Alternative afforestation options on sandy heathland result in minimal long-term changes in mineral soil layers

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Abstract

Extensive afforestation is currently being widely promoted as a key nature-based solution for climate change mitigation. Fundamental to this strategy is the sequestration of carbon into long-term stable storage, either in wood products or the soil. However, the long-term effects of tree planting on soil carbon, or other soil properties, has rarely been examined. Importantly, afforestation can take many different forms, with differing effects on soil properties. Here, we evaluate how the historical afforestation of sandy heathland adopting a range of management options – including different combinations of conifers and broadleaves in monocultures and mixtures – have affected soil pH, total carbon and nitrogen concentrations, the C:N ratio, and carbon and nitrogen stocks almost a century later. We analyse these properties at a range of soil depths through the organic (litter, F and grass layers) and upper mineral soil profiles (0-5 cm, 5-10 cm and 10-20 cm depth). In comparison to the historical heathland sites, afforestation decreased soil pH, most dramatically under conifers, and increased the C:N ratio. However, there was overall little difference in carbon and nitrogen concentrations between alternative management options. While the total carbon and nitrogen concentrations were much higher in the organic layers of the forest options compared to the open sites, this did not translate into differences in the mineral layers. Furthermore, although we found some evidence of the transferral of carbon and nitrogen into the uppermost soil mineral layers, this was minimal in comparison to the concentrations of the organic layers. The soils at our study site are low quality and sandy, and are therefore unfavourable for incorporating organic matter, but it is still notable how little was incorporated after nearly a century of afforestation. Given the current emphasis on tree planting as a means to tackle climate change, these results demonstrate the fundamental importance of the appropriate consideration of both the afforestation management option and underlying soil type.

1 Introduction

Tree planting is widely advocated as a critical way of combating climate change (Bastin et al., 2019; Popkin, 2019). It is a focus of numerous international agreements (such as the Bonn Challenge and the New York Declaration on Forests), national government-led initiatives (such as the UK government's aim to plant 30,000 ha of new woodland every year as part of its net zero by 2050 target) and programmes led by multilateral organisations or charities (such as the Trillion Tree Campaign) (Burton et al., 2018; Chazdon et al., 2017; Committee on Climate Change, 2020). Afforestation and reforestation have considerable potential to mitigate climate change through capturing and sequestering atmospheric carbon, although a number of important trade-offs and caveats must be considered (such as competition with agricultural land, tree species choice, previous land use and high potential water use) (Doelman et al., 2020; Griscom et al., 2017; Lewis et al., 2019). Fundamental to the ability of woodland to act as a carbon sink is long-term carbon storage, either in wood (by converting harvested wood to long-lived wood products or leaving trees unharvested) or transferred to soil carbon (slow turnover) pools. However, the ability of soils to accumulate and fix carbon, and the wider impacts of afforestation on soil quality, are seldom the focus of tree planting schemes (Friggens et al., 2020).

Afforestation can take many different forms. Monoculture plantations are often favoured as they can sequester carbon rapidly, although many studies have shown that more diverse forests store more carbon and have greater long-term resilience and stability of the carbon stocks (Lewis et al., 2019; Osuri et al., 2020; Seddon et al., 2019). Therefore, recommendations for the use of nature-based solutions to help mitigate climate change include the avoidance of non-native monocultures and a preference for the restoration of natural forests and forest diversification (Seddon et al., 2020b, 2020a; Watson et al., 2018).

However, most studies investigating the effects of tree species richness on carbon focus on above-ground assessments (Li et al., 2019; Liu et al., 2018). This is despite the fact that the soil carbon stock normally contains an equivalent, or even greater proportion, of the carbon stock than above-ground biomass (De Vos et al., 2015; Lal, 2005; Smith et al., 2006; Vanguelova et al., 2013). Understanding how different types of afforestation – such as with conifers or broadleaves and in monocultures or mixtures – and subsequent forest management affects below-ground carbon storage is an important dimension to the debate.

Where the effects of afforestation on soil carbon have been investigated, the results have been variable, with a range of studies finding an increase, decrease or no effect of afforestation on soil carbon (Ashwood et al., 2019; Burton et al., 2018; Deng et al., 2014; Li et al., 2017; Mayer et al., 2020; Smal et al., 2019; Whitehead, 2011). Generally, there is an initial decrease in soil organic carbon immediately following afforestation due to soil disturbance, with a gradual increase in the subsequent years and decades back to pre-disturbance levels and (sometimes) beyond (Deng et al., 2014; Deng and Shangguan, 2017; Vanguelova et al., 2019). The magnitude and duration of these different stages varies and is dependent on factors such as ground preparation practices, soil type, forest type and forest management, but is an important consideration if tree planting aims to mitigate climate change (Mayer et al., 2020). Most studies investigating the effects of afforestation focus on young plantings (< 20 years); studies that focus on older afforestation are scarce (Ashwood et al., 2019; Mayer et al., 2020; Smal et al., 2019; Wang et al., 2016). However, these long-term studies are particularly valuable to understand how our current rapid afforestation goals may translate into long-term carbon storage.

Soils perform a wide range of functions and deliver a variety of ecosystem services beyond carbon storage (Baveye et al., 2016; Drobnik et al., 2018). Soil formation is itself an important supporting service, underpinning the delivery of many other ‘final’ ecosystem services, although soil formation is generally such a slow process that many suggest soil should be managed as a non-renewable resource (Bardgett et al., 2011; FAO, 2015; Natural Capital Committee, 2020). Soil quality supports soil functions, soil health and is defined as an ecosystem service, due to its important role in regulating the environment, such as capturing nutrients, purifying water and buffering against atmospheric pollutants (Smith et al., 2011). Despite the focus on the benefits of afforestation for climate mitigation, it can also be a means of increasing soil quality (particularly after degradation from intensive land use) and it is important to understand the effects of alternative tree planting options on other vital soil functions.

Typical indicators of soil quality are total carbon concentration, total nitrogen concentration, and the carbon to nitrogen ratio (C:N) (Boerema et al., 2017; Muñoz-Rojas, 2018). Total carbon concentration and total nitrogen concentration usually correlate with each other and with soil quality. Soil carbon has a major role in influencing other important biological, chemical and physical soil properties and is an indicator of soil organic matter content (Lal, 2005; Masciandaro et al., 2018). Soil organic matter is an important source of soil fertility, is a nutrient store, provides energy and substrate to microorganisms, buffers against pH changes, and increases soil aeration and water holding capacity (Jones et al., 2005; Smith et al., 2011). Soil organic matter can be separated into particulate organic matter (relatively undecomposed plant-derived material that persists in soil through occlusion in large aggregates) and mineral-associated organic matter (microscopic fragments of organic matter or single molecules that are chemically bonded to minerals) (Cotrufo et al., 2019; Lavallee et al., 2020). Although less readily available, mineral-associated organic matter is more nutrient dense and can be more easily assimilated by plants and microbes than particulate organic matter (Lavallee et al., 2020). The avoidance of leaching and increasing the retention of nitrogen are both important soil functions as nitrogen is an essential nutrient for tree growth (Vanguelova et al., 2011; Vesterdal et al., 2008). During decomposition of organic matter, nitrogen is largely retained and recycled within the soil and the trees whereas carbon is mineralised to carbon dioxide, so a lower C:N ratio indicates more thorough decomposition of organic matter (Veum et al., 2011). A low C:N ratio may relate to better soil quality as there is more nitrogen available for vegetation uptake; in contrast, a high C:N ratio may be the result of microbial nitrogen immobilisation, leading to lower productivity (Berthrong et al., 2009). However, while high nitrogen availability can indicate better soil quality, it can also lead to increased nitrogen leaching (particularly in soils with C:N ratio of less than 25), with negative implications for water quality (Sutton et al., 2011).

Afforestation is also well known to affect soil pH (Hornung, 1985). Changes in soil pH affect soil properties and biogeochemical processes, with repercussions on the wider ecosystem functioning, structure and diversity (Hong et al., 2018; Janssens et al., 2010; Kunito et al., 2016; Stevens et al., 2010). The effects of afforestation on soil pH vary by tree species. In general, forest soils tend to be more acidic than equivalent soils under grassland vegetation (Berthrong et al., 2009; Chapin et al., 2002; Hong et al., 2018; Jackson et al., 2005), which seems to be caused mainly through the redistribution of cations (increased cation uptake by trees causing localised acidification in the upper soil layers) (Berthrong et al., 2009; Jobbágy and Jackson, 2003). Trees are also effective at scavenging atmospheric pollutants, leading to increased deposition and acidification under forest canopies where air pollution is high (Guerrieri et al., 2015; Vanguelova et al., 2011, 2010). Due to both a greater canopy surface area and aerodynamic roughness, conifers scavenge atmospheric deposition more efficiently than broadleaved species (Augusto et al., 2002; De Schrijver et al., 2007; Guerrieri et al., 2015). Conifers also have a more acidic leaf litter than broadleaves. Taking these two factors together, conifers therefore tend to acidify soils more than broadleaved species (De Schrijver et al., 2007; Hornung, 1985). A global meta-analysis found that afforestation with *Eucalyptus*, *Pinus*, and other conifers significantly decreased pH, while there was no change for other angiosperms (Berthrong et al., 2009). The impact of afforestation on soil pH may also vary by location. A large study in China found that afforestation neutralises soil pH as it raises pH in acidic soil but lowers pH in alkaline soil (Hong et al., 2018). Despite recognition of the fundamental importance of soil for forests, it is often not routinely monitored within the commercial forestry industry. Understanding the localised and specific impact of past management on soil properties is important for considering future management, so this represents a key opportunity for improvement.

Here we explore how alternative historical afforestation options on sandy heathland have affected soil properties, including pH, and carbon and nitrogen concentrations and stocks. We compare a range of combinations of broadleaves and conifer species in mixtures and monocultures, as well as historical and recently reverted heathland sites. Sandy soils have a number of properties that make them less amenable to change through land management. For example, they are less able to bind and accumulate carbon and are therefore already close to their carbon saturation potential (i.e. the maximum carbon that can be sequestered and stored by the soil) (Angers et al., 2011). They are also prone to the leaching of nutrients. It is therefore particularly interesting to evaluate the effects of afforestation on sandy soil properties, especially over long time periods.

