



Tree planting in organic soils does not result in net carbon sequestration on decadal timescales

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Abstract

Tree planting is increasingly being proposed as a strategy to combat climate change through carbon (C) sequestration in tree biomass. However, total ecosystem C storage that includes soil organic C (SOC) must be considered to determine whether planting trees for climate change mitigation results in increased C storage. We show that planting two native tree species (*Betula pubescens* and *Pinus sylvestris*), of widespread Eurasian distribution, onto heather (*Calluna vulgaris*) moorland with podzolic and peaty podzolic soils in Scotland, did not lead to an increase in net ecosystem C stock 12 or 39 years after planting. Plots with trees had greater soil respiration and lower SOC in organic soil horizons than heather control plots. The decline in SOC cancelled out the increment in C stocks in tree biomass on decadal timescales. At all four experimental sites sampled, there was no net gain in ecosystem C stocks 12–39 years after afforestation—indeed we found a net ecosystem C loss in one of four sites with deciduous *B. pubescens* stands; no net gain in ecosystem C at three sites planted with *B. pubescens*; and no net gain at additional stands of *P. sylvestris*. We hypothesize that altered mycorrhizal communities and autotrophic C inputs have led to positive ‘priming’ of soil organic matter, resulting in SOC loss, constraining the benefits of tree planting for ecosystem C sequestration. The results are of direct relevance to current policies, which promote tree planting on the assumption that this will increase net ecosystem C storage and contribute to climate change mitigation. Ecosystem-level biogeochemistry and C fluxes must be better quantified and understood before we can be assured that large-scale tree planting in regions with considerable pre-existing SOC stocks will have the intended policy and climate change mitigation outcomes.

KEYWORDS

afforestation, *Betula pubescens*, carbon stocks, climate change mitigation, mycorrhiza, *Pinus sylvestris*, soil carbon dynamics, tree planting

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1 | INTRODUCTION

Anthropogenic climate change has been described as the greatest current threat to ecosystems and all that depends on them (Nolan et al., 2018). World-wide strategies to mitigate climate change have therefore been proposed (Paris Agreement, 2015). Notable among these is the growing international momentum behind tree planting, and the extensive afforestation of areas with future climates potentially suitable for forest cover (Bastin et al., 2019; Lewis, Wheeler, Mitchard, & Koch, 2019; New York Declaration of Forests, 2014; UNEP, 2011). These proposed mitigation steps rely on sequestration of carbon dioxide (CO₂) by the production of tree biomass, but rarely consider the fate and storage of C in soils. Soil C storage is critically important, however, as more C is stored in soil globally than in vegetation and the atmosphere combined (Tarnocai et al., 2009). Furthermore, a large proportion of this is stored in high latitude regions (De Deyn, Cornelissen, & Bardgett, 2008; Köchy, Hiederer, & Freibauer, 2015; Wookey et al., 2009) and is vulnerable to loss through climate warming (Karhu et al., 2014). Across humid temperate, boreal and sub-Arctic regions of the northern hemisphere, high densities of C are found in organic soils of uplands and tundra (Bradley et al., 2005; Crowther et al., 2019; Hartley et al., 2012). The persistence of these significant C reserves depends in part on climatic conditions but also significantly on land use and vegetation cover (Bradley et al., 2005; Karhu et al., 2014). At high latitudes, significantly greater ecosystem C-stores are associated with low-stature, non-woody vegetation (tundra and ericaceous heathland vegetation), rather than with forests (Hartley et al., 2012; Parker, Subke, & Wookey, 2015). Similarly, trends of soil C loss following afforestation have also been reported in the context of forest plantations on grasslands (Guo & Gifford, 2002; Zerva, Ball, Smith, & Mencuccini, 2005). Changes in land use and vegetation cover thus have the potential to influence biological and biogeochemical processes that can reduce soil and hence ecosystem C storage, even resulting in a net C source to the atmosphere.

Planting trees in previously un-forested areas (or areas which have been deforested for centuries) creates profound changes to plant communities. This ultimately affects below-ground microbial communities, resulting in a reshaping of the ecosystem with consequences for stored

soil C (Kyaschenko, Clemmensen, Hagenbo, Karlton, & Lindahl, 2017; Wardle et al., 2004; Wurzbürger, Brookshire, McCormack, & Lankau, 2017). These consequences remain poorly quantified and understood. Both above- and below-ground organisms play an important role in C sequestration (Wardle et al., 2004), and it is vital to understand the combined responses of these communities to climate warming, and how they might be managed to facilitate climate mitigation (Amundson & Biardeau, 2018; Luyssaert et al., 2018). Although afforestation has potential positive effects on C sequestration through the generation of plant biomass, it may have variable effects on soil C depending on tree and associated mycorrhizal species (Craig et al., 2018), forest management (Kyaschenko, Clemmensen, Karlton, & Lindahl, 2017), land use practices prior to afforestation (Guo & Gifford, 2002; Zerva et al., 2005) and underlying soil characteristics (Jandl et al., 2006). It remains critically important to understand the consequences of afforestation for whole ecosystem C stocks, both above- and below-ground. This is also important in the context of climate-driven tree encroachment onto C-rich soils in northern boreal and low-Arctic tundra regions (Hagedorn et al., 2014; Reichle, Epstein, Bhatt, Reynolds, & Walker, 2018; Tømmervik et al., 2009) around the circumpolar north, which may increasingly attract the attention of policy-makers and ecosystem managers in coming decades.

Here, we report direct measurements of the decadal-scale impact of tree planting at sites with organic-rich soils on the whole-ecosystem carbon balance. We use an experimental research platform, where the oldest sites were established nearly 40 years ago, to address our key hypothesis that gains in tree biomass following afforestation do not lead to a net increase in ecosystem C storage at sites with high soil organic matter (SOM) content.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

The four experimental sites used in this study—Ballogie, Craggan, Delnalyne and Kerrow—form part of the Moorland Colonisation experimental platform (MOORCO, 2018) and are located across Northern Scotland (Figure 1). Stands of the native tree species

FIGURE 1 Map of experimental sites used across Northern Scotland, with detailed site map of Ballogie, showing block and plot layout (not to scale). Plots and blocks used for soil respiration and C stock measurements are indicated with separate icons (key in figure). Note that the placement of these icons does not equate to the position of the relevant measurements, merely that these measurements were taken at the plot in question. The hashed birch plot in Block 1 indicates failed tree growth. The detailed plot layout at other sites differed (see text)

