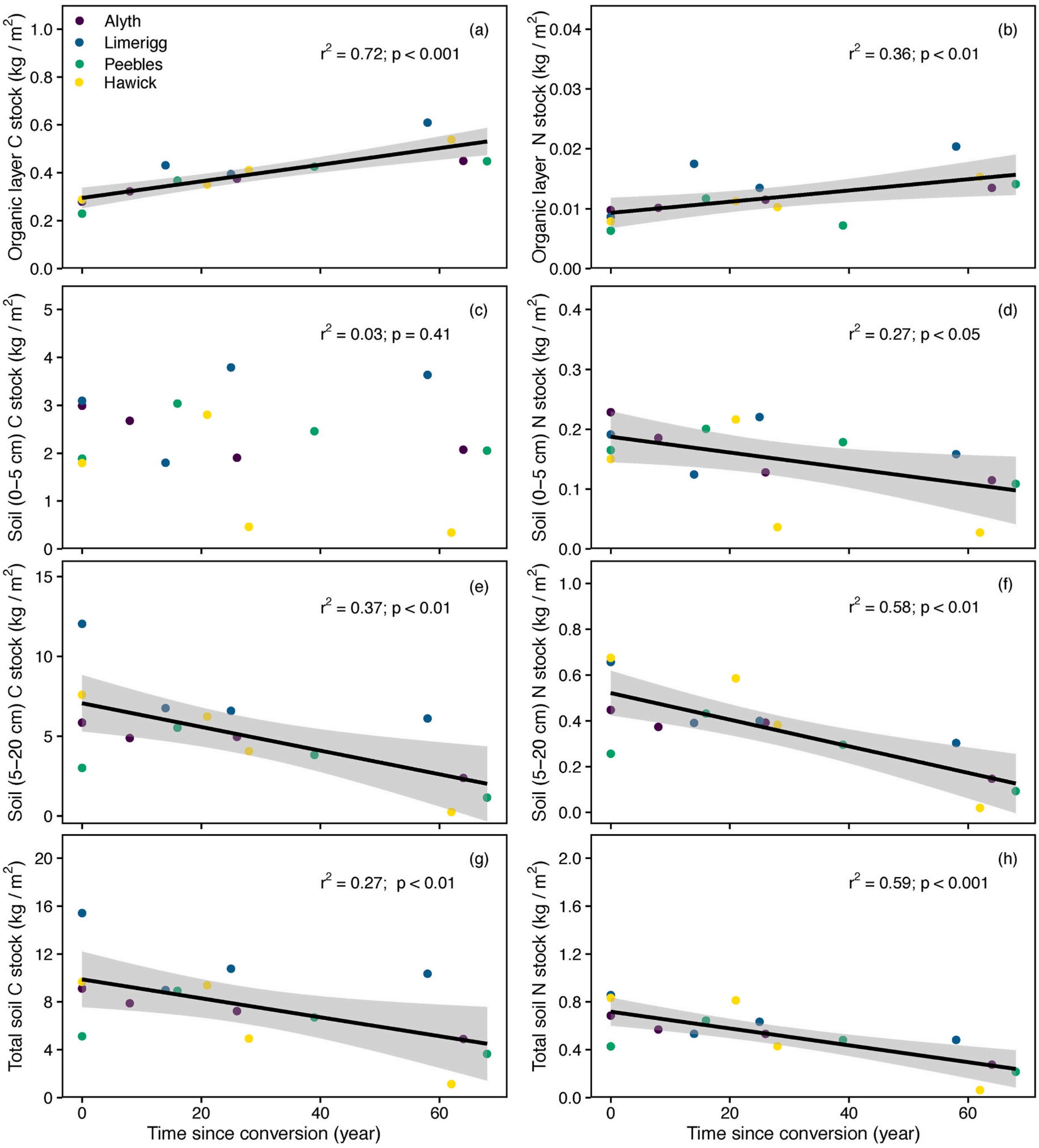

Fig. 3. Changes in C and N stocks in different soil layers as a function of time since grassland-to-pine forest conversion. Changes in C and N stocks in the organic layer (a) and (b), the 0–5 cm (c) and (d) and the 5–20 cm mineral soil layer (e) and (f), and overall belowground changes in total C and N stocks (g) and (h), respectively.