2 Methods

2.1 Study site

We collected soil samples from Thetford Forest, an extensive forest landscape in the Breckland region of East Anglia, UK. Nearly 18,000 hectares was planted between 1922 and 1950 as part of a government drive to create a strategic national timber reserve following

World War I (Dannatt, 1996). Prior to afforestation, most of the land was covered in heath or rough grass vegetation and described as marginal agricultural land. A range of conifer and broadleaved species were planted, but the establishment success with the pioneer species Scots pine *Pinus sylvestris* and Corsican pine *Pinus nigra* meant that it was, and continues to be, a predominantly pine plantation. Remaining historical heathland sites are characterised by a grass-heath vegetation, which is a mixture of acidophilous grassland, calcareous grassland and lowland heath assemblages, adapted to nutrient poor and drought-prone soils (Dolman et al., 2010). The Breckland Forest Site of Special Scientific Interest recognises an important vascular plant and invertebrate assemblage associated with these grass-heath sites (Natural England, 2000).

The soils across the landscape are a combination of chalk-sand drift (with highly variable chalk content), sand and gravels, and wind-blown sand, creating a mosaic of calcareous soils (where chalk is near the surface) and acidic soils (where there is deep sand over chalk) (Corbett, 1973). Soils across the majority of the landscape are arenosols (UK soilscape 11: freely draining sandy Breckland soils), with some smaller areas of leptosols and podzols. The parent material is chalk and glacial till.

The region is semi-continental. It is relatively cool and dry compared to the rest of the UK. Monthly average temperatures are between 0.1°C (February minimum temperature) and 22.5°C (July maximum temperature) (30-year average for 1981-2010) (Met Office). Temperatures tend to be extreme compared to the rest of the UK, with common late frosts and high summer temperatures. Average annual rainfall is 664.6 mm.

2.2 Plot selection

We selected forest plots to represent a variety of different land use and management options across the forest based on a GIS analysis (Table 1). We used the soil map from the 1973

Breckland Soil Survey to ensure that a range of historic soil types were identified for soil sampling (although note that these largely fall within the broader arenosol classification) (Corbett, 1973). Plots were only selected if the main tree component was planted more than 15 years ago, to ensure that the current crop was well established. Although the ages of stands varied between plots (as some stands had secondary rotations or planting since the original afforestation, Table A.1), we are confident that each plot would have had near-continual tree cover for at least 65 years. Plots that exceeded 2 ha were selected (with the exception of one plot that was found to be sub-divided by species and therefore each section was smaller). The conifer monocultures comprised of Corsican pine, Scots pine, hybrid larch *Larix x marschlinsii*, Douglas fir *Pseudotsuga menziesii* or Weymouth pine *Pinus strobus*. Species in broadleaved monocultures were sweet chestnut *Castanea sativa*, eucalyptus *Eucalyptus spp.*, oak *Quercus spp.*, beech *Fagus sylvatica* and birch *Betula pendula*. Full information on the plots is given in Table A.1.

Management option	Category description	Number of plots
Conifer monoculture	One species, conifer	6
Conifer mixture	3+ species, all conifer	6
Broadleaved monoculture	One species, broadleaved	5
Broadleaved mixture	3+ species, all broadleaved	5
Mixture (primary conifer)	3+ species, combination of broadleaved and conifers, largest component is conifer	5
Mixture (primary broadleaved)	3+ species, combination of broadleaved and conifers, largest component is broadleaved	5
Open	Sites recently cleared from forestry to revert to heathland (~15 years ago)	5
Heathland	Historical heathland sites, never planted	5
Total		**42**

Table 1: Summary of survey plots

The historical heathland sites, which had never been planted, were used as a control against which to compare the different afforestation scenarios.

2.3 Sampling procedure

Soil sampling took place in November and December 2016. At each plot, we selected three sub-plots by randomly generated coordinates. We collected samples from the organic and mineral layers (Figure 1a). In forested sites, the organic layers were separated into the leaf litter layer (intact leaves or needles) and the fermentation (F) layer (partially broken-down leaf material and humus). In open sites, the organic layers also included a grass layer, but leaf litter was sometimes not present. The mineral layers were separated into three different depths below the F layer: 0-5 cm, 5-10 cm, 10-20 cm. Within the upper 20 cm of mineral soils that we sampled, the soils were uniform and sandy with no clear development of different mineral horizons.

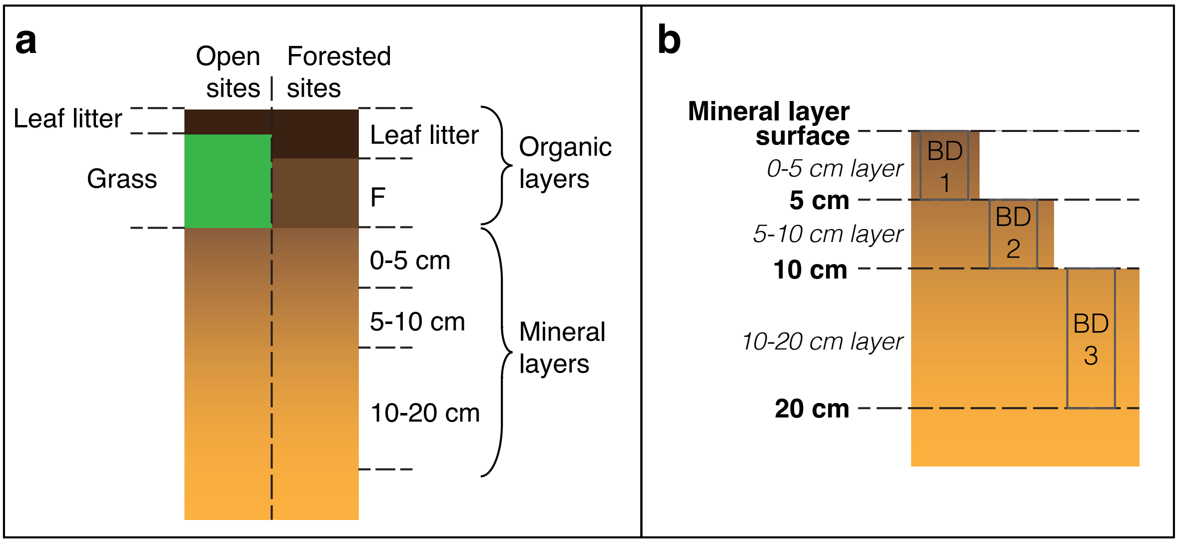

Figure 1: Diagram of soil samples. a) All soil layers sampled. The leaf litter and F layers may vary in depth. b) Samples taken to calculate bulk density of different layers. BD1, BD2 and BD3 indicate different bulk density samples, in increasing order of depth.

At each sub-plot, we tapped down a 2-inch diameter soil corer until the top of the core was level with the top of the leaf litter (the full length of the soil corer including the nose was 35.5 cm). While still in the ground, we unscrewed the top of the corer and measured the compression of the sample by placing a marked metal tube in the top of the corer. We then dug up the corer and carefully lifted it from the ground so that soil was not lost from the bottom of the corer. We collected mineral layers from the corer for all sites, and also the organic layers from the corer in open sites. In forested sites, we collected all organic layer material within a 25 x 25 cm quadrat adjacent to the corer to calculate layer densities.

In addition, at the first sub-plot, we took extra samples to calculate mineral soil bulk density. We cleared the surface litter and F-layer from the soil and tapped the corer down to 5 cm (0-5 cm sample – BD1 in Figure 1b). We then excavated an adjacent area of soil to 5 cm depth and tapped the corer down another 5 cm (5-10 cm sample – BD2 in Figure 1b). Finally, we excavated an area of soil to 10 cm depth and tapped the corer down another 10 cm (10-20 cm sample – BD3 in Figure 1b). This ensured that each bulk density sample was minimally affected by compression as the corer was tapped down; if all samples were taken from one core, the top of the sample would undergo more compression than the bottom, affecting bulk density calculations.

We recorded the time, date and GPS location of each sub-plot. We transferred samples to a fridge as soon as possible on the sampling day and stored them at 4°C until analysis.

2.4 Laboratory analysis

Samples were transferred to the Forest Research chemical laboratory at Alice Holt. All samples were analysed separately. Therefore, for each plot there were three samples (one from each sub-plot) for each of the different soil layers. The bulk density samples were weighed, dried at 105°C, and then re-weighed. We calculated dry bulk density of the mineral soil layers by dividing the dry weight by the volume of the sample (based on the corer dimensions). Moisture content of the organic layer samples were determined from the weights of wet and oven-dried (at 40°C) samples. We calculated the litter, F and grass layer densities by dividing the dry weight by the volume of the sample (25 x 25 cm quadrat multiplied by measured thickness of the layer).

Soil samples for chemical analysis were also oven-dried at 40°C until dry (assessed using visual inspection). Litter, F-layer and soil samples were then individually sieved (2-mm) and milled. The samples were then analysed for total carbon (separated into organic carbon and inorganic carbon) and total nitrogen by dry combustion at 900°C, with a Carlo Erba CN analyser (Flash1112 series) (reference methods ISO 10694 and 13878). As there is always some remaining soil moisture in samples even after oven-drying, these values were then corrected for the residual soil moisture content in each sample (by drying subsamples at 105°C overnight and measuring weight loss to determine the residual moisture content of samples). Soil pH (in water) was also measured in each sample using a suspension of 25 ml of distilled water with either 5 g of mineral soil or 3 g of organic soil, shaken on an orbital shaker for 15 minutes and rested for 45 minutes, with pH analysis using a Sentek pH electrode (reference method ISO 10390).