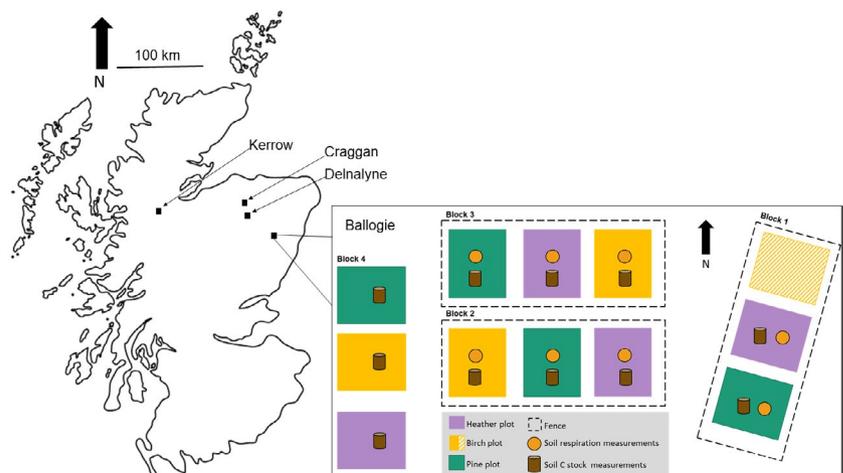


TABLE 1 Summary information for the four experimental sites

Site	Location	Elevation (m a.s.l.)	Soil type	O _h -horizon depth (mean ± SD cm) ^a	Forest stand age (years)	Species planted	Measurements in current study
Ballogie	Lamahip Hill, Aberdeenshire: 57°01'53.5"N, 2°43'53.5"W	230	Peaty podzol	7.9 ± 2.0	12	<i>Betula pubescens</i> , <i>Pinus sylvestris</i>	SOC, soil respiration, hyphal and root production, understorey biomass, tree height and diameter ^b
Kerrow	Fasnakyle, Beaulieu: 57°19'48.0"N, 4°45'55.0"W	379	Humus-iron podzol	7.9 ± 1.7	39	<i>B. pubescens</i> , <i>Betula pendula</i>	SOC stocks, tree DBH ^b
Craggan	Ballindalloch, Moray: 57°22'31.0"N, 3°20'14.0"W	206	Humus-iron podzol	38.7 ± 13.9	39	<i>B. pubescens</i>	SOC stocks, tree DBH ^b
Delnalyne	Lagganvoulain, Glenlivet: 57°14'27.0"N, 3°20'38.0"W	433	Humus-iron podzol	17.2 ± 3.2	39	<i>B. pubescens</i>	SOC stocks, tree DBH ^b

Abbreviation: DBH, diameter at breast height; SOC, soil organic carbon.

^aData for heather control plots only, measured in 2018–2019. O-horizon depth here refers to depth following removal of the L (litter) layer.

^bUsed to calculate tree biomass using allometric equations in Table S2.

downy birch (*Betula pubescens* Ehrh.), silver birch (*Betula pendula* Roth), or Scots pine (*Pinus sylvestris* L.) were planted in replicated paired-plot designs onto *Calluna vulgaris* (L.) Hull dominated heather moorland areas 12 or 39 years previously (Table 1). Tree planting and heather control treatments were randomly assigned to plots within blocks, following measurement of baseline soil parameters (bulk density, organic (O_h) horizon depth and %C), to ensure no underlying systematic bias between plots. Statistical analysis of these baseline data revealed no statistically significant initial differences between the subsequent planting treatments in any of the measured parameters ($p > .05$; Table S1).

The Ballogie experiment was established in 2005 (site map in Figure 1) and consists of three fenced blocks, each containing three plots (18 m × 15 m). Treatments of birch (*B. pubescens*) and Scots pine (*P. sylvestris*), both planted with 1 m spacing, and heather-dominated (*C. vulgaris*) controls, were randomly assigned to the plots. Trees, 20–40 cm high Scots pine saplings and 40–60 cm high birch saplings, both of local provenance, were slot-planted with a spade, causing minimal disturbance to the soil profile. The birch plot in block 1 failed to establish and was therefore omitted from this study. Because of this, a fourth unfenced block, with the same treatments as the fenced blocks, was used for carbon stock measurements but not soil respiration measurements. The presence/absence of fencing was accounted for in the data analysis and block design. Within each planted and heather control plot (not applicable to Block 4), three 2 × 2 m subplots have been established and systematically weeded every year. The three weeding treatments were removal of (a) ericoid species (WR), (b) graminoid species (WM) and (c) understorey species predicted to be dominant in future forest successional stages (WD), for example, *Vaccinium myrtillus* and various grasses as described in figure 1 of Hester,

Miles, and Gimingham (1991). Weeding treatments were applied to investigate the effects of understorey vegetation change on soil C cycling during forest succession.

At Delnalyne and Craggan, 12 plots were established on heather moorland in a paired-plot design, with one of each pair randomly assigned to a *B. pubescens* treatment. The experimental design at Kerrow had six groups of three plots with three treatments: heather control, planted with *B. pubescens*, and planted with *Betula pendula* (silver birch). Seedlings for all three sites were grown in pots at the Centre for Ecology and Hydrology (CEH) Edinburgh from a local seed source (John Miles letters, recorded by RJM). Tree saplings were planted at 0.5 m spacing between 1979 and 1981 and all three sites were fenced from grazing by large herbivores. See Mitchell et al. (2007) for further details of experiment design. At Kerrow, the establishment of an overhead power line through the site in 2012 led to trees being felled in eight of the 12 birch plots (felled plots were excluded from analyses). Of the four planted plots remaining, two were *B. pubescens* and two were *B. pendula*, and both were used for carbon stock sampling. No difference in SOC stocks was found between the two species ($p = 1.00$), consistent with previous findings from the same plots (Mitchell et al., 2007).

2.2 | Soil respiration measurements

Soil respiration (Ballogie only) was measured at the edge and 4.5 m inside plots from the N, W, S and E edges of each plot (pooled by plot during data analysis) using a portable EGM-4 infrared gas analyser with a darkened CPY-4 chamber (PP Systems International). Respiration rates were calculated from the rate of CO₂ increase

within the closed system over a period of 96 s. Respiration was measured from 15 cm diameter and 5 cm high PVC collars which were secured to the soil surface using non-setting plumber's putty (Plumber's Mait[®], Bostik Ltd) to minimize disturbance of the soil and prevent severing of any roots or fungal hyphae (Parker et al., 2015). All vegetation was excluded from the collars; therefore, respiration in this study is defined as the sum of microbial and root respiration within the chamber, and represents forest soil respiration. Respiration measurements at all collars were taken 12 times between 24 May 2017 and 16 October 2018. Soil temperature and moisture were measured at 5 cm soil depth at each collar using a hand-held Traceable[®] probe (Fisher Scientific) and a HH1 ThetaMeter (Delta-T Devices) at the same time as the respiration measurements were made.

2.3 | Carbon stocks: Sampling and analysis

Tree carbon was inventoried using allometric equations (Table S2). Tree size (height and girth) was measured in 2 m radius subplots ($n = 4$ per plot at Ballogie and $n = 2$ per plot at Kerrow, Craggan and Delnalyne), centred on the location from which the soil core was taken, within each planted plot. At Craggan, Delnalyne and Kerrow, tree girth was DBH (diameter at breast height), and at Ballogie diameter at 10% height was measured (instead of DBH due to the large variation in tree height with many shorter than 1.3 m [standard 'breast height']). Tree above-ground biomass was converted into C stock using a conversion factor of 0.54 (Renou-Wilson, Pöllänen, Byrne, Wilson, & Farrell, 2010).

Ground flora above-ground C (including shrubs, forbs and grasses) at Ballogie was inventoried by destructive harvest of three 50 × 50 cm quadrats within each plot, of all fresh biomass above the moss layer (if present), air-dried for 14 days and oven-dried for 24 hr at 60°C. Above-ground biomass of shrub, forb and grass dry weight was converted into C stock using conversion factors; 0.48 for shrubs (Allen, Harris, & Marrs, 2013) and 0.45 for forbs and grasses (Vogt, 1991). Above- and below-ground C stocks of ground flora vegetation at Kerrow, Craggan and Delnalyne were not measured. For control plots at these three sites, vegetation C stocks are assumed to be equal to those inventoried at Ballogie, given the similarity in vegetation cover (Figure S1), comparability to vegetation stocks at a range of other moorland sites in the UK (Quin, Artz, Coupar, Littlewood, & Woodin, 2014), and relatively low contribution to total organic C stocks. In birch plots at Kerrow, Craggan and Delnalyne, there was little, and predominantly herbaceous, ground flora present (Figure S1), in accordance with succession from moorland vegetation to birch woodland (Hester et al., 1991). The sparse ground flora present in these plots was considered to contribute a negligible amount of C to ecosystem C stocks.