C concentrations (p-value = 0.022, $r^2 = 0.18$) and soil N concentrations (p-value = 0.006, $r^2 = 0.18$), by 37.6 and 41.1%, respectively (Fig. S1). Additionally, the marginally significant increase in rock content in the 5–20 cm layer, which led to a decrease in rock-free mass by 38.5%, could have also contributed to this decrease. In turn, the significant decrease in N stock in the 0–5 cm layer by 44.3% could not be explained by changes in soil N concentrations, which did not significantly change in this layer (p-value = 0.25, $r^2 = 0.04$) (Fig. S1e), but could be associated with the marginally significant decrease in bulk density in the 0–5 cm layer which decreased the rock-free soil mass by 25.4%. This decrease in rock-free soil mass in the 0–5 cm layer, however, did not lead to a decrease in soil C stock despite a lack of significant change in soil C concentration (Fig. S1d) along chronosequences, similar to soil N concentration. Notably, these changes in C and N concentrations did not lead to a change in the C:N ratio in the organic layer (p = 0.67, $r^2 = 0.01$, Fig. S1c), but led to increases in C:N ratio in the mineral soil layers, both in the 0–5 cm layer (p-value = 0.002, $r^2 = 0.32$), by 37.5% (Fig. S1f), and in the 5–20 cm layer (p-value = 0.020, $r^2 = 0.05$) by 12.8% (Fig. S1).

3.4. Changes in C and N stocks in soil fractions

In both the 0–5 and the 5–20 cm soil layers, C stocks in specific fractions only decreased significantly following grassland-to-pine forest conversion for the MAOM fraction (Fig. 4a–e), from 1.37 to 0.80 kg C m^{-2} in the 0–5 cm layer, and from 4.72 to 1.76 kg C m^{-2} in the 5–20 soil cm layer, representing declines by 41.8% and 62.8% in the 0–5 and the 5–20 cm layers, respectively. In turn, C stocks in the form of WEOM, fPOM and oPOM did not significantly change (Fig. 4b, c, d, f, g, h). Still,