Across all samples, the proportion of total carbon concentration that was inorganic was minimal (mean value of 2.31%). No inorganic carbon at all was recorded in 504 of the 600 total samples (hence we only analysed organic carbon content).

2.5 Data analysis

The C:N ratio was calculated as the total organic carbon concentration divided by the total nitrogen concentration. For each soil layer, we calculated the mean value of each variable per plot from the values at each of the three sub-plots. For some litter, F and grass samples there was insufficient material to accurately assess pH, so means were taken of the available data. For each plot and soil layer, we calculated carbon stocks by multiplying the mean moisture-corrected total carbon concentration (organic and inorganic carbon), the mean thickness of the layer, and the mean density (bulk density for mineral soil layers, and density for litter, F and grass layers). We calculated total soil profile carbon stock by summing the carbon stocks of each sample layer. We followed the equivalent method to calculate nitrogen stocks.

Henceforth, *total carbon concentration* refers to moisture-corrected total organic carbon concentration (%). *Layer carbon stock* refers to the total carbon stock in each soil layer, and *total carbon stock* refers to the sum of carbon stocks from the whole topsoil profile sampled. The equivalent terms are used for nitrogen.

For each dependent variable, we fitted a linear model and then used an ANOVA to test for significance. Within these main categories, we also fitted separate linear models to compare different subsets of data, for example, only mineral soil samples (see Table 2). Management option, soil layer and pH were included as predictors. To improve the model fit, we transformed dependent variables using a logarithmic function (model fitting was evaluated using the DHARMa R package to assess the normality of model residuals). We used a type II ANOVA on the models to determine which predictors were significant. Where predictors had a significant effect, we then used a Tukey-Kramer post-hoc test to find pairwise interactions that were significant (although pH could not be included as a predictor at this stage as it was a continuous variable). Before running the Tukey-Kramer we excluded all non-significant predictors from the model (at the 0.05 significance level).

Dependent variable	**Subset of data included in different linear models**
pH	All plots
Total carbon concentration	All soil layers; only organic soil layers; only mineral soil layers
Total nitrogen concentration	All soil layers; only organic soil layers; only mineral soil layers
C:N ratio	All soil layers; only organic soil layers; only mineral soil layers

Thickness of layer	Only organic soil layers
Carbon stock in each layer	All soil layers
Carbon stock of plot	All soil layers; only organic soil layers; only mineral soil layers
Nitrogen stock in each layer	All soil layers
Nitrogen stock of plot	All soil layers; only mineral soil layers

Table 2: The different linear models included in statistical analysis.

To account for the possibility of increased type I errors through multiple testing of the same dataset, we used a Benjamini-Hochberg procedure to reduce the *P* value (Benjamini and Hochberg, 1995; Pike, 2011). We collated all *P* values for linear models (41 in total); with a false discovery rate set at 5% the corrected significance *P* value was 0.027.

All data was analysed using R (R Core Team, 2018).

3 Results

3.1 pH

Management option significantly affected pH ($P < 0.0001$; Table 3). Conifer monoculture had the lowest average pH (4.36) while heathland had the highest average pH (6.53) (Figure 2). Pure broadleaved stands (i.e. broadleaved monoculture or mixture) had higher average pH than pure conifer stands (i.e. conifer monoculture or mixture). Post-hoc Tukey-Kramer comparisons showed that the pH of conifer monoculture was significantly lower than mixtures (where the primary component was broadleaved), pure broadleaved plots (i.e. monoculture or mixture), open and heathland sites. In addition, heathland sites had a pH significantly higher than open, mixtures (where the primary component was conifer) and pure conifer stands (Figure 2).

3.2 Total carbon and nitrogen concentrations

Both total carbon and total nitrogen concentrations significantly varied between soil layers (P < 0.0001 for both; Table 3). The forest litter and F layers had the highest average total carbon and total nitrogen concentrations (litter layer greatest for total carbon concentration, F layer greatest for total nitrogen concentration), followed by the grass layer, and then the mineral soil samples in order of depth (Figure 3). When a model was fitted solely to organic soil samples (i.e. litter, grass and F layers), management option had a significant effect on total carbon concentration (P < 0.0001; Table 3). Between management options the total carbon concentration in the organic samples of heathland and open sites were significantly lower than all the forested sites (Figure 4). There was the same pattern with total nitrogen concentration (P = 0.002), with the exception that the nitrogen concentration of the open sites was not significantly lower than the broadleaved monoculture sites.

3.3 C:N ratio

The C:N ratio significantly varied between soil layers (P < 0.0001; Table 3). Similarly to total carbon and total nitrogen concentrations, the litter layer had the greatest C:N ratio, followed by the F layer, grass layer and then mineral soil samples in order of increasing depth (Figure 3). Management option had a significant effect on the C:N ratio, both when all samples were included in the same model (P = 0.011) and when samples were split into organic and mineral layers (P = 0.003 and P = 0.0005, respectively, Table 3). In the organic layers, the pure conifer sites (conifer monoculture or mixture) had a significantly higher C:N ratio than heathland sites (Figure 4). In the mineral layers, the heathland sites had a significantly lower C:N ratio than all management options except the pure broadleaved sites (broadleaved monoculture or mixture). Additionally, pH had a significant effect on the C:N ratio for models including all layers or only mineral layers (P < 0.0001 for both) but not for only organic layers when the Benjamini-Hochberg correction factor was applied (Table 3); increasing pH was correlated with decreasing C:N ratio (Figure A.1).

Response variable	Data subset	Predictor variable		
		Management option	Soil layer	pH
pH	All plots	***	n.s.	
Total carbon concentration	All layers	n.s.	***	n.s.
	Only organic layers	***	‡	×
	Only mineral layers	n.s.	***	n.s.
Total nitrogen concentration	All layers	*	***	n.s.
	Only organic layers	**	‡	***
	Only mineral layers	n.s.	***	*
C:N ratio	All layers	*	***	***
	Only organic layers	**	‡	×
	Only mineral layers	***	**	***
Layer thickness	Only litter and F layers[#]	n.s.	*	***
Layer carbon stock	All layers	×	***	n.s.
Layer nitrogen stock	All layers	n.s.	***	n.s.
Total carbon stock	All layers	*		§
	Only organic layers	***		§
	Only mineral layers	n.s.		§
Total nitrogen stock	All layers	n.s.		§
	Only organic layers	***		§
	Only mineral layers	n.s.		§

*Table 3: Significance of predictor variables included in linear models for different data subsets. Symbols indicate significance as follows; n.s. not significant, × $P \leq 0.05$, * $P \leq 0.027$ (i.e. the Benjamini-Hochberg corrected significance level), ** $P \leq 0.01$, *** $P \leq 0.001$. Light grey shading indicates that variables were not included in the models, either because it was a key feature of the response variable or as indicated by the following symbols; ‡ not possible to test for influence of soil layer as plot management option determines which samples were collected (i.e. only grass in open sites), § pH varies across soil layers so not included. [#]The test for layer thickness included the plots with corresponding data, excluding open sites.*

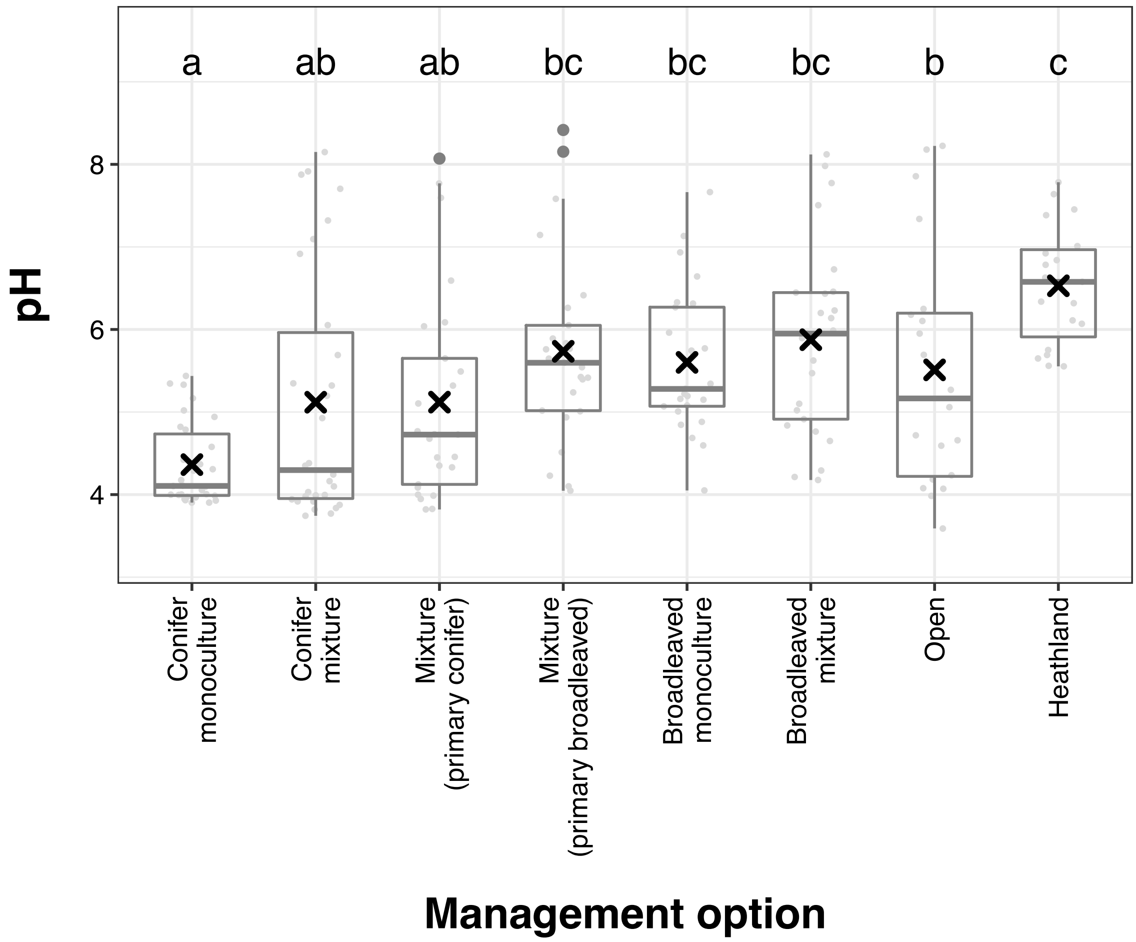

Figure 2: pH values for different management options. Letters show significant differences between groups (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different at P = 0.05. Black crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Light grey points show raw data points, dark grey points indicate values that are beyond the whiskers.