Root C at all plots was inventoried using a combination of root plucking and applying conversion factors to above-ground C. Tree root C was estimated at all planted plots as 35% of above-ground tree C (26% of total tree C), as found by Renou-Wilson et al. (2010)

in plots of afforested peaty soils of applicable age classes. Root C stocks in heather control plots at Ballogie were directly inventoried by plucking, washing and drying (at 65°C for 72 hr) the roots from three soil cores (4 cm diameter, 20 cm depth) taken within the centre of each plot. To avoid damage in these permanent experimental plots, roots >10 mm diameter were not excavated. Root dry weight was converted to C stocks using a 0.5 g C (g SOM)⁻¹ conversion factor (Vogt, 1991). Ground flora associated root C in the 12-year-old birch and pine plots (Ballogie) was estimated using a 0.86 above:-below-ground C conversion factor derived from heather control plots (i.e. representative ground flora communities). This conversion factor was applied to the measured above-ground ground flora C in birch and pine plots to account for the contribution of ground flora root C to total root C.

Carbon in the organic (O) horizon (hereafter referred to as soil organic carbon [SOC]) was inventoried in all plots at all sites by taking soil cores using a stratified random approach within the plots ($n = 4$ per plot at Ballogie and Kerrow, $n = 2$ per plot at Craggan and Delnalyne). Where $n = 4$ cores, the location was randomized within each quarter of the plot, and where $n = 2$ cores, the location was randomized within each half of the plot. O-horizon depth (excluding litter layer, but including fermentation and humus layers) was recorded and cores were oven dried for 96 hr at 50°C. Soil C in mineral horizons was not inventoried, therefore references to 'ecosystem C stocks' do not include mineral soil C. SOM content for each sample was determined by loss on ignition in a furnace at 550°C for 4 hr (Ball, 1964) and a subset of samples ($n = 3$ for each soil layer from each plot type from each site; 66 samples in total) was analysed for C content using a FLASH SMART elemental analyser (ThermoFisher Scientific). SOM was converted to SOC using a standard curve: $\text{SOC (kg/m}^2\text{)} = \text{SOM (kg/m}^2\text{)} \times 0.5291$, ($R^2 = .95$), based on elemental analysis results.

Methodological contrasts between baseline and current soil sampling protocols (see Supplementary Materials) reflect evolving research priorities in the intervening 12- to 42-year period. Together with the contrasting dates for baseline sampling (Table S1), this prevent a direct comparison of SOC stocks between initial and current estimates.

2.4 | Root and mycorrhizal hyphae production

At Ballogie, in-growth techniques were used to assay root and hyphal production as a proxy measure of the relative contribution of root and hyphal respiration to total soil respiration. For hyphae, four sand-filled 5 cm × 5 cm bags of 41 μm mesh were deployed at 5 cm depth within each plot from May to October 2017 (181 days). Upon harvest, in-growth bags were freeze-dried for 72 hr and hyphae were extracted by suspending 1.5 g sand in deionized water and sonicating for 10 min before filtering onto glass microfiber filters (Whatman TM) and analysing C content using a FLASH SMART elemental analyser (ThermoFisher Scientific). Five laboratory blank samples were processed as controls. For roots, four bags of organic soil (from Ballogie) of 2 mm plastic mesh with height = 5 cm and plan

view area = 2.95 cm² were deployed at 5 cm soil depth in each plot from May to October 2018 (147 days). All roots were plucked and washed within 24 hr of harvest and dried for 72 hr at 50°C.

2.5 | Data analysis

All analyses were carried out using R Version 3.4.0 (R Core Team, 2017). Variation in soil respiration, soil and vegetation C stocks, root production and hyphal production was investigated using nested ANOVA following a linear mixed effects model (Pinheiro, Bates, DebRoy, & Sarkar, 2012). If interactions between fixed effects were not significant ($p > .05$), they were removed to maximize degrees of freedom (Crawley, 2007). Covariates that did not significantly improve the model fit, as measured by Akaike information criterion (Akaike, 1998) values, were removed from the model. In the soil respiration model, treatment (birch, pine or heather control), soil temperature and moisture were included as fixed effects and block and collar (physical point where respiration measurement was taken) assigned as random effects, accounting for variation between block sampling dates (Harrison et al., 2018). Tree basal area was removed from the soil respiration model as it did not significantly improve the model fit. In the C stock model, treatment (birch, pine or heather control) was included as a fixed effect and block (Ballogie) or plot pair (Kerrow, Craggan and Delnalyne) a random effect. In the root and hyphal production models, treatment (birch, pine or heather control) was included as a fixed effect and block as random effects. Variation in soil

respiration through time was modelled using a generalized additive model with a mixed effects structure (Pedersen, Miller, Simpson, & Ross, 2019) as described above.

3 | RESULTS

At Ballogie, SOC stocks in birch plots were 58% less ($p = .02$) than in the un-planted heather control plots 12 years after planting (Figure 2). This loss of soil C from organic horizons in birch plots at Ballogie was not compensated for by C in above-ground tree and ground flora biomass as the combined above- and below-ground C (ecosystem C stock) in the birch plots was lower than the total C in the heather control plots ($p = .028$). No significant change in SOC stocks was seen in the Scots pine plots (Ballogie) 12 years after planting ($p = .48$), and, although in these plots a substantial amount of C has been sequestered as tree biomass (Figure 2), the whole ecosystem C stock was not significantly different ($p = .79$) between pine and heather control plots 12 years after planting. At Kerrow, SOC stocks in birch plots were 50% less ($p = .03$) than in the un-planted heather control plots while ecosystem C stock (excluding ground flora C) was not significantly different in birch plots relative to heather controls after 39 years ($p = .66$; Figure 2). At both the Craggan and Delnalyne sites, there was no significant difference in SOC ($p = .34$ and $p = .18$, respectively), or ecosystem C stock ($p = .84$ and $p = .77$, respectively; Figure 2), between birch and heather control plots 39 years after planting. At all sites, tree planting was associated with a trend for

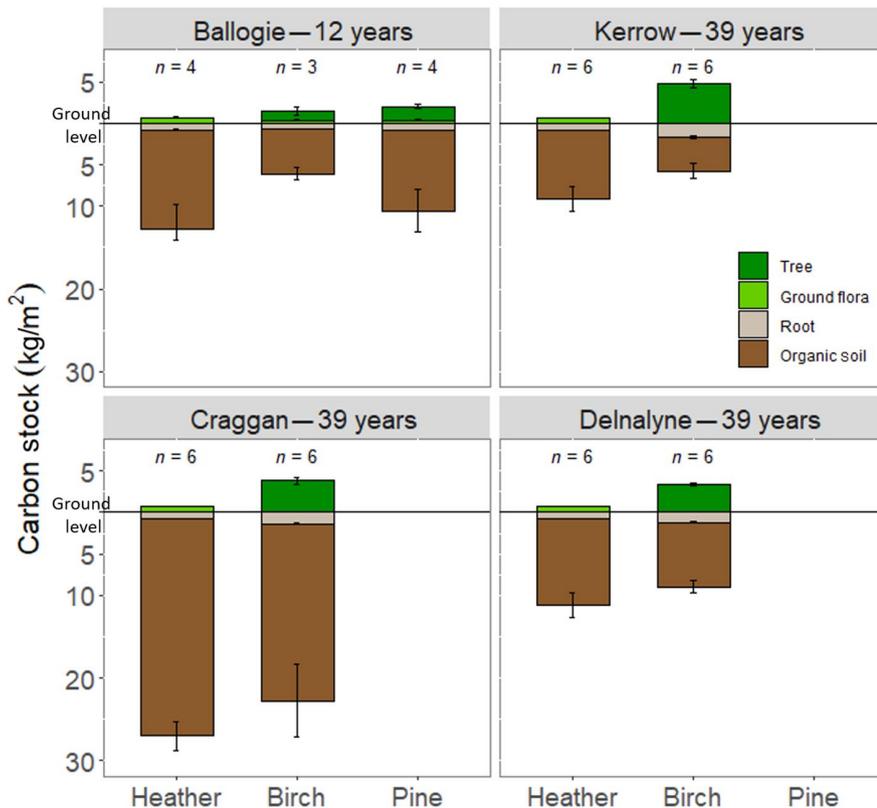


FIGURE 2 Mean ecosystem C stocks from four sites across Northern Scotland. Roots and organic horizon C stocks are represented beneath the zero-line on the y-axis and tree and ground flora above the line in planted birch and pine plots as well as in un-planted heather moorland ('Heather') control plots. Error bars are 1 SE of each constituent C stock mean