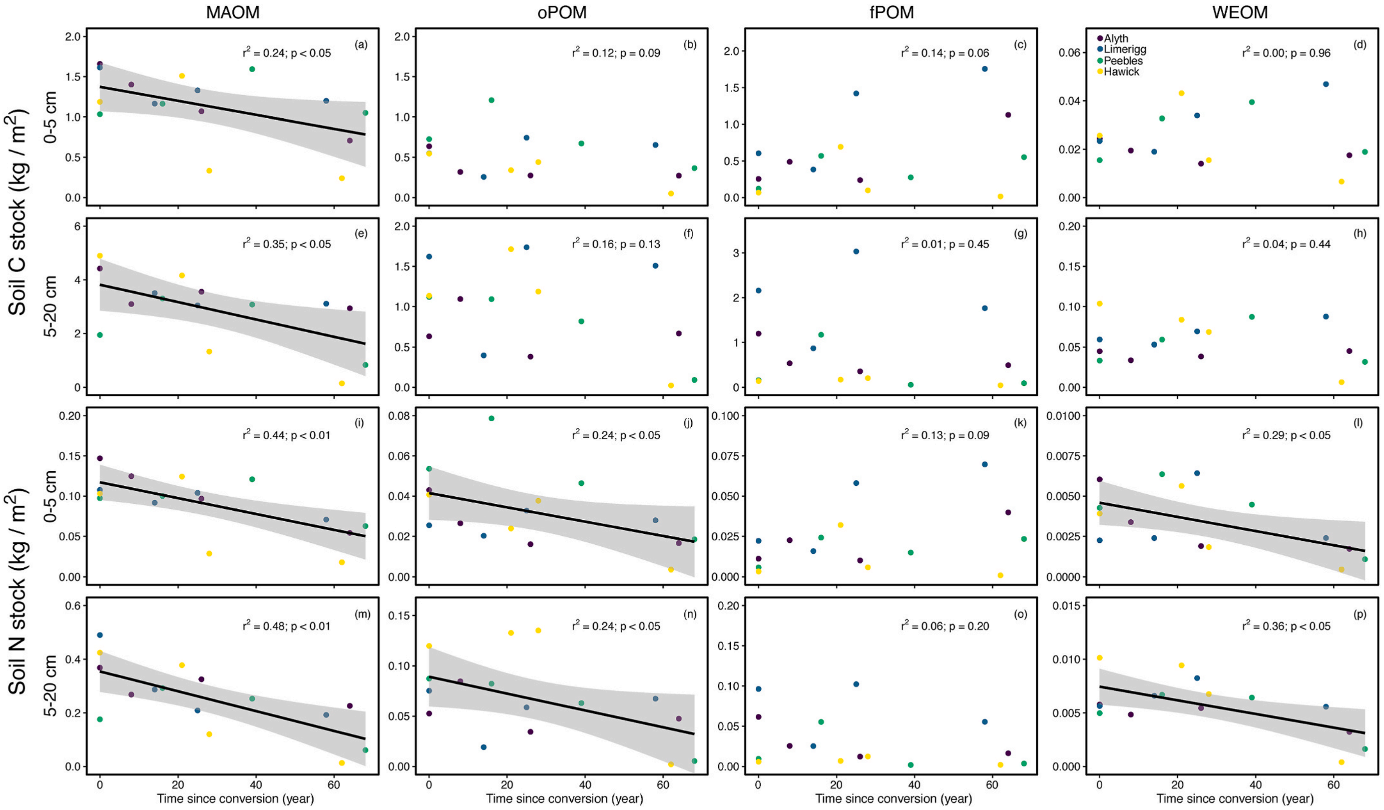

Fig. 4. Changes in C and N stocks in different soil fractions as a function of time grassland-to-pine forest conversion. Changes in C (a–h) and N stocks (i–p) in contrasting soil fractions in the 0–5 (a-d, i-l) and 5–20 cm (e-h, m-p) mineral soil layers as a function of time since grassland to Scots pine forest conversion. MAOM: mineral-associated OM; oPOM: occluded particulate OM; fPOM: free light particulate OM; WEOM: water-extractable OM.

we observed a moderate, marginally significant increase in the fPOM C stock in the 0–5 cm layer (Fig. 4c). Nitrogen stocks in specific soil fractions decreased significantly following grassland-to-pine forest conversion for all fractions except the fPOM, in both the 0–5 and 5–20 cm layers. Specifically, for the 0–5 and 5–20 cm layers, respectively, N decreased by 54.8% and 66.2% in the MAOM fractions, by 59.0% and 63.4% in the oPOM fraction, and by 65.8% and 59.2% in the WEOM fractions. Instead, in the fPOM fractions, we observed a marginally significant increase in N stocks ($p = 0.09$), by 216.2%, in the 0–5 cm layer (Fig. 4k).

3.5. Modelled increase in tree C stocks

According to the ForestYield model, the modelled tree carbon stock, including stem, crown, and roots increased linearly following grassland-to-pine forest conversion, by 0.23 kg C m^{-2} $year^{-1}$, reaching an average of around 13.9 kg C m^{-2} in the oldest Scots pine forests (Fig. 5).

4. Discussion

4.1. Soil carbon changes following grassland-to-pine forest conversion

Our study provides evidence for significant losses of mineral soil C and N following grassland-to-pine forest conversion. The halving of bulk soil C and N stocks, from 9.83 kg C m^{-2} and 0.70 kg N m^{-2} in grasslands to 5.01 kg C m^{-2} and 0.26 kg N m^{-2} in 58–68 year-old Scots pine forests, confirms our hypothesis that land-use conversion results in overall losses of C and N from the soil. Even when the marginal gain in the organic layer was accounted for, we observed sustained soil C and N losses of 49.1% and 63.1% respectively across four spatially replicated chronosequences. Whilst our full C budget indicate that forestry does result in net C gains by 9.08 kg C m^{-2} over 58–68 years, the magnitude of soil C losses equivalent to 34.7% of tree C gains means that these losses must be considered for tree-planting projects to accurately predict their C sequestration potential. A particular concern is that the vulnerability of the remaining soil C stocks to ongoing climate change increased with afforestation, as the observed soil C loss was largely attributed to a MAOM loss, which is predicted to be more resistant to climate change than POM in European forests (Angst et al., 2021; Lavallee et al., 2020;