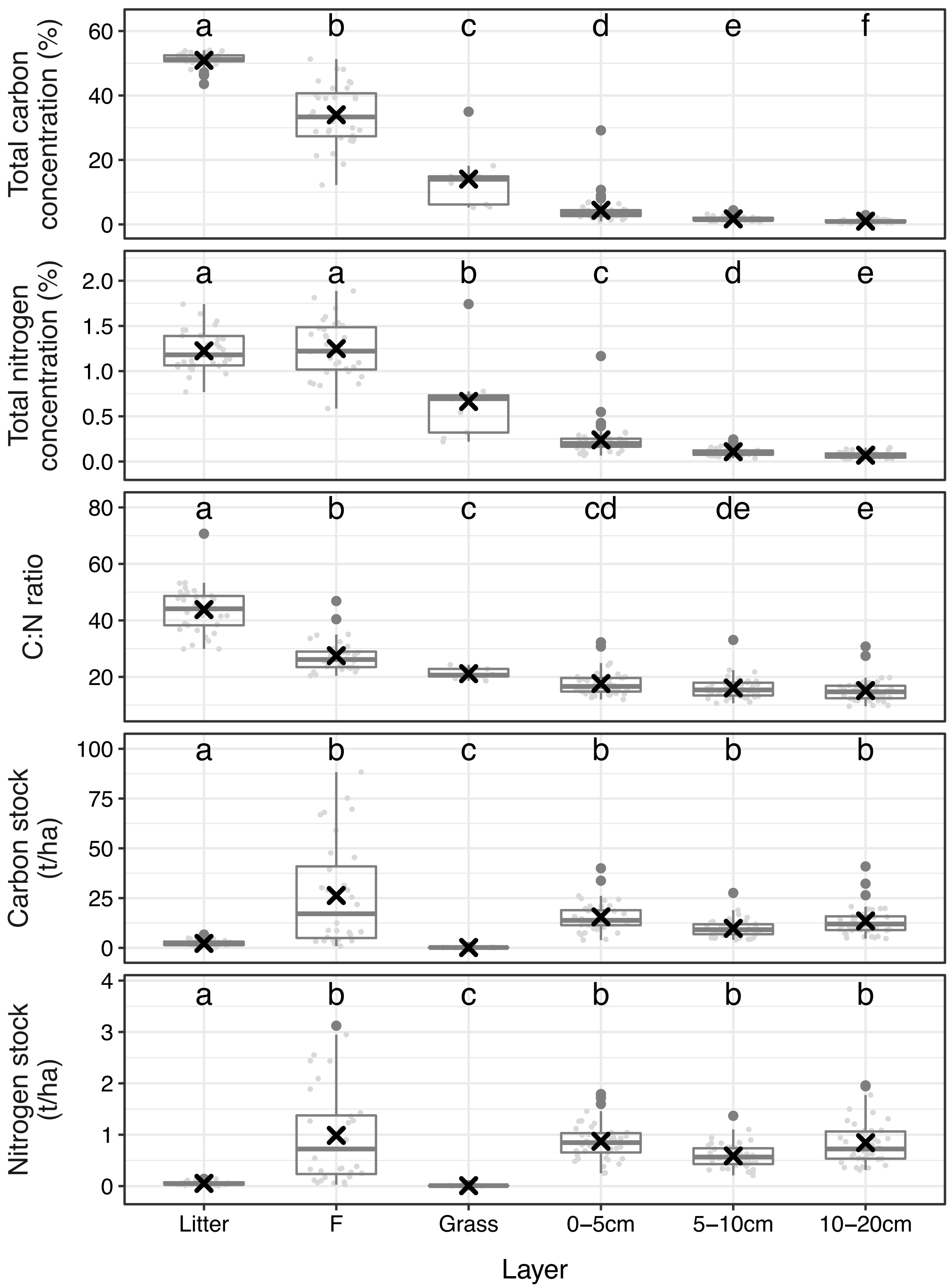

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Figure 3: Measured values for different layers across all management options. Letters show significant differences between groups (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different at P = 0.05. Black crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Light grey points show raw data points, dark grey points indicate values that are beyond the whiskers.

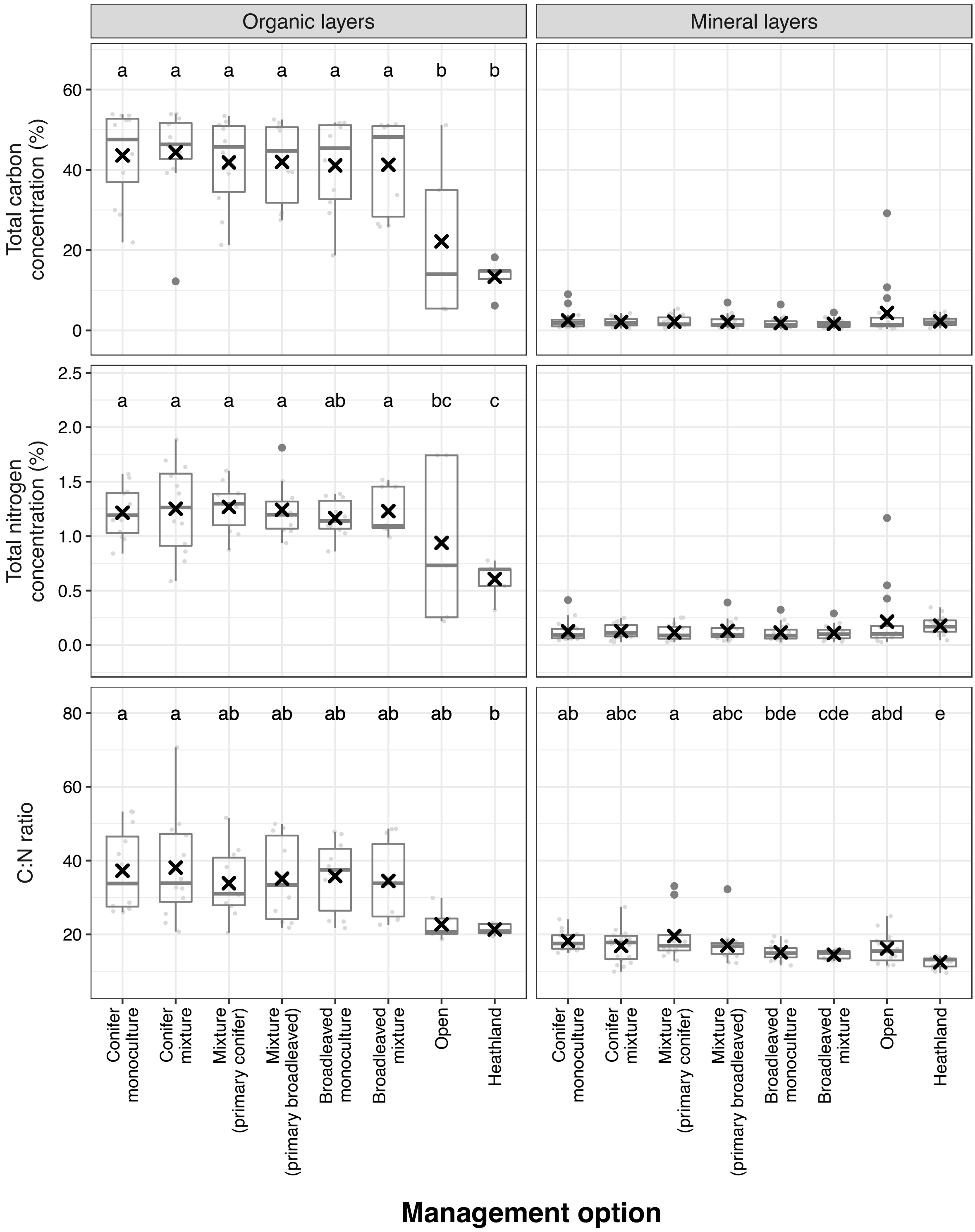
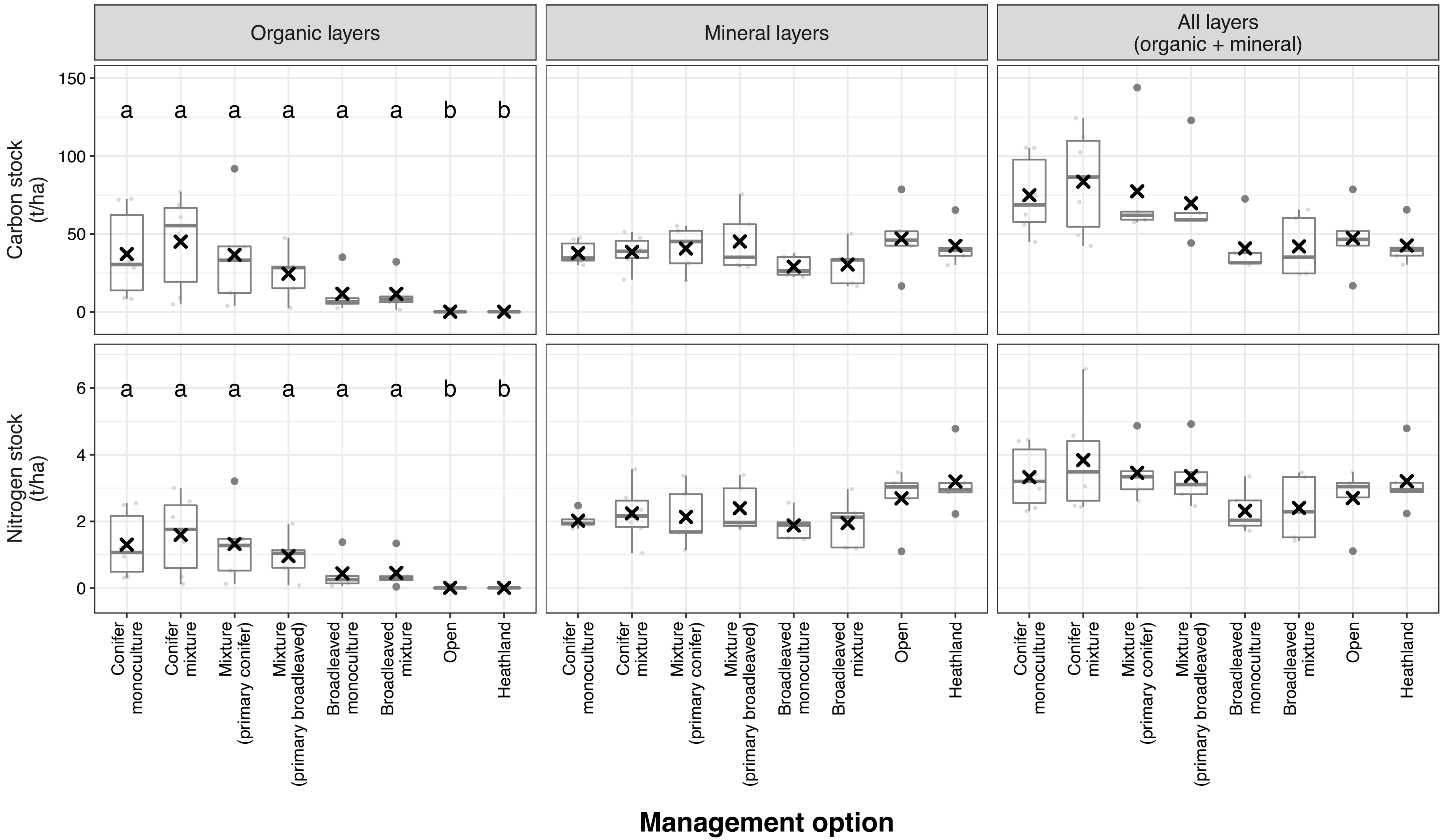