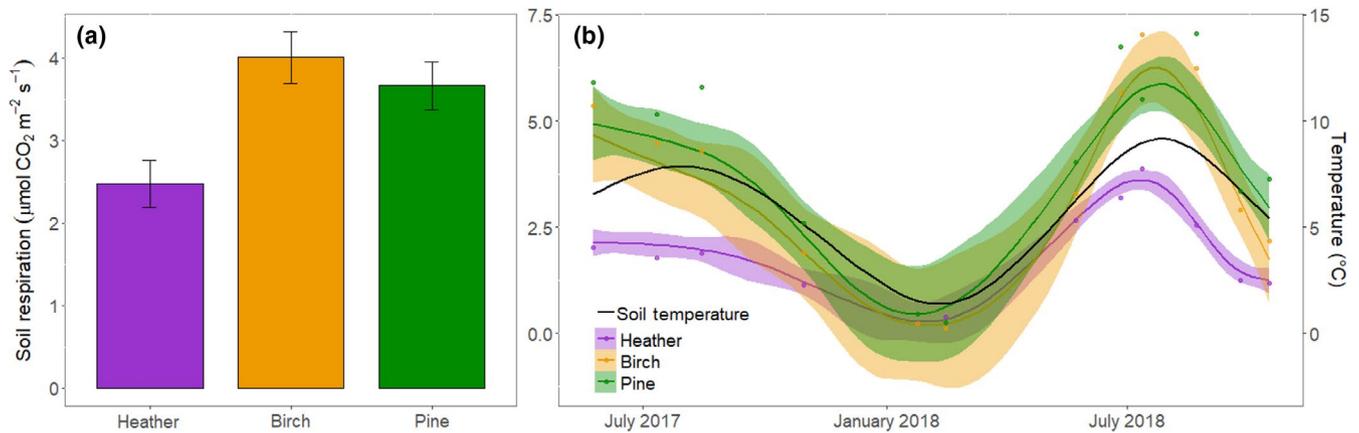


FIGURE 3 Modelled mean soil respiration in planted birch and pine plots and heather moorland ('Heather') control plots based on measurements conducted over 2017–2018 at the Ballogie site. (a) Modelled mean for total measurement period from mixed effects models with block and plot as random effects, tree size, soil moisture and temperature as fixed effects and an interaction term between date and plot. (b) Modelled mean over time with soil temperature averaged across all plots, together with measured data (points) using a generalized additive model with a mixed effects structure as in (a). Output error bars/ribbons are standard error of the mean ($n = 3$)

lower SOC stocks, although this was only significant at two of four sites.

Soil respiration was significantly ($p < .01$) higher in the birch and pine stands compared to the heather control plots across the measurement period at the Ballogie site, 12 years after planting (Figure 3a). Soil respiration showed a seasonal pattern, with apparent differences between the planted and control plots May–September ($p < .05$) and no difference between planted and control plots October–April ($p > .1$; Figure 3a). The seasonal pattern corresponded with soil temperature variations (Figure 3b). There was no significant difference in the amount of roots produced in the heather control plots and planted birch ($p = .69$) or planted pine ($p = .11$) plots over one growing season (Figure S2). There was also no significant difference in the amount of mycorrhizal hyphae produced in the heather control plots and planted birch ($p = .37$) or planted pine ($p = .72$) plots over one growing season.

At Ballogie, where subplots were systematically weeded, none of the weeding treatments were associated with significantly altered soil respiration compared to un-weeded controls in Heather (WD: $p = .93$, WM: $p = .53$, WR: $p = .50$), birch (WD: $p = .17$, WM: $p = .18$, WR: $p = .16$) or pine (WD: $p = .19$, WM: $p = .21$, WR: $p = .25$) plots (Figure S4).

4 | DISCUSSION

4.1 | Whole ecosystem (above- and below-ground) carbon stocks

Planting replicated stands of two native tree species onto heather moorlands was associated with significantly lower O-horizon SOC stocks at two sites, and no change in SOC stocks at two other sites (Figure 2). As baseline soil parameters did not differ significantly or systematically between planting treatments (Table S1), we conclude

that any current differences in SOC stocks between un-planted heather control plots and planted plots are caused by tree planting. Despite increased above-ground C associated with tree biomass, the loss of SOC in planted plots resulted in no net increase in ecosystem C stock at any site over the duration of the experiment, and a net loss at one site (Figure 2). When considering both above- and below-ground C stocks, these data show no net gain in whole ecosystem C stock as a result of planting trees, over the decadal timescales observed here. At one site, Kerrow, above-ground tree C gains offset the significant SOC losses associated with planting trees (Figure 2), indicating that initial loss of SOC associated with planting trees may be compensated for by tree C gains after 39 years. As the birch stands continue to age and grow, they may eventually lead to net ecosystem C sequestration after 39 years, assuming no further SOC loss.

Differences in SOC between heather and birch plots may be explained by different rates of C lost as CO_2 (Figure 3a) or as dissolved organic carbon (DOC, Figure 4). We did not quantify the latter, but early evidence from similar experimental plots suggests that DOC loss is 43% greater from planted birch plots than adjacent heather moorlands (Dawson et al., 2007). An assessment of the extent to which organic materials—originating from leaf and root litter, rhizodeposition and O-horizon SOM—are transferred to mineral horizons was beyond the scope of the current study, although we note the potential value of this for future research at these plots.

Plots planted with birch 39 years previously showed a significant decline in SOC stocks from O-horizons relative to adjacent heather moorlands at one of three sites (Kerrow, Figure 2). Furthermore, there was no evidence of significant net ecosystem C accumulation in forested plots at any of the sites investigated (Kerrow, Craggan and Delnalyne). These results mirror those found when these three sites were surveyed in 2007 (Smith et al., 2007). As these experimental plantings are more than three times older