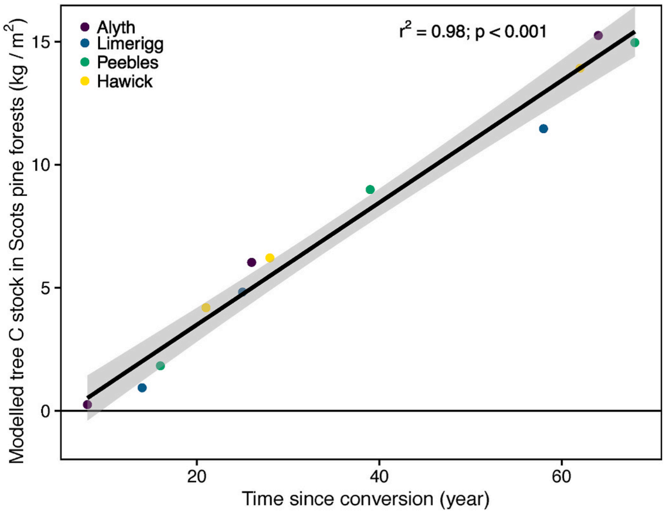

Fig. 5. Total tree carbon stocks as a function of time since grassland to Scots pine forest conversion. Carbon stocks were modelled for *Pinus sylvestris* for each individual stand included in the study based on yield class, soil type and stand age.

Lugato et al., 2021). The magnitude of C and N stock changes are larger than previously reported (Guo and Gifford, 2002; Li et al., 2023; Poeplau et al., 2011), and provide evidence for a sustained loss of soil C and N stocks, with no net uptake of soil C after 30–50 years in plantations unlike reported in previous studies (Bárcena et al., 2014; Li et al., 2012; Poeplau et al., 2011; Ražauskaitė et al., 2020; Speckert et al., 2023), or of lower rates in soil C losses following afforestation.

These more pronounced reductions than previously observed may result from the fact that we studied spatially-replicated chronosequences, as opposed to paired plots where forest treatments are not necessarily planted on former grasslands (Buczko et al., 2023; Li et al., 2023). This is important as C and N changes depend on past levels, and paired plots may not be as informative to predict such changes following land-use change. In turn, our results echo a similar report of reductions in soil C stocks following afforestation of pine or birch on heather moorlands (Friggens et al., 2020). Because heather moorlands have extremely organic-rich soils, their potential for C and N losses is particularly high, and the authors reported a 50% decrease in C stocks within 10 years of tree planting, compared to 58–68 years in our study. Our findings that such losses also occur in plantations on grasslands with mineral soils, albeit at a slower pace, suggests that this pattern may be more general.

4.2. Implications for net carbon sequestration

The documented decrease in soil C amounts to 4.82 kg C m^{-2} (i.e., 48.2 t C ha^{-1}) over 58–68 years and indicates that projected net C gains from tree planting are significantly overestimated if they do not consider soil C changes. In parallel, tree biomass on our plots is expected to capture c. 13.9 kg C m^2 of C (Fig. 5). The resulting reduction in net C sequestration by c. 34.7% is likely a conservative estimate, since we do not include grassland aboveground and belowground biomass in our direct C stock comparison, nor was forest understorey vegetation considered as it was scarce and made a negligible contribution to stand biomass. This finding, together with others from organic soils (Friggens et al., 2020), is a significant caveat to the potential of afforesting grasslands to sequester CO_2. Furthermore, it is important to note that we were only able to consistently sample the 0–20 cm mineral soil layer due to extreme rockiness in most plots (Table S1), thus possibly underestimating soil C and N losses if the trend continues deeper. Losses of C with stand age in deeper soil horizons (up to c. 70 cm) have been reported previously (Ražauskaitė et al., 2020), in line with our observations, whilst observed increases in DOC under forest plantations compared to non-forested control sites (Sawicka et al., 2021) indicate a possible mechanism of C losses through microbial processing and subsequent leaching of DOC. Overly optimistic projections for the potential of sequestering CO_2 through tree-planting schemes (e.g., Bastin et al., 2019) have sparked a new debate regarding the effectiveness of tree-planting actions as nature-based solutions to mitigate climate change. Whilst the scientific debate has highlighted many limitations to tree planting as a climate change mitigation strategy (Kirschbaum et al., 2024), our results show that equating biomass accumulated in vegetation with net C sequestration is too simplistic and inaccurate. Our observed C losses in the mineral soil and increased climate vulnerability of the remaining C stock indicate that soil C stock changes, and changes in C distribution across SOM fraction need to be taken into account when considering afforestation as a CO_2 draw-down strategy. Additionally, large-scale, map-based estimates ignore ecological interactions between plants, soil biota and soil minerals, and a more robust approach that considers the long-term net C balance of ecosystems, not just vegetation, is needed for potential C capture through land management.