Figure 4: Carbon, nitrogen and C:N values for different management options. Data are displayed separately for organic and mineral layers. Letters show significant differences between groups (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different at P = 0.05. Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers. Light grey points show raw data points, dark grey points indicate values that are beyond the whiskers.



330 *Figure 5: Carbon and nitrogen stocks for different management options. Data are displayed separately for organic and mineral layers (1st and 2nd column) and then for all layers combined (3rd column). Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers. Light grey points show raw data points, dark grey points indicate values that are beyond the whiskers.*

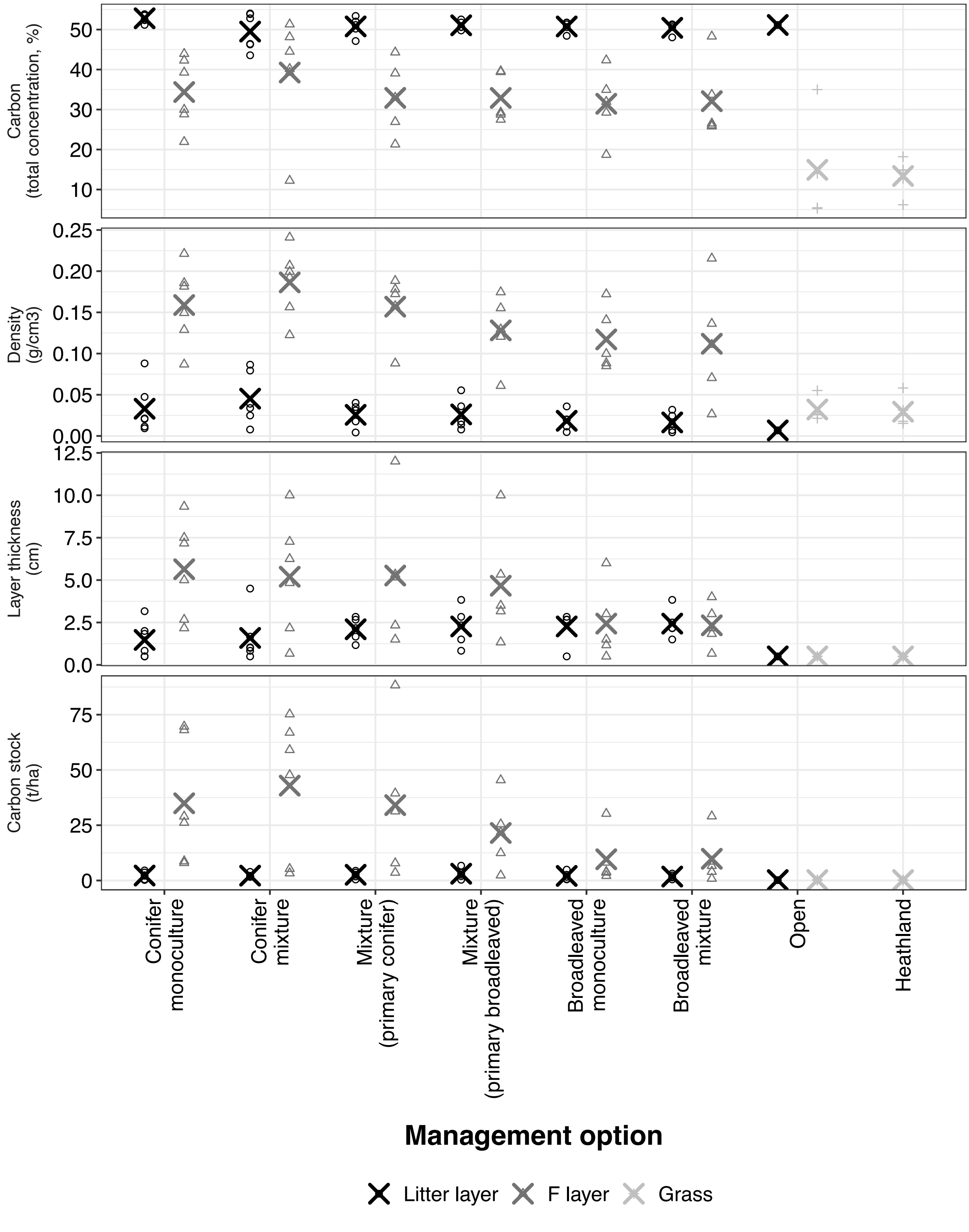


Figure 6: Carbon stock data of the organic layers of different management options. Total carbon stock (bottom panel) is the product of the carbon concentration (including organic and inorganic carbon), density and thickness of each layer. Individual data are indicated by the small points (circle – litter layer, triangle – F layer, cross – grass layer). Large diagonal crosses indicate means.

3.4 Depth of layers

Although management options with conifers appeared to have a thicker F layer than broadleaved sites, management option did not have a significant effect on layer thickness, although the soil layer type (whether it was litter or F) did (P = 0.013, Table 3). The overall average litter layer depth was 2.0 cm (range of 0.5-4.5 cm), whereas the F layer was generally deeper (overall average was 4.3 cm, range of 0.5-12.0 cm). Broadleaved mixture had the largest average litter layer depth (2.4 cm), whereas conifer monoculture had the smallest average litter layer depth (1.5 cm) (excluding the open site where there was scattered leaf litter) (Figure 6). In contrast, the opposite was true for F layer depth, with conifer monoculture having the greatest average thickness (5.6 cm) and broadleaved mixture having the smallest average thickness (2.3 cm) (Figure 6).

3.5 Carbon and nitrogen stocks

The carbon stock was greatest in the F layer for all plot types with a conifer component (i.e. pure conifer stands and mixtures), the 0-5 cm layer for pure broadleaved stands and the open plots, and the 10-20 cm layer for the heathland plots (Table A.2). Soil layer had a significant effect on layer carbon stocks, whereas management option did not at the Benjamini-Hochberg corrected significance level (Table 3, see Table A.3 for precise P values). When all types of management options were grouped together, a post-hoc Tukey-Kramer showed that overall the F layer and mineral soil layers had the largest carbon stock, followed by the litter layer; grass had the smallest stocks (Figure 3).

Nitrogen stocks followed a similar pattern. The nitrogen stock was greatest in the F layer for conifer stands and mixtures where the primary component was conifer, the 0-5 cm layer for mixtures where the primary component was broadleaved, pure broadleaved stands or open plots, and the 10-20 cm layer for the heathland plots (Table A.2). Soil layer had a significant effect on layer nitrogen stocks ($P < 0.0001$, Table 3); as for the carbon stocks the management option was not significant ($P = 0.063$, Table A.3). The Tukey-Kramer test showed differences between soil layers that followed the same pattern as for the carbon stocks (Figure 3).

When carbon stock and nitrogen stock were combined across all layers (i.e. mineral and organic) for each plot, conifer mixture had the greatest average total carbon and nitrogen stocks, followed by mixtures (where the primary component is conifer) (Figure 5). The pure broadleaved plots had the lowest total carbon and nitrogen stocks. The differences were so pronounced that, on average, conifer mixture had over twice the total carbon stock than broadleaved monoculture, and over 1.5 times the total nitrogen stock. Management option had a significant effect on total carbon stocks (although a post-hoc Tukey-Kramer test did not find any significant pairwise differences) but not total nitrogen stock (Table 3), due to extensive spatial variation.

In contrast, when only mineral soil layers were added together, open sites had the highest total carbon stock and heathland had the highest total nitrogen stock, and there was overall relatively little difference between management options (Figure 5, Table A.2). This demonstrates the importance of the organic soil layers – particularly the F layer – in determining the overall total carbon and nitrogen stocks in all forest management options. It had high total carbon and nitrogen concentration, and was also thicker and denser than the litter layer (Figure 3 and Figure 6). The thickness and density of the litter layer was so low that its contribution to total stocks was negligible (Figure 6), whereas for conifer mixture the F layer alone contributed a greater carbon stock than all the mineral layers combined.