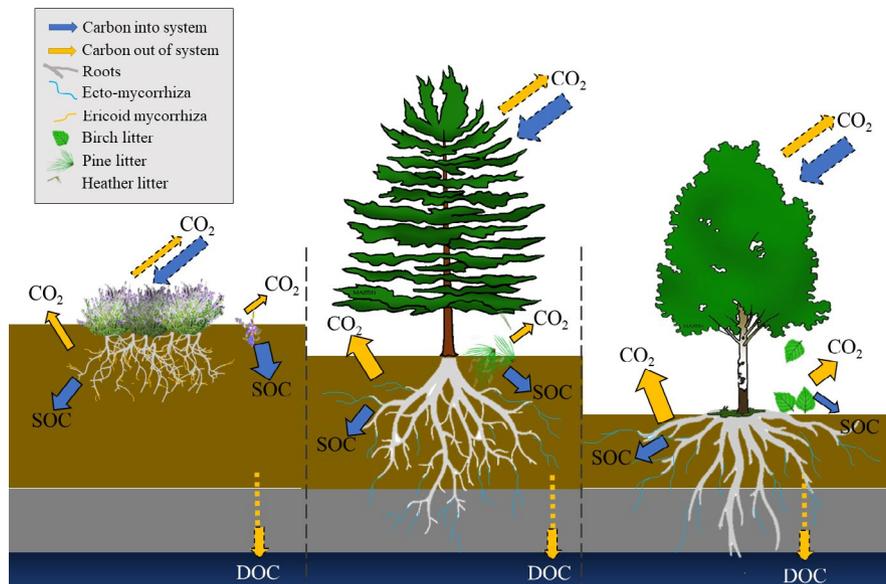


FIGURE 4 Conceptual diagram representing the relative differences in magnitude (represented by arrow width) of carbon fluxes into and out of the ecosystem in birch, pine and heather moorland plots. Carbon dioxide (CO_2) is fixed by plants and released back into the atmosphere through plant and soil (root, mycorrhiza and decomposer) respiration. Plant litter decomposition and root exudations are influxes of carbon into the soil and lead to soil organic carbon (SOC) formation, an unknown fraction of which is leached from the system in the form of dissolved organic carbon (DOC). Litter inputs may also, however, lead to accelerated decomposition ('priming') of pre-existing SOC. Dashed arrows indicate fluxes not quantified in this study. Organic and mineral soil horizons represented by brown (scaled to SOC stocks found at Ballogie in Figure 2) and grey boxes, respectively

than those at Ballogie, there may be regeneration of SOC stocks as forest stands age. However, at Kerrow, where the trees are the same age as trees at Craggan and Delnalyne (39 years), SOC stocks from organic horizons declined by 50% in planted birch plots relative to heather control plots (Figure 2). The direction of this trend is similar to Ballogie, and, although there is a slowing of SOC loss ($4.8\% \text{ year}^{-1}$ at Ballogie vs. $1.3\% \text{ year}^{-1}$ at Kerrow), this is still a highly significant loss of SOC from the system. This may, in part, be explained by a reduction in mycorrhizal C use efficiency as forest stands age and N availability decreases (Hagenbo et al., 2019). A similar study (using some of the sites studied in the current work) found a decrease in SOC stocks by 20.6% in 20-year-old birch plantations relative to heather moorland (Mitchell et al., 2007), and declines in organic matter in the top 5 cm of soil were reported in birch forests (compared to adjacent heather moorland) of 21%, 27%, 38% and 50% in 18-, 26-, 38- and 90-year-old forests (Miles, 1981), respectively. These results suggest high rates of organic matter decline in young forests, which slow as forest stands age. Using a modelling approach, Poeplau et al. (2011) estimate that afforestation of temperate grasslands results in SOC loss in the first 50 years after plantation but then gradually leads to SOC gain in the forest floor. Although the specific land use change explored in that paper is different from the current work, the change in the magnitude, and direction, of the SOC trend over time may be relevant in the current context. We found lower SOC stocks in birch forests than in adjacent heather moorlands in two sites (Ballogie and Kerrow). However, the magnitude of this change was different, with younger stands depleting SOC stocks more, and

tree-associated C stocks offsetting SOC loss in older stands, but, crucially, not leading to net ecosystem C gain.

As all plots (within site) showed no significant difference in baseline soil parameters prior to tree planting, the differences in stocks between planted and control plots found here are likely driven by the presence of planted trees. However, we note that there are significant differences in SOC stocks between sites, despite being established at the same time and using the same method (Figure 2). This suggests that abiotic factors, such as moisture, topography/aspect and pre-existing soil conditions can affect the absolute magnitude of the change in SOC stock following planting of birch trees onto heather moorlands. Combined, this evidence shows that (a) careful consideration must be taken when choosing sites for future tree planting schemes and (b) a more nuanced approach to an evaluation of SOC stocks prior to planting is warranted, rather than simply whether peat horizons are greater than 50 cm deep (Forestry Commission Scotland, 2014).

4.2 | Soil and mycorrhizosphere processes

Consistent with the inventories of SOC (Figure 2), planting two native tree species onto heather moorlands resulted in greater release of CO_2 from the soil (soil respiration) relative to the unplanted heather moorlands 12 years post-planting (Figure 3a). This increase in soil respiration in planted plots relative to heather control plots occurred despite similar rates of root and mycorrhizal hyphae production between planted plots and heather

control plots (Figure S1); that is, root respiration potential is similar. Combined, this may indicate positive soil 'priming', whereby recent C inputs into the soil, mediated by carbon assimilation above-ground, stimulate the soil microbial community, enabling decomposition of pre-existing soil C stores and release of CO₂ into the atmosphere (Fontaine et al., 2007). This phenomenon has been detected from temperate peatlands (Walker et al., 2016) to arctic permafrost soils (Street et al., 2020; Wild et al., 2016) and may become a more prevalent mechanism, causing increased CO₂ release and soil C loss in regions with large soil C pools (Hartley et al., 2012) affected by climate driven changes in plant communities. The loss of organic horizon SOC in moorland with tree planting coincides with a shift in the dominance of mycorrhizal type from ericoid mycorrhizal (ERM) fungi to ectomycorrhizal (ECM) fungi. This key difference may lead to faster hyphae turnover (Clemmensen et al., 2015), and less diverse extracellular enzymes (Read & Perez-Moreno, 2003) but with potentially higher expression (Sterkenburg, Clemmensen, Ekblad, Finlay, & Lindahl, 2018), especially SOM-degrading peroxidases that may be used to liberate N from complex organic matter (Bödeker et al., 2014). Priming of organic matter may be particularly important for trees as they colonize uplands and tundra as the N that they require for growth is typically bound to organic matter (Shaver et al., 1992). A key question remains concerning the role of mycorrhizal fungi in priming of upland and tundra soils as well as more widely across other ecosystems (Frey, 2019; Zak et al., 2019). It should also be noted that many soils in these regions may be particularly vulnerable to the direct effects of warming (Karhu et al., 2014). Higher soil respiration rates in the planted plots relative to the unplanted heather moorland controls were seasonal, with apparent differences in the spring and summer months (May–September; Figure 3b) and no difference between planted and unplanted plots in the autumn and winter months (October–April; Figure 3b). This seasonality corresponds with higher temperatures and photosynthetic activity leading to more C resources being allocated below-ground by the plants. Soil moisture also exhibited clear seasonality across all treatments, with wetter soils in the autumn and winter months, followed by drying during spring and summer; however, there was no difference between treatment types (Figure S3, $p > .05$), possibly due to the relatively small scale of the experimental plantings and the likely importance of lateral soil water recharge at these sites. However, at the landscape scale, large-scale afforestation is likely to impact the ecosystem water balance, affecting soil moisture substantially (Roberts, 1999). In organic-rich soils, significant soil drying together with rhizosphere priming may accentuate rates of SOC loss further (Birch, 1958; Fontaine et al., 2007), both to the atmosphere and to ground- and surface-waters.