4.3. Destabilisation of soil C stocks following grassland-to-pine forest conversion

An important finding of our study is that soil C and N stocks following grassland-to-pine forest conversion were driven by losses from the MAOM fraction (of C and N), and the oPOM fraction (of N). These fractions are considered to be relatively more stable due to close associations (e.g. direct chemical binding) of OM to minerals (MAOM), or to a lesser extent, physical occlusion of OM within aggregates (oPOM), both of which can protect OM from microbial access. The MAOM fraction is considered less accessible to microbial degradation, a process which may increase with global warming (Benbi et al., 2014; Lugato et al., 2021; Rocci et al., 2021) and global estimates show that there is potential for significant C sequestration in this specific fraction (Georgiou et al., 2022). The MAOM is, however, the larger reservoir of N in soil and expected to be decomposed when N becomes limiting, i.e., because of increased C:N of the vegetation input (Daly et al., 2021). Our results support this hypothesis, with MAOM accumulating under grasslands, where the higher N availability can support the increased storage of N-rich OM associated to minerals (Spohn, 2024), and POM accumulating in forests under conditions of N limitation and immobilization of N into the POM fraction (Cotrufo et al., 2021). Interestingly, these decreases occurred despite marginal increases in C ($p = 0.06$) and N stocks ($p = 0.09$) in the fPOM fraction. The fact that soil C and N gains along chronosequences were in the form of fPOM, with marginal increases in C ($p = 0.06$) and N stocks ($p = 0.09$), which is more susceptible to decomposition and responsive to warming in forest ecosystems (Lugato et al., 2021), means that these are conservative estimates of reductions in ecosystem C storage based on the climatic conditions of recent decades. Overall, these changes support our hypothesis, and echo reports of lower C and N stocks in MAOM and higher stocks in POM in European forests compared to grasslands (Cotrufo et al., 2019). Our observation of this trend on four spatially-replicated chronosequences provides strong support for the view that MAOM formation is less efficient in coniferous forests than grasslands. Ongoing climate change may increase C and N loss in the form of fPOM and consequently further decrease soil C stocks, thereby reducing the ability of tree-planting projects to sequester CO_2.

4.4. Mycorrhizal association shift as driver of soil C destabilisation following grassland afforestation

We propose that the switch from AM-to ECM-dominated vegetation as a result of grassland-to-pine forest conversion is responsible for this decrease in the amount of C and N stored as MAOM (Fig. 6). While AM fungi depend on saprotrophic decomposition of OM to obtain N (Hodge and Fitter, 2010) and are thus typically abundant in mineral N-rich environments (Phillips et al., 2013), ECM fungi have the enzymatic ability to degrade OM themselves to satisfy their N demand (Lindahl and Tunlid, 2015; Read and Perez-Moreno, 2003). A change from AM-dominated grasslands to ECM-dominated Scots pine forest can thus induce uptake of N from OM by ECM fungi, thus reducing the C use efficiency of saprotrophic fungi (Averill and Hawkes, 2016; Fernandez and Kennedy, 2016), increasing microbial respiration, decreasing microbial necromass production and reducing MAOM formation. Our observation that decreases in mineral soil C and N stocks were associated with a parallel increase in the soil C:N ratio support this functional shift following a change in dominant mycorrhizal associations, driven by an increased demand for N in the coniferous forest canopy (Tang et al., 2023).

We conceptualise the proposed processes centred around a shift from AM-to ECM-dominated vegetation as evidenced by our results (Fig. 6). This mechanism also fits with the observation from soils of the LUCAS database (Tóth et al., 2013), that AM-dominated ecosystems stored more C as MAOM than ECM-dominated ecosystems (Cotrufo et al., 2019). The amount of N stored as MAOM was also reported to be negatively related to ECM-dominance in temperate American forests (Craig et al., 2018). Other changes following grassland-to-pine forest conversion may also have impacted the decomposition and SOM formation dynamics, including changes in litter lability (Joly et al., 2023), rhizosphere C input (Angst et al., 2018), soil microbial community (Cleveland et al.,