4 Discussion

4.1 Soil pH

The results from this study support the general observation that afforestation lowers soil pH (Berthrong et al., 2009), with conifers having a greater acidification effect than broadleaves. We found that all sites managed as forest had a lower average soil pH than heathland sites, although this difference was significant only for sites that were entirely, or mostly, coniferous (Figure 2). In contrast to other studies we did not find a pH neutralisation effect of afforestation (Hong et al., 2018), although this was probably because no sites were initially acidic enough to show an increase in pH through afforestation.

We found evidence that the de-coniferisation of sites and reversion back to heathland was increasing soil pH back towards the pH of historical heathland. The open sites are part of a heathland reversion programme, which aims to restore habitats akin to sites that have always been open. These sites – which were cleared of forest approximately 15 years prior – had significantly higher soil pH than conifer monocultures (what most of these sites were before clearance), but with an average pH lower than broadleaved sites and significantly lower than the heathland sites (Figure 2). During clearance, high disturbance and clearing of the organic layers would have caused acidification, through both nitrification (resulting in the release of H^+) and subsequent leaching of anions (nitrites, NO_2^-, and nitrates, NO_3^-) as water input increased due to loss of canopy cover (Moffat et al., 2011). However, high soil disturbance events in Thetford Forest (such as tree stump harvesting) have been observed to increase soil pH through disturbance of chalk (Crow et al., n.d.). Our results suggest that at least partial recovery of soil pH is possible, although it remains to be seen whether, and over what timespan, pH reaches pre-afforestation levels. This has important ramifications for the conservation management objectives of the heathland reversion programme. Both calcareous and acidic heathland have high biodiversity value – Breckland is designated as a Special Area of Conservation for its varied dry heaths (Dolman et al., 2010; JNCC, 2005) – and they support different plant communities. These results demonstrate the importance of giving careful consideration to the type of heathland – acidic or calcareous – that is the objective of the intervention, as site choice, soil type and clearance operations have a crucial influence. For example, when creating calcareous heathland, selecting sites that have chalk closer to the surface and using clearance techniques that will expose and disturb the chalk may counter the acidification caused more generally through nitrification and leaching after forest clearance, and raise pH. In contrast, where acidic heathland is the objective, removing organic material and leaving the site fallow over the winter months when there will be high rainfall input would encourage leaching and further acidification of the site.

4.2 Carbon

When evaluating the capacity of a woodland to sequester and store carbon, consideration of the soil is essential, particularly as the soil carbon stock is often more substantial than the above-ground stock (De Vos et al., 2015; Vanguelova et al., 2013). Here we found that, although soil layer significantly affected total carbon concentration (with decreasing carbon concentration with depth) and layer carbon stock (Table 3), there was little difference between the mineral soil layers (Figure 3). Additionally, total carbon concentration in any of the mineral soil layers was very low compared to the litter and F layers. Although it was not possible to look at changes over time, these results suggest that carbon is only very slowly being transferred into mineral soil pools from the litter and F layers.

On heathland or cropland sites, there is some evidence from northern Europe that afforestation leads to significant increases in soil organic carbon stocks in the uppermost soil mineral layers (Bárcena et al., 2014). However, we found no significant effect of management option on either total carbon concentration or carbon stock within the mineral soil layers (Table 3). Results from other studies of existing UK forests also find either no, or small, increases in total carbon concentration and carbon stocks over time in upper soil layers (Alton et al., 2007; Benham et al., 2012; Chamberlain et al., 2010; Kirby et al., 2005; Ražauskaitė et al., 2020). Nevertheless, it is striking that there is such little incorporation of carbon into the mineral soils after almost a century of afforestation. This is likely to be due to the soil at the study site being sandy (so unable to easily bind and accumulate carbon) in combination with low regional rainfall (with very low drainage and hence limited leaching) and high average annual air temperature, which collectively make unfavourable conditions for soil carbon dynamics and incorporation (Vanguelova et al., 2010; Villada, 2013). According to the carbon saturation concept, there is an upper limit of stable soil organic carbon storage, dependent on soil textural and mineralogical properties (Six et al., 2002). The capacity and efficiency of a soil to sequester carbon is determined not just by the rate of carbon input, but also by the saturation deficit (how far a soil is from the carbon saturation) (Stewart et al., 2008, 2007). Furthermore, micro-environmental and disturbance factors that affect decomposition rates can reduce the effective carbon stabilisation capacity to below the theoretical carbon saturation level (Stewart et al., 2007). Sandy soils, with a very small fine fraction (clay and fine silt), appear to be very close to their carbon saturation (Angers et al., 2011). These concepts further explain why there was relatively little difference between the carbon content of the mineral soils, despite the higher input of carbon to forest soils compared to heathlands (visible in the accumulation of organic layers).

This lack of carbon incorporation into lower mineral soil layers is only likely to be exacerbated in future. The Breckland region has some of the highest dry deposition rates of ammonia in Great Britain, largely as a result of intensive pig and poultry farming in the region*,* with localised nitrogen deposition in Thetford Forest up to four times as high as the critical load (Sutton et al., 2001; Vanguelova et al., 2007; Vanguelova and Pitman, 2019). This can hinder organic matter decomposition and cycling, particularly in low quality litter (such as twigs, branches, and leaves or needles with high lignin content); while this may increase carbon storage in upper soil layers it will decrease transport of carbon into the lower mineral soil layers (Janssens et al., 2010; Vanguelova and Pitman, 2019). Additionally, soil carbon tends to be less stable in sandy textured soils such as those at our study site. Carbon in the mineral soil layers of sandy soils contain more labile and interaggregate carbon fractions and thus is less stable compared to carbon associated with clay minerals in heavy mineral soils, where stable carbon could make up to 70% of total carbon (Villada, 2013). This has further implications for the capacity of the site to sequester and store carbon in stable soil pools.

Our study has demonstrated the importance of the F layer in determining the soil carbon stock, especially under conifers, where F layer carbon stock was much greater than under broadleaves (Figure 6). This is in contrast to averaged findings from national studies but not a surprising result: conifers have lower litter quality and generally slower decomposition rates than broadleaves, which is exacerbated at our study site by the local soil and climatic conditions (Mayer et al., 2020; Vanguelova et al., 2013; Vanguelova and Pitman, 2009). Carbon stored in the F layer is particularly vulnerable to being lost through aeration or leaching if disturbed and under favourable environmental conditions. At Thetford Forest, such conditions could be introduced if the forest is felled and left cleared, for example during fallow periods before restocking or in heathland conversion. Given that the majority of the total carbon stock was in the F layer, this highlights the fragility of soil carbon accumulation, even after many decades of afforestation. The UK Forestry Standard outlines guidelines to minimise soil disturbance during forestry operations (Forestry Commission, 2017) – these results emphasise their importance if tree planting is to result in significant and stable carbon sequestration.

4.3 Nitrogen

Thetford Forest receives some of the highest nitrogen deposition in the United Kingdom (13-19 kg N ha^{-1} yr^{-1}, with hot spots up to 46 kg N ha^{-1} yr^{-1}) and various areas of the forest are nitrogen saturated (Guerrieri et al., 2015; Vanguelova et al., 2010; Vanguelova and Pitman, 2019). This is well above the critical nitrogen load for woodlands in the UK of 10-12 kg N ha^{-1} yr^{-1} (RoTAP, 2012) and the European threshold of nitrogen input at which there is likely to be significant shift in ectomycorrhizal fungi diversity (5-10 kg N ha^{-1} yr^{-1}) (van Der Linde et al., 2018). Increased nitrogen inputs to temperate forests can lead to soil acidification, increase leaching, affect understorey vegetation, vertically redistribute soil organic carbon pools and alter soil microbial communities and biomass (Forstner et al., 2019a, 2019b; Gundale et al., 2014; Morrison et al., 2016; Schleppi et al., 2017). Foliar sampling of pine trees in Thetford Forest has shown that, while some of the younger, actively growing trees in second planting rotations show nitrogen deficiency in needles, the majority of older trees have accumulated nitrogen in their needles to such an extent that nitrogen concentration is above the optimal level (Crow et al., n.d.). This may cause imbalances with other nutrients, such as phosphorus (Jonard et al., 2015; Prietzel and Stetter, 2010; Tarvainen et al., 2016). The results from our study support and add to these observations. Although there was no significant difference between the nitrogen stock of the F and mineral layers (as a product of the layers' thickness), the litter and F layers had significantly higher total nitrogen concentration than the mineral soil layers (Figure 3). As with carbon, while there is some evidence that nitrogen is being incorporated into the uppermost soil layers (the three mineral layers had significantly different total nitrogen concentrations, decreasing with depth), the majority of the high nitrogen input is clearly accumulating in the organic layers. In particular, the total nitrogen concentration of the F layer was more than five times greater than the 0-5 cm layer and almost 18 times greater than the 10-20 cm layer. In addition to the difficulty of incorporating nutrients into sandy soils due to lower binding capacity, this could be due to nitrogen addition inhibiting litter decomposition, particularly in low litter quality sites (for example, where lignin content is high, such as conifer needles) (Knorr et al., 2005).

These results have a range of important management implications. Low regional rainfall means that leaching is generally limited (Vanguelova et al., 2010). However, the sandy soil texture lends itself to extreme leaching events over prolonged wet periods. The accumulation of nitrogen could then lead to extremely high nitrate concentrations, with concerns for water quality issues (mean annual nitrate concentrations are three times the UK water drinking standard) (Vanguelova et al., 2010). Equally, disturbance of organic matter is likely to lead to mineralisation and associated long-term loss of nutrients from the system as it is not incorporated into the soil. Therefore, soil cultivation operations, such as ploughing, should be restricted as much as possible. As mineralisation and leaching is most likely after felling events due to a loss of canopy cover and increased rainfall input to the soil, it would also be advisable to leave areas fallow for as short a duration as possible and to schedule this for dry periods, and to use alternative to clearfell management such as shelterwood systems that maintain tree cover. Where sites are being permanently converted to heathland, leaching of nutrients is not so problematic as the conservation value of such sites is associated with nutrient poor soils (assuming the desired pH can also be achieved, as discussed above). However, in places where forestry continues to be the objective, loss of nutrients would reduce future productivity and undermine the viability of a site for forestry.