Although we find similar rates of root production between planted and unplanted treatments (Figure S2a), the increase in soil respiration seen in planted plots may represent the rapid cycling of recently fixed C back to the atmosphere via root respiration, which can be the fate of a large fraction of fixed C (Högberg et al., 2001; Pumpanen, Heinonsalo, Rasilo, Hurme, & Ilvesniemi, 2009; Ryan &

Law, 2005). The contribution of understorey species to this CO₂ efflux, assessed through systematic weeding treatments with sustained removal of key understorey species from subplots within all plots, is not significant (Figure S4). This result is similar to that found by Kritzler, Artz, and Johnson (2016), where prevention of photosynthate allocation to the rhizosphere (through the implementation of 'girdling'; the removal of phloem tissues around stems) in *C. vulgaris* did not alter soil CO₂ efflux. Furthermore, it has recently been found that mountain birch and associated fungi are responsible for the majority of soil respiration in peak growing season in a sub-Arctic treeline forest (Parker et al., 2020). Taken together, these results indicate that the canopy-forming tree species have a larger net contribution to the return flux of C (soil respiration) than understorey species, although rhizosphere processes associated with the latter are too poorly understood at present to reach firm conclusions.

The difference in soil respiration and SOC stocks between birch and heather control plots is likely driven by contrasting mycorrhizal types (Figure 4), from the ERM heathland shrubs, with recalcitrant litter, slow hyphal turnover and suppression of saprotrophic decomposers, to the ECM birch and pine trees, with faster hyphal turnover and more generalist saprotrophic decomposers (Clemmensen et al., 2015; Hazard & Johnson, 2018; Read & Perez-Moreno, 2003). The difference in SOC accumulation between birch and pine plots found here may also be explained by differences in quality of leaf litter (Brovkin et al., 2012; Dorrepaal, Cornelissen, Aerts, Wallén, & Van Logtestijn, 2005; Epps, Comerford, Reeves, Cropper, & Araujo, 2007; Parker et al., 2018) and root exudates (Smith, 1976), resulting in slower C turnover in the coniferous pine stands relative to the deciduous birch stands (Melvin et al., 2015; Figure 4). The combined above- and below-ground C stocks in the pine plots were similar to heather control plots 12 years after planting, indicating that planting pine trees onto heather moorlands may lead to little change in ecosystem C sequestration in the short to medium term (~12 years).

4.3 | Synthesis

This study contributes to the debate on scenarios of change in soil and ecosystem C stocks in northern circumpolar boreal and low arctic ecosystems with similar plant functional types and controls on SOM dynamics. Indeed, model analyses (Pearson et al., 2013) indicate that substantial regions of the ~1.63 million km² of circum-polar arctic vegetation communities which currently have sedge, shrub and moss-dominated vegetation have the potential to shift to forest (Raynolds et al., 2019) and have recently been identified as areas for potential tree restoration/afforestation (Bastin et al., 2019). These are also systems where SOC densities are remarkably high (Hugelius et al., 2013) and potentially vulnerable to both the direct (Karhu et al., 2014) and indirect effects of warming. This long-term planting experiment, with ECM trees growing on former ERM heather moorland, provides the most informative empirical evidence to date for

the potential effects of tree establishment in ericaceous heathlands, including tundra heaths. In the Scottish context, our data suggest that the current policy not permitting afforestation on peats >50 cm deep (Forestry Commission Scotland, 2014) should be reviewed and tightened; recommendations (to the Scottish Government's Woodland Expansion Advisory Group) that 34% of Scotland's land area may have potential for woodland expansion (Sing, Towers, & Ellis, 2013) risk jeopardizing soil (and ecosystem) C stocks on the extensive heather moorlands and heathlands with organic horizons of <50 cm depth. Growing interest in afforestation as a means of climate mitigation both locally and globally necessitates that ecosystem-level biogeochemistry and C fluxes are better quantified and understood before we can be assured that large scale tree planting in regions with large pre-existing SOC stocks have the intended policy and climate outcomes.

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CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

AUTHOR CONTRIBUTION

All authors contributed to the design of the study. N.L.F. and T.C.P. collected the data and N.L.F. conducted analyses. All authors contributed to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be freely accessible in due course but in the meantime, please contact the corresponding author for access to data.

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REFERENCES

- Akaike, H. (1998). Information theory and an extension of the maximum likelihood principle. In E. Parzen, K. Tanabe, & G. Kitagawa (Eds.), *Selected papers of Hirotugu Akaike*. Springer Series in Statistics (Perspectives in Statistics) (pp. 199–213). New York, NY: Springer.
- Allen, K. A., Harris, M. P. K., & Marrs, R. H. (2013). Matrix modelling of prescribed burning in *Calluna vulgaris*-dominated moorland: Short burning rotations minimize carbon loss at increased wildfire frequencies. *Journal of Applied Ecology*, 50(3), 614–624. <https://doi.org/10.1111/1365-2664.12075>
- Amundson, R., & Biardeau, L. (2018). Opinion: Soil carbon sequestration is an elusive climate mitigation tool. *Proceedings of the National Academy of Sciences of the United States of America*, 115(46), 11652–11656. <https://doi.org/10.1073/pnas.1815901115>
- Ball, D. (1964). Loss-On-Ignition as estimate of organic matter + organic carbon in non-calcareous soils. *Journal of Soil Science*, 15(1), 84–92. <https://doi.org/10.1111/j.1365-2389.1964.tb00247.x>
- Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., ... Crowther, T. W. (2019). The global tree restoration potential. *Science*, 364(6448), 76–79. <https://doi.org/10.1126/science.aax0848>
- Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil*, 10(1), 9–31. <https://doi.org/10.1007/BF01343734>
- Bödeker, I. T. M., Clemmensen, K. E., de Boer, W., Martin, F., Olson, Å., & Lindahl, B. D. (2014). Ectomycorrhizal Cortinari species participate in enzymatic oxidation of humus in northern forest ecosystems. *New Phytologist*, 203(1), 245–256. <https://doi.org/10.1111/nph.12791>
- Bradley, R. I., Milne, R., Bell, J., Lilly, A., Jordan, C., & Higgins, A. (2005). A soil carbon and land use database for the United Kingdom. *Soil Use and Management*, 21(4), 363–369. <https://doi.org/10.1079/SUM2005351>
- Brovkin, V., van Bodegom, P. M., Kleinen, T., Wirth, C., Cornwell, W. K., Cornelissen, J. H. C., & Kattge, J. (2012). Plant-driven variation in decomposition rates improves projections of global litter stock distribution. *Biogeosciences*, 9(1), 565–576. <https://doi.org/10.5194/bg-9-565-2012>
- Clemmensen, K. E., Finlay, R. D., Dahlberg, A., Stenlid, J., Wardle, D. A., & Lindahl, B. D. (2015). Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. *New Phytologist*, 205(4), 1525–1536. <https://doi.org/10.1111/nph.13208>
- Craig, M. E., Turner, B. L., Liang, C., Clay, K., Johnson, D. J., & Phillips, R. P. (2018). Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Global Change Biology*, 24(8), 3317–3330. <https://doi.org/10.1111/gcb.14132>
- Crawley, M. J. (2007). *The R book*. Chichester, UK: Wiley.
- Crowther, T. W., van den Hoogen, J., Wan, J., Mayes, M. A., Keiser, A. D., Mo, L., ... Maynard, D. S. (2019). The global soil community and its influence on biogeochemistry. *Science*, 365(6455), eaav0550. <https://doi.org/10.1126/science.aav0550>
- Dawson, L., Hester, A. J., Ross, J., Hood, K., Gwatkin, R., Potts, J. M., ... Sommerkorn, M. (2007). *Carbon dynamics in heather moorland – Impact of tree establishment (poster)*. Aberdeen, UK: Macaulay Land Use Research Institute. Retrieved from http://www.hutton.ac.uk/webfm_send/607
- De Deyn, G. B., Cornelissen, J. H. C., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes.