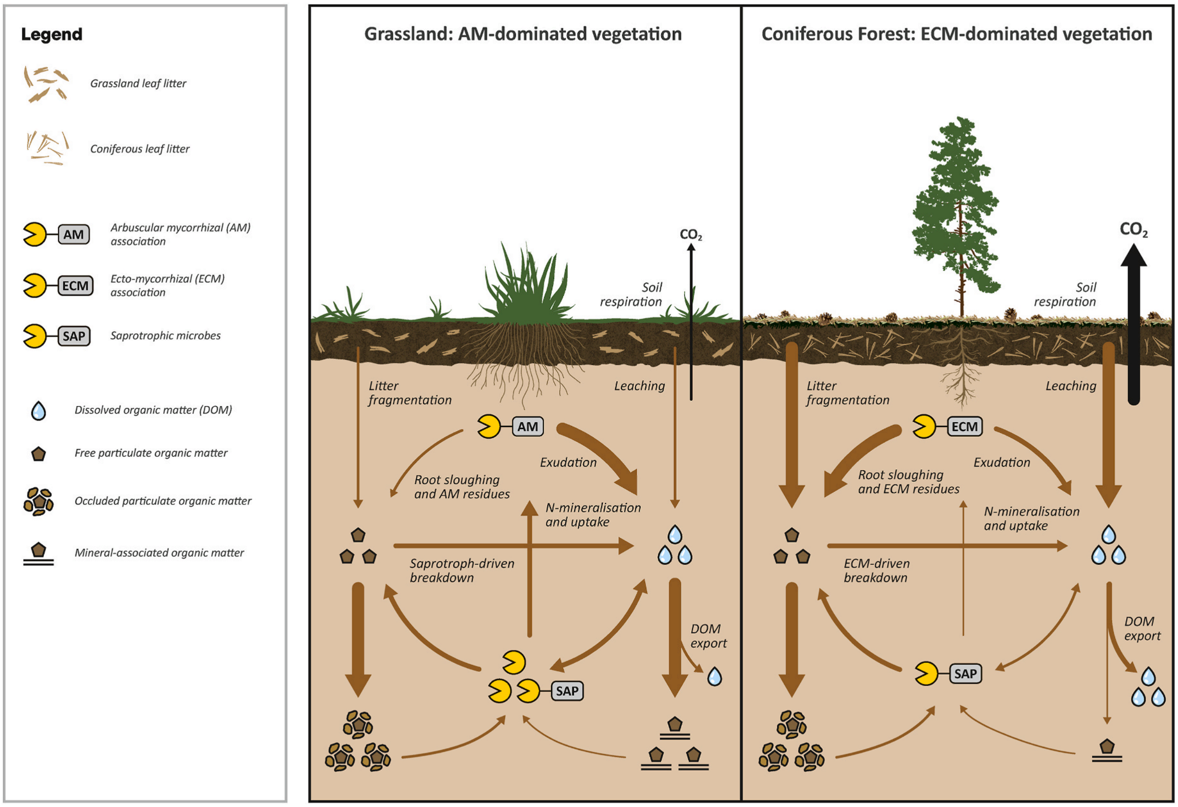

Fig. 6. Conceptual diagram representing hypothesised mechanisms leading to observed differences in SOM pools between grasslands and coniferous forests. Differences in flux sizes are represented by varying arrow widths. Differences in the size of functionally distinct litter and SOM pools are represented by varying icon numbers.

2014), and soil faunal activity (Angst et al., 2024; Joly et al., 2020). Disentangling the mechanisms underlying this change in SOM fractions is challenging yet essential to predict the circumstances when afforestation can be used as an effective solution to mitigate climate change.

5. Conclusions

Collectively, our results highlight that C gains from tree biomass do not equate to net ecosystem C gains, and that long-term grasslands hold an important soil C sequestration value and warrant conservation and restoration efforts (Bardgett et al., 2021; Bai and Cotrufo, 2022). Current financial incentives for tree planting, such as the Woodland Carbon Code in the UK (Jenkins et al., 2011), consider soil C stocks prior to afforestation, but do not yet include an assessment of possible changes of soil C stocks following afforestation. Our findings add to a growing body of evidence (e.g., Bossio et al., 2020; Friggens et al., 2020) suggesting that whole ecosystem C stocks, not just tree biomass, must be considered for full C accounting.

CRediT authorship contribution statement

François-Xavier Joly: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis. **M. Francesca Cotrufo:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Mark H. Garnett:** Writing – review & editing. **David Johnson:** Writing – review & editing, Funding acquisition, Conceptualization. **Jocelyn M. Lavallee:** Writing – review & editing. **Carsten W. Mueller:** Writing – review & editing. **Mike P. Perks:** Writing – review & editing, Investigation. **Jens-Arne Subke:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.124149.

Data availability

The data that support the findings of this study are openly available in the NERC EIDC at https://doi.org/10.5285/ad3d4c0a-66d5-4367-a41c-5f3cdff752f7.

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