Conifers are more efficient scavengers of atmospheric pollutants than broadleaves (Vanguelova and Pitman, 2019). Tree planting is advocated as an effective way to reduce the environmental impacts of ammonia emissions from agriculture, by increasing dry deposition and reducing the long-range export of pollutants (Bealey et al., 2016). Targeted tree planting can be used to scavenge pollutants at their source and protect more vulnerable semi-natural habitats. Although we did not detect a significant difference in the total nitrogen concentration of mineral or organic layers between conifers and broadleaved management options, there was a clear and significant difference between the organic layers of the forested and the historical heathland sites (Figure 4). However, this did not translate into the mineral soil layers, with the heathland and open sites having the highest total nitrogen concentration and nitrogen stock (although this was not significant) (Figure 4 and Figure 5). In contemplating the use of afforestation to scavenge ammonia in this region, consideration must also be given to the potential for extreme leaching events as a result of locking up nitrogen in organic material and implications for other issues such as water quality.

4.4 C:N ratio

Different tree species are known to influence the C:N ratio of soil through variability in the lignin and nitrogen content of their leaf litter (Cools et al., 2014; Hansson et al., 2011; Vesterdal et al., 2008). The C:N ratio in the mineral soils was significantly lower in heathland sites than any management option that contained conifers (i.e. conifer monocultures or mixtures and conifer and broadleaved mixtures; Figure 4). Furthermore, the C:N ratios of the mineral soil layers of pure broadleaved stands (monocultures and mixtures) was significantly lower than mixtures (where the primary component was conifer), and the means were universally lower than pure conifer stands (although not significant due to high variation). This confirms the trend increasingly reported in other studies that a higher C:N ratio in mineral soils is found under conifers than broadleaves (Cools et al., 2014; Dawud et al., 2017). This is attributed to higher foliar and litterfall C:N ratios in conifers compared to broadleaves, due to greater nitrogen use efficiency by conifers and thus lower nitrogen content in litter (Dawud et al., 2017, 2016; Yang and Luo, 2011). Although our data did not show significant pairwise differences in organic layers between conifers and broadleaves, the mean C:N ratio of the litter layer was higher in conifers than broadleaves, supporting this hypothesis (Table A.4).

In combination with the effect of tree species, increasing pH had a negative effect on the C:N ratio, related to increasing mineralisation and decomposition of organic matter (Figure A.1). Less acidic soils (e.g. under broadleaves) have higher microbial diversity and therefore are expected to have more efficient nutrient cycling and higher organic matter decomposition. Our data support this generalisation, with soils under conifers being more acidic and having a higher C:N ratio than soils under broadleaves or open space. Soil acidity status has a pivotal role in organic matter and carbon cycling. Recovery from historical acidification has resulted in increased mineralisation and decomposition rates and thus release of stored carbon from both organic and mineral soils (Clark et al., 2011; Sawicka et al., 2016). This phenomenon should be taken into account in carbon cycling and the carbon budget accounting of alternative land use change scenarios.

5 Conclusions

Afforestation is widely promoted as a tool for both climate mitigation and increasing soil quality. In this study, combining the different indicators commonly used for soil quality does not give a unified indication of the effects of different management options. Higher carbon and nitrogen concentrations were found in the organic layers of forested sites but a lower C:N ratio was observed in the heathland sites. Overall, the differences between alternative afforestation options were marginal. In terms of carbon sequestration, despite a significant accumulation of carbon in the organic layers under forest, this did not translate to the mineral soil layers and greater carbon storage stability. The soils at our study site are sandy in texture and low quality, so not amenable to change through land management. While our results are therefore not entirely surprising in the local context, it is striking how little change has occurred in soil chemistry despite nearly a century of afforestation. This is particularly salient given the current emphasis on tree planting to tackle climate change; soil properties must be a key consideration if afforestation is to be an effective strategy for long-term carbon sequestration and stable storage.

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Appendix A. Supplementary material

Table A.1: Full information on plots visited

Category	Species composition (year of planting)	No. of species	Area (ha)	Average GPS point of sub-plots	
				Longitude	Latitude
Conifer monoculture	100% Scots pine (1960)	1	2.65	580928.3	288735
Conifer monoculture	100% Corsican pine (1965)	1	4.22	580956.7	290745
Conifer monoculture	100% Scots pine (1927)	1	5.06	581648.3	291781.7
Conifer monoculture	100% Douglas fir (1928)	1	8.82	580990	287222.5
Conifer monoculture	100% Hybrid larch (1999)	1	3.96	578502.5	282080
Conifer monoculture	100% Weymouth pine (1964)	1	0.53	580797.5	276760
Conifer mixture	42% Grand fir (1966), 40% Corsican pine (1966), 18% Scots pine (1929)	3	5.65	576203.3	291816.7
Conifer mixture	48% Scots pine (1970), 48% Corsican pine (1970), 4% mixed conifers (1926)	3+	9.2	583660	283445
Conifer mixture	40% Corsican pine (1911), 40% Scots pine (1911), 20% Douglas fir (1911)	3	2.66	588717.5	287752.5
Conifer mixture	50% Scots pine (1927), 30% European larch (1927), 20% Douglas fir (1927)	3	2.66	579562.5	306040
Conifer mixture	45% Scots pine (1995), 35% Corsican pine (1995), 10% European silver fir (2014), 10% Douglas fir (2014)	4	4.55	581785	282435
Conifer mixture	60% Douglas fir (1932, 1980), 40% Grand fir (1932, 1980)	2	5.49	581130	290962
Broadleaved monoculture	100% Sweet chestnut (1979)	1	4.56	579675	293280
Broadleaved monoculture	100% Eucalyptus (1980)	1	2.76	580018.8	290111.3
Broadleaved monoculture	100% Oak (1933)	1	2.76	595350	283942.5
Broadleaved monoculture	100% Beech (1932)	1	4.55	595650	283410
Broadleaved monoculture	100% Birch (1953)	1	2.61	583887.5	273995
Broadleaved mixture	50% Beech (1949), 20% Ash (1949), 25% mixed broadleaves (1900, 1985), 5% Oak (1850)	5+	6.33	579495	289457.5

Broadleaved mixture	51% Beech (1939), 29% Sycamore (1900), 20% Oak (1900)	3	3.86	582744	286330
Broadleaved mixture	50% mixed broadleaves (1975), 25% Lime (1966), 25% Sycamore (1966)	3+	3.21	597100	283902.5
Broadleaved mixture	49% Oak (1970), 33% Beech (1960), 11% Ash (1970), 7% Sycamore (1970)	4	5.92	598175	284430
Broadleaved mixture	80% Beech (1951, 1960), 11% Birch (1951), 9% Sycamore (1951)	3+	3.43	581375	272940
Mixed (primary conifer)	53% Scots pine (1932), 26% mixed broadleaves (1932), 21% Ash (1932)	3+	9.38	580764	290822
Mixed (primary conifer)	60% Scots pine (1930), 30% Sycamore (1985), 10% Sweet chestnut (1975)	3	4.72	581530	291937.5
Mixed (primary conifer)	50% European Larch (1926), 30% Scots pine (1926), 20% Beech (1926)	3	16.55	583777.5	283507.5
Mixed (primary conifer)	50% Corsican pine (1988), 45% Scots pine (1988), 5% Birch (1988)	3	13.87	588940	288252.5
Mixed (primary conifer)	49% Scots pine (1938), 25% Oak (1938), 20% Beech (1938), 6% Sweet chestnut (1938)	4	8.83	597257.5	284752.5
Mixed (primary broad)	40% Beech (1907, 1950), 29% European larch (1907), 20% Scots pine (1907), 11% Douglas fir (1907)	4	5.29	579165	284820
Mixed (primary broad)	54% Beech (1948), 30% Scots pine (1948), 10% Oak (1948), 6% Birch (1948)	4	7.14	580524	288210
Mixed (primary broad)	40% Sweet chestnut (1975), 30% Scots pine (1927), 15% mixed broadleaves (1975), 15% Sycamore (1990)	4+	2.76	581757.5	291905
Mixed (primary broad)	50% Oak (1934), 40% Scots pine (1934), 10% Beech (1934)	3	3.61	597245	285055
Mixed (primary broad)	60% Beech (1910), 25% Corsican pine (1955), 15% Scots pine (1955)	3	3.95	583075	274050
Open			17.72	577212.5	294127.5
Open			13.28	575225	289282.5
Open			10.18	578322.5	293305
Open			4.42	582170	287920
Open			8.21	598240	283240
Heathland			10.3	577465	294125
Heathland			2.36	580838	275722
Heathland				575810	288102.5
Heathland				591544	288162
Heathland				584905	279600

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Table A.2: Mean layer stocks for carbon and nitrogen. Means are calculated across all plots in tonnes per hectare. Numbers in brackets are the standard deviation. Grey highlighting indicates the soil layer with the greatest stock for each management option.