- Ecology Letters*, 11(5), 516–531. <https://doi.org/10.1111/j.1461-0248.2008.01164.x>
- Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallén, B., & Van Logtestijn, R. S. P. (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology*, 93(4), 817–828. <https://doi.org/10.1111/j.1365-2745.2005.01024.x>
- Epps, K. Y., Comerford, N. B., Reeves III, J. B., Cropper Jr., W. P., & Araujo, Q. R. (2007). Chemical diversity – Highlighting a species richness and ecosystem function disconnect. *Oikos*, 116(11), 1831–1840. <https://doi.org/10.1111/j.2007.0030-1299.15853.x>
- Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 450(7167), 277–280. <https://doi.org/10.1038/nature06275>
- Forestry Commission Scotland. (2014). *Forestry on peatland habitats. Supplementary guidance to support the FC forests and peatland habitats guideline note (2000)*. Edinburgh, UK: Scottish Forestry, 5 pp. Retrieved from <https://forestry.gov.scot/publications/forests-and-the-environment/protecting-and-managing-soil-in-forests/5-supplementary-guidance-to-support-the-fc-forests-and-peatland-habitats-guideline-note>
- Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. *Annual Review of Ecology, Evolution, and Systematics*, 50, 237–259. <https://doi.org/10.1146/annurev-ecolsys-110617-062331>
- Guo, L. B., & Gifford, R. M. (2002). Soil carbon stocks and land use change: A meta analysis. *Global Change Biology*, 8(4), 345–360. <https://doi.org/10.1046/j.1354-1013.2002.00486.x>
- Hagedorn, F., Shiyatov, S. G., Mazepa, V. S., Devi, N. M., Grigor'ev, A. A., Bartysh, A. A., ... Moiseev, P. A. (2014). Treeline advances along the Urals mountain range – Driven by improved winter conditions? *Global Change Biology*, 20(11), 3530–3543. <https://doi.org/10.1111/gcb.12613>
- Hagenbo, A., Hadden, D., Clemmensen, K. E., Grelle, A., Manzoni, S., Mölder, M., ... Fransson, P. (2019). Carbon use efficiency of mycorrhizal fungal mycelium increases during the growing season but decreases with forest age across a *Pinus sylvestris* chronosequence. *Journal of Ecology*, 106(6), 2808–2822. <https://doi.org/10.1111/1365-2745.13209>
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., ... Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 5, 1–32. <https://doi.org/10.7717/peerj.4794>
- Hartley, I. P., Garnett, M. H., Sommerkorn, M., Hopkins, D. W., Fletcher, B. J., Sloan, V. L., ... Wookey, P. A. (2012). A potential loss of carbon associated with greater plant growth in the European Arctic. *Nature Climate Change*, 2(12), 875–879. <https://doi.org/10.1038/nclimate1575>
- Hazard, C., & Johnson, D. (2018). Does genotypic and species diversity of mycorrhizal plants and fungi affect ecosystem function? *New Phytologist*, 220, 1122–1128. <https://doi.org/10.1111/nph.15010>
- Hester, A. J., Miles, J., & Gimingham, C. H. (1991). Succession from heather moorland to birch woodland. II. Growth and competition between *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Agrostis capillaris*. *Journal of Ecology*, 79(2), 317–327.
- Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., ... Read, D. J. (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, 411(June), 789–792. <https://doi.org/10.1038/35081058>
- Hugelius, G., Tarnocai, C., Broll, G., Canadell, J. G., Kuhry, P., & Swanson, D. K. (2013). The northern circumpolar soil carbon database: Spatially distributed datasets of soil coverage and soil carbon storage in the northern permafrost regions. *Earth System Science Data*, 5(1), 3–13. <https://doi.org/10.5194/essd-5-3-2013>
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., ... Byrne, K. A. (2006). How strongly can forest management influence soil carbon sequestration? *Geoderma*, 137(3–4), 253–268. <https://doi.org/10.1016/j.geoderma.2006.09.003>
- Karhu, K., Auffret, M. D., Dungait, J. A. J., Hopkins, D. W., Prosser, J. I., Singh, B. K., ... Hartley, I. P. (2014). Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature*, 513(7516), 81–84. <https://doi.org/10.1038/nature13604>
- Köchy, M., Hiederer, R., & Freibauer, A. (2015). Global distribution of soil organic carbon – Part 1: Masses and frequency distributions of SOC stocks for the tropics, permafrost regions, wetlands, and the world. *Soil*, 1(1), 351–365. <https://doi.org/10.5194/soil-1-351-2015>
- Kritzler, U. H., Artz, R. R. E., & Johnson, D. (2016). Soil CO₂ efflux in a degraded raised bog is regulated by water table depth rather than recent plant assimilate. *Mires and Peat*, 17, 1–13. <https://doi.org/10.19189/MaP.2015.OMB.203>
- Kyaschenko, J., Clemmensen, K. E., Hagenbo, A., Karlton, E., & Lindahl, B. D. (2017). Shift in fungal communities and associated enzyme activities along an age gradient of managed *Pinus sylvestris* stands. *The ISME Journal*, 11(4), 863–874. <https://doi.org/10.1038/ismej.2016.184>
- Kyaschenko, J., Clemmensen, K. E., Karlton, E., & Lindahl, B. D. (2017). Below-ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecology Letters*, 20(12), 1546–1555. <https://doi.org/10.1111/ele.12862>
- Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A., & Koch, A. (2019). Restoring natural forests is the best way to remove atmospheric carbon. *Nature*, 568, 25–28. <https://doi.org/10.1038/d41586-019-01026-8>
- Luyssaert, S., Marie, G., Valade, A., Chen, Y.-Y., Njakou Djomo, S., Ryder, J., ... McGrath, M. J. (2018). Trade-offs in using European forests to meet climate objectives. *Nature*, 562(7726), 259–262. <https://doi.org/10.1038/s41586-018-0577-1>
- Melvin, A. M., Mack, M. C., Johnstone, J. F., David, M. G. A., Genet, H., & Schuur, E. A. G. (2015). Differences in ecosystem carbon distribution and nutrient cycling linked to forest tree species composition in a mid-successional boreal forest. *Ecosystems*, 18(8), 1472–1488. <https://doi.org/10.1007/s10021-015-9912-7>
- Miles, J. (1981). *Effect of birch on moorlands* (pp. 1–18). Cambridge, UK: Institute of Terrestrial Ecology.
- Mitchell, R. J., Campbell, C. D., Chapman, S. J., Osler, G. H. R., Vanbergen, A. J., Ross, L. C., ... Cole, L. (2007). The cascading effects of birch on heather moorland: A test for the top-down control of an ecosystem engineer. *Journal of Ecology*, 95(3), 540–554. <https://doi.org/10.1111/j.1365-2745.2007.01227.x>
- MOORCO. (2018). James Hutton Institute. Retrieved from <https://www.hutton.ac.uk/research/groups/ecologicalsciences/researchfacilities/moorco>
- New York Declaration of Forests. (2014). *UN climate summit 2014*. New York, NY: United Nations.
- Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., ... Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361(August), 920–923. <https://doi.org/10.1126/science.aan5360>
- Paris Agreement. (2015). Paris Agreement. FCCC/CP/2015/L.9/Rev1. UNFCCC. Retrieved from <http://unfccc.int/resource/docs/2015/cop21/eng/l09>
- Parker, T. C., Clemmensen, K. E., Friggens, N. L., Hartley, I. P., Johnson, D., Lindahl, B. D., ... Wookey, P. A. (2020). Rhizosphere allocation by canopy-forming species dominates soil CO₂ efflux in a subarctic landscape. *New Phytologist*. <https://doi.org/10.1111/nph.16573>
- Parker, T. C., Sanderman, J., Holden, R. D., Blume-Werry, G., Sjögersten, S., Large, D., ... Wookey, P. A. (2018). Exploring drivers of litter decomposition in a greening Arctic: Results from a transplant experiment across a treeline. *Ecology*, 99(10), 2284–2294. <https://doi.org/10.1002/ecy.2442>
- Parker, T. C., Subke, J. A., & Wookey, P. A. (2015). Rapid carbon turnover beneath shrub and tree vegetation is associated with low soil

- carbon stocks at a subarctic treeline. *Global Change Biology*, 21(5), 2070–2081. <https://doi.org/10.1111/gcb.12793>
- Pearson, R. G., Phillips, S. J., Lorant, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3(7), 673–677. <https://doi.org/10.1038/nclimate1858>
- Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, 7, e6876. <https://doi.org/10.7717/peerj.6876>
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2012). nlme: Linear and nonlinear mixed effects models. R package version 3.0.
- Poelau, C., Don, A., Vesterdal, L., Leifeld, J., Van Wesemael, B., Schumacher, J., & Gensior, A. (2011). Temporal dynamics of soil organic carbon after land-use change in the temperate zone – Carbon response functions as a model approach. *Global Change Biology*, 17(7), 2415–2427. <https://doi.org/10.1111/j.1365-2486.2011.02408.x>
- Pumpanen, J. S., Heinonsalo, J., Rasilo, T., Hurme, K. R., & Ilvesniemi, H. (2009). Carbon balance and allocation of assimilated CO₂ in Scots pine, Norway spruce, and Silver birch seedlings determined with gas exchange measurements and ¹⁴C pulse labelling. *Trees*, 23(3), 611–621. <https://doi.org/10.1007/s00468-008-0306-8>
- Quin, S. L. O., Artz, R. R. E., Coupar, A. M., Littlewood, N. A., & Woodin, S. J. (2014). Restoration of upland heath from a graminoid- to a *Calluna vulgaris*-dominated community provides a carbon benefit. *Agriculture, Ecosystems and Environment*, 185, 133–143. <https://doi.org/10.1016/j.agee.2013.12.022>
- R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Raynolds, M. K., Walker, D. A., Balsev, A., Bay, C., Campbell, M., Cherosov, M. M., ... Troeva, E. (2019). A raster version of the Circumpolar Arctic Vegetation Map (CAVM). *Remote Sensing of Environment*, 232, 111297. <https://doi.org/10.1016/j.rse.2019.111297>
- Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – A journey towards relevance? *New Phytologist*, 157(3), 475–492. <https://doi.org/10.1046/j.1469-8137.2003.00704.x>
- Reichle, L. M., Epstein, H. E., Bhatt, U. S., Raynolds, M. K., & Walker, D. A. (2018). Spatial heterogeneity of the temporal dynamics of arctic tundra vegetation. *Geophysical Research Letters*, 45(17), 9206–9215. <https://doi.org/10.1029/2018GL078820>
- Renou-Wilson, F., Pöllänen, M., Byrne, K., Wilson, D., & Farrell, E. P. (2010). The potential of birch afforestation as an after-use option for industrial cutaway peatlands. *Suo*, 61(3–4), 59–76.
- Roberts, J. (1999). Plants and water in forests and woodlands. In A. J. Baird & R. L. Wilby (Eds.), *Eco-hydrology: Plants and water in terrestrial and aquatic environments* (pp. 181–236). New York, NY: Routledge.
- Ryan, M. G., & Law, B. E. (2005). Interpreting, measuring, and modeling soil respiration. *Biogeochemistry*, 73(1), 3–27. <https://doi.org/10.1007/s10533-004-5167-7>
- Shaver, G. R., Billings, W. D., Chapin, F. S., Giblin, A. E., Nadelhoffer, K. J., Oechel, W. C., & Rastetter, E. B. (1992). Global change and the carbon balance of arctic ecosystems. *BioScience*, 42(6), 433–441. <https://doi.org/10.2307/1311862>
- Sing, L., Towers, W., & Ellis, J. (2013). Woodland expansion in Scotland: An assessment of the opportunities and constraints using GIS. *RSFS Scottish Forestry*, 67(4), 18–25.
- Smith, P., Smith, J., Flynn, J., Killham, K., Rangel-Castro, I., Foereid, B., ... Bell, J. (2007). ECOSSE: Estimating carbon in organic soils – Sequestration and emissions. Edinburgh, UK: Scottish Executive Environment and Rural Affairs Department.
- Smith, W. H. (1976). Character and significance of forest tree root exudates. *Ecology*, 57(2), 324–331. <https://doi.org/10.2307/1934820>
- Sterkenburg, E., Clemmensen, K. E., Ekblad, A., Finlay, R. D., & Lindahl, B. D. (2018). Contrasting effects of ectomycorrhizal fungi on early and late stage decomposition in a boreal forest. *The ISME Journal*, 12(9), 2187–2197. <https://doi.org/10.1038/s41396-018-0181-2>
- Street, L. E., Garnett, M. H., Subke, J.-A., Baxter, R., Dean, J. F., & Wookey, P. A. (2020). Plant carbon allocation drives turnover of old soil organic matter in permafrost tundra soils. *Global Change Biology*. <https://doi.org/10.1111/gcb.15134>
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23(2), 1–11. <https://doi.org/10.1029/2008GB003327>
- Tømmervik, H., Johansen, B., Riseth, J. Å., Karlsen, S. R., Solberg, B., & Høgda, K. A. (2009). Above ground biomass changes in the mountain birch forests and mountain heaths of Finnmarksvidda, northern Norway, in the period 1957–2006. *Forest Ecology and Management*, 257(1), 244–257. <https://doi.org/10.1016/j.foreco.2008.08.038>
- UNEP. (2011). The Bonn challenge. Retrieved from <http://www.bonncchallenge.org/>
- Vogt, K. (1991). Carbon budgets of temperate forest ecosystems. *Tree Physiology*, 9(1–2), 69–86. <https://doi.org/10.1093/treephys/9.1-2.69>
- Walker, T. N., Garnett, M. H., Ward, S. E., Oakley, S., Bardgett, R. D., & Ostle, N. J. (2016). Vascular plants promote ancient peatland carbon loss with climate warming. *Global Change Biology*, 22(5), 1880–1889. <https://doi.org/10.1111/gcb.13213>
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304(5677), 1629–1633. <https://doi.org/10.1126/science.1094875>
- Wild, B., Gentsch, N., Čapek, P., Diáková, K., Alves, R. J. E., Bárta, J., ... Richter, A. (2016). Plant-derived compounds stimulate the decomposition of organic matter in arctic permafrost soils. *Scientific Reports*, 6(1), 1–11. <https://doi.org/10.1038/srep25607>
- Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H. C., ... Shaver, G. R. (2009). Ecosystem feedbacks and cascade processes: Understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, 15(5), 1153–1172. <https://doi.org/10.1111/j.1365-2486.2008.01801.x>
- Wurzburger, N., Brookshire, E. N. J., McCormack, M. L., & Lankau, R. A. (2017). Mycorrhizal fungi as drivers and modulators of terrestrial ecosystem processes. *New Phytologist*, 213(3), 996–999. <https://doi.org/10.1111/nph.14409>
- Zak, D. R., Pellitier, P. T., Argiroff, W. A., Castillo, B., James, T. Y., Nave, L. E., ... Tunlid, A. (2019). Exploring the role of ectomycorrhizal fungi in soil carbon dynamics. *New Phytologist*, 223(1), 33–39. <https://doi.org/10.1111/nph.15679>
- Zerva, A., Ball, T., Smith, K. A., & Mencuccini, M. (2005). Soil carbon dynamics in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) chronosequence on a peaty gley. *Forest Ecology and Management*, 205(1–3), 227–240. <https://doi.org/10.1016/j.foreco.2004.10.035>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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