Carbon

Soil layer	Conifer monoculture	Conifer mixture	Mixture (primary conifer)	Mixture (primary broadleaved)	Broadleaved monoculture	Broadleaved mixture	Open	Heathland
Litter layer	2.24 (1.69)	2.19 (0.85)	2.58 (1.53)	3.05 (2.35)	2.06 (1.8)	1.77 (1)	0.17 (NA)	NA
Grass	NA	NA	NA	NA	NA	NA	0.19 (0.13)	0.18 (0.07)
F layer	34.92 (27.67)	42.9 (31.27)	34.09 (33.89)	21.49 (16.1)	9.6 (11.74)	9.82 (11.14)	NA	NA
0-5cm depth	16.84 (4.84)	9.83 (3.47)	17.26 (5.44)	18.31 (4.7)	12.84 (5.67)	12.26 (5.1)	23.41 (13.94)	14.54 (5.67)
5-10cm depth	9.46 (2.86)	11.89 (8.17)	10.28 (4.06)	9.95 (4.96)	6.61 (2.05)	7.93 (3.19)	10.25 (5.17)	11.68 (2.03)
10-20cm depth	11.42 (2.27)	16.78 (8.84)	13.16 (5.98)	16.94 (13.83)	9.64 (3.89)	10.26 (5.86)	13.46 (6.51)	16.19 (6.95)
Organic layers total	37.16 (28.94)	45.09 (30.83)	36.66 (34.46)	24.54 (16.76)	11.67 (13.30)	11.59 (11.96)	0.24 (0.21)	0.18 (0.07)
Mineral layers total	37.72 (7.54)	38.50 (10.85)	40.71 (14.83)	45.19 (20.19)	29.09 (6.80)	30.45 (13.70)	47.12 (22.18)	42.42 (13.51)
All layers total	74.87 (25.56)	83.60 (34.29)	77.38 (37.30)	69.74 (30.59)	40.76 (18.02)	42.04 (19.60)	47.31 (22.13)	42.60 (13.50)

Nitrogen

Soil layer	Conifer monoculture	Conifer mixture	Mixture (primary conifer)	Mixture (primary broadleaved)	Broadleaved monoculture	Broadleaved mixture	Open	Heathland
Litter layer	0.05 (0.04)	0.05 (0.02)	0.07 (0.05)	0.07 (0.05)	0.05 (0.04)	0.04 (0.02)	0.01 (NA)	NA
Grass	NA	NA	NA	NA	NA	NA	0.01 (0.01)	0.01 (0.003)
F layer	1.25 (0.97)	1.55 (1.20)	1.26 (1.18)	0.90 (0.67)	0.39 (0.50)	0.41 (0.49)	NA	NA
0-5cm depth	0.81 (0.18)	0.56 (0.22)	0.88 (0.36)	0.97 (0.32)	0.79 (0.32)	0.78 (0.28)	1.21 (0.54)	1.05 (0.39)
5-10cm depth	0.52 (0.11)	0.66 (0.39)	0.53 (0.21)	0.53 (0.20)	0.45 (0.14)	0.52 (0.19)	0.57 (0.20)	0.91 (0.13)
10-20cm depth	0.69 (0.13)	1.02 (0.56)	0.73 (0.37)	0.89 (0.55)	0.63 (0.23)	0.65 (0.32)	0.91 (0.39)	1.24 (0.54)
Organic layers total	1.30 (1.00)	1.69 (1.19)	1.32 (1.19)	0.96 (0.68)	0.44 (0.54)	0.46 (0.51)	0.01 (0.01)	0.01 (0.003)
Mineral layers total	2.02 (0.24)	2.24 (0.86)	2.13 (0.92)	2.40 (0.74)	1.88 (0.44)	1.95 (0.76)	2.69 (0.93)	3.20 (0.95)
All layers total	3.33 (0.94)	3.84 (1.58)	3.46 (0.86)	3.36 (0.95)	2.32 (0.67)	2.41 (0.97)	2.70 (0.93)	3.20 (0.95)

Response variable	Data subset	Predictor variable		
		Management option	**Soil layer**	**pH**
pH	All layers	<0.0001	0.2265	NA
Total carbon concentration	All layers	0.2927	<0.0001	0.1464
	Only organic layers	<0.0001	NA*	0.0400
	Only mineral layers	0.3417	<0.0001	0.8391
Total nitrogen concentration	All layers	0.0266	<0.0001	0.1760
	Only organic layers	0.0024	NA*	<0.0001
	Only mineral layers	0.0971	<0.0001	0.0144
C:N ratio	All layers	0.0113	<0.0001	<0.0001
	Only organic layers	0.0031	NA*	0.0439
	Only mineral layers	0.0005	0.0015	<0.0001
Layer thickness	Only litter and F layers (plots with corresponding data, excluding open sites)	0.0955	0.0132	<0.0001
Layer carbon stock	All layers	0.0424	<0.0001	0.1349
Layer nitrogen stock	All layers	0.0636	<0.0001	0.3686
Total carbon stock	All layers	0.0134	NA	NA[+]
	Only organic layers	<0.0001	NA	NA[+]
	Only mineral layers	0.4887	NA	NA[+]
Total nitrogen stock	All layers	0.1545	NA	NA[+]
	Only organic layers	<0.0001	NA	NA[+]
	Only mineral layers	0.2688	NA	NA[+]

*Table A.3: P values for the significance of predictors in all linear models. Dark grey shading indicates significance at the Benjamini-Hochberg corrected significance level (0.027); light grey shading indicates significance at the traditional P = 0.05 significance level. * Not possible to test for influence of soil layer as plot management option determines which samples were collected (i.e. only grass in open sites). + pH varies across soil layers so not included.*

Table A.4: Average C:N ratio of different samples. Values are mean ± standard deviation.

Depth	Conifer monoculture	Conifer mixture	Mixture (primary conifer)	Mixture (primary broadleaved)	Broadleaved monoculture	Broadleaved mixture	Open	Heathland
Litter layer	47.16 ± 6.08	45.54 ± 14.75	41.11 ± 7.40	45.29 ± 5.50	42.82 ± 5.12	42.83 ± 7.42	29.89 ± NA	NA
Grass	NA	NA	NA	NA	NA	NA	20.93 ± 2.40	21.32 ± 1.60
F layer	27.35 ± 1.14	30.64 ± 9.64	26.61 ± 3.94	24.92 ± 3.30	28.81 ± 8.30	26.13 ± 4.36	NA	NA
0-5cm depth	20.28 ± 2.23	17.47 ± 3.01	20.48 ± 6.08	20.33 ± 6.75	15.87 ± 2.07	14.97 ± 0.85	17.82 ± 4.80	13.54 ± 0.66
5-10cm depth	17.77 ± 2.18	16.80 ± 3.33	19.71 ± 7.68	15.69 ± 1.63	14.75 ± 2.28	14.37 ± 1.12	16.70 ± 40	12.19 ± 1.25
10-20cm depth	16.59 ± 1.75	16.35 ± 6.75	18.45 ± 7.05	14.91 ± 2.64	14.79 ± 2.62	14.13 ± 1.41	13.97 ± 2.59	11.54 ± 1.81

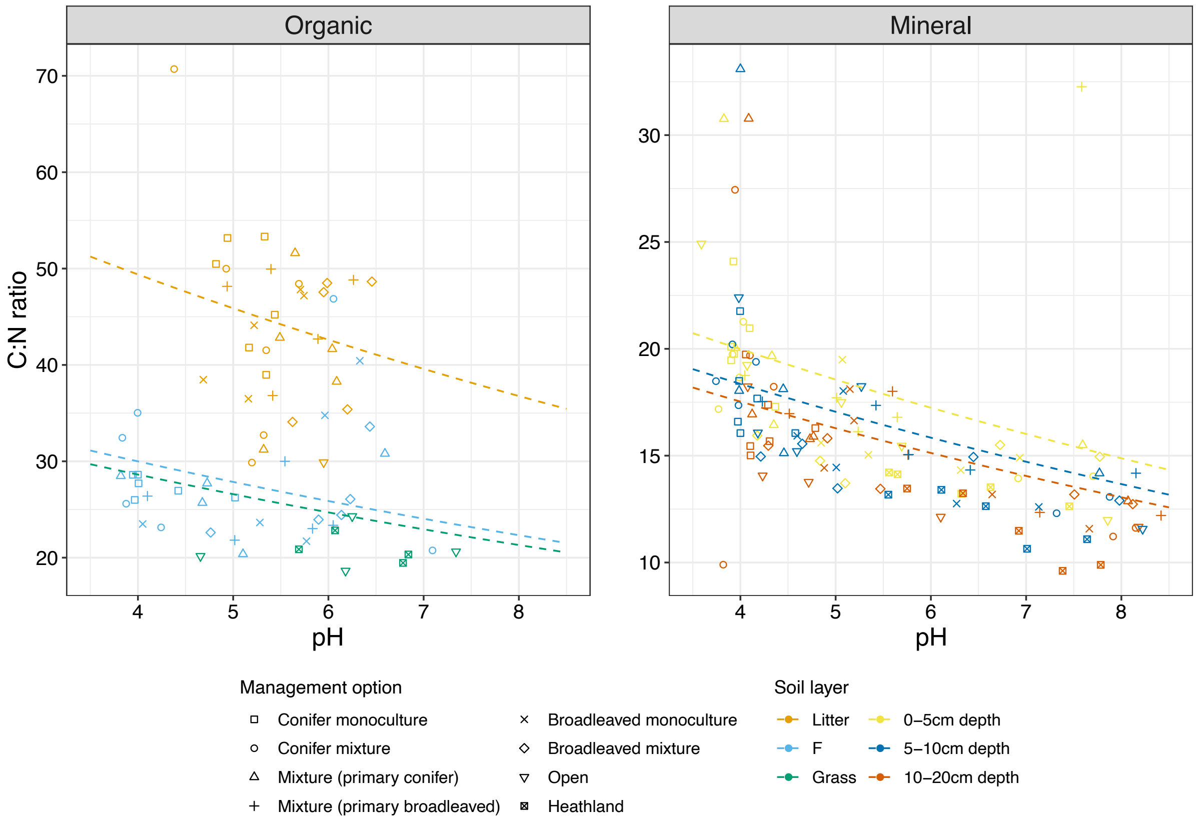

Figure A.1: Relationship between pH and the C:N ratio. Dashed lines indicate the predicted relationship from the fitted linear model for each soil layer (with the management option held as mixed (primary broadleaved) for illustration).