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Soil carbon in the South Atlantic United States: Land use change, forest management, and physiographic context

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ABSTRACT

Evidence-based forest carbon (C) management requires identifying baseline patterns and drivers of soil organic carbon (SOC) stocks, and their responses to land use change and management, at scales relevant to landowners and resource professionals. The growth of datasets related to SOC, which is the largest terrestrial C pool, facilitates use of synthesis techniques to assess SOC stocks and changes at management-relevant scales. We report results from a synthesis using *meta*-analysis of published studies, as well as two large databases, in which we identify baseline patterns and drivers, quantify influences of land use change and forest management, and provide ecological context for distinct management regimes and their SOC impacts. We conducted this, the fourth in a series of ecoregional SOC assessments, for the South Atlantic States, which are disproportionately important to the national-scale forest C sink and forest products industry in the U.S. At the ecoregional level, baseline SOC stocks vary with climatic, topographic, and soil physical factors such as temperature and precipitation, slope gradient and aspect, and soil texture. Land use change and forest management modestly influence SOC stocks. Reforestation on previously cultivated lands increases SOC stocks, while deforestation for cultivation has the opposite effect; for continuously forested lands, harvesting is associated with SOC increases and prescribed fire with SOC declines. Effects of reforestation are large and positive for upper mineral soils (+30%) but not detectable in lower mineral soils. Negative effects of prescribed fire are due to significant C losses from organic horizons (-46%); fire and harvest have no impacts on upper mineral soils but both increase SOC in lower mineral soils (+8.2 and +46%, respectively, with high uncertainty in the latter). Inceptisols are generally more negatively impacted by prescribed fire or harvest than Ultisols, and covariance between inherent factors (including soil taxonomy) and management impacts indicates how interior vs. coastal physiographic sections differ in their management regimes and SOC trends. In the cooler, wetter, topographically rugged interior hardwood forests, which have larger baseline SOC stocks, prescribed fire and even light harvesting generally decrease SOC; in contrast, intensively managed coastal plain pine plantations begin with small initial SOC stocks, but exhibit rapid gains over even a single rotation. This covariance between place (physiography) and practice (management regime) suggests that distinct approaches to forest C management may be complementary to other ecological or production goals, when implemented as part of wider (e.g., state-level) forest C or climate policy.

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1. Introduction

Soil organic carbon (SOC) is important because it is connected to soil properties, biogeochemical and hydrologic processes fundamental to forest ecosystems, and the fiber, fuel, and food that they provide humanity (Nave et al., 2019a; Vance, 2000). Recognizing that SOC is critically important within ecosystems and increasingly connected to strategies to mitigate climate change, there is growing interest in the potential impact of land use change and forest management on SOC (Harden et al., 2018).

A mature and extensive review literature has reported the general effects of land use change and forest management on SOC (e.g., Certini, 2005; Dignac et al., 2017; James and Harrison, 2016; Jandl et al., 2007; Mayer et al., 2020; Post and Kwon, 2000; Smith et al., 2016). Numerous review papers have quantified the direction, magnitude, and variability in management effects upon SOC, as well as their drivers at broad scales (Laganiere et al., 2010; Lorenz and Lal, 2014; Nave et al., 2010; 2011; Thiffault et al., 2011). Nevertheless, these papers that have contributed so much to our foundational understanding consistently identify a substantial knowledge gap between broad syntheses and site-level studies. This knowledge gap between synthesis and specificity thus requires research to address SOC management at intermediate scales, which are often the focus of decision making by landowners, forest managers, and policy makers.

It has recently become possible to use synthesis approaches to address SOC management at intermediate to localized scales, thanks to increased data availability and the flexibility of the approaches themselves. For example, *meta*-analysis quantifies major treatment effects by synthesizing across individual studies, while using minor differences within and between studies to provide insights into the factors that drive differences in those effects (Hedges et al., 1999). However, even data-rich *meta*-analyses are constrained by the specific studies they synthesize, making them good for identifying trends at select sites, but unable to address the diversity of conditions across intervening spaces (Gurevitch et al., 2001). With this limitation in mind, it is possible to use more extensive observational data (e.g., soil survey or forest inventory programs) to validate and contextualize *meta*-analysis results. Observational datasets lack experimental control, may not possess desired auxiliary variables, and introduce other sources of variation that may obscure or confound treatments of interest. Nonetheless, these observational data enable comparisons and inferences over those intervening areas that have not been reported in the literature, and furthermore, auxiliary variables can be obtained from other sources to create datasets that complement *meta*-analysis in scale, scope, and approach (Fick et al., 2020). This combined approach has proven useful for downscaling soil C management assessments from broad patterns (e.g., Nave et al., 2010, 2018) to the physiography, land use and management regimes of distinct ecoregions (Nave et al., 2019b, 2021, 2022), and promises to find applications in still more.

The South Atlantic U.S. is a physiographically and biologically diverse region, and its forests are disproportionately important to the forest-based economy and land sector C budget of the U.S. as a whole. From mountains to piedmont and coastal plain to seacoast, the forests of North and South Carolina alone represent 5% of the forest land in the conterminous U.S. (CONUS), despite these two states representing under 3% of the land area. On an annual basis, forests of North and South Carolina comprise 7% of the annual U.S. forest sector C sink, which overall offsets the equivalent of more than 11% of annual U.S. greenhouse gas emissions (Domke et al., 2021). More broadly, the southern U. S. produces nearly 2/3 of U.S. timber, much of which comes from its nearly 170,000 km^2 of managed plantations, which are 71% of all planted U.S. forestland (Wear and Greis, 2013; Oswalt et al., 2019). Coastal plain plantations of loblolly pine (*Pinus taeda*) and other pines are optimized and intensively managed to produce wood products over harvest rotations that are among the shortest in North America due to the region's warm, humid climate (Fox, 2000). The slower growing, mixed mesophytic forests in the cooler, topographically rugged interior of the region also support a significant forestry industry (Griffith et al., 2003; Napton et al., 2010).

Forest C stocks of the South Atlantic States are, like most ecoregions, dominated by soils. For reference, in North and South Carolina, soils to a depth of 1 m hold more than 46% of the forest C, compared to 39% in aboveground live biomass (Domke et al., 2021). Thus, understanding the role of land use and management in the land sector C budget of the South Atlantic States requires assessing baseline stocks and stock changes, and placing both in the context of how C persists, or is emitted, from forests themselves and through related land sector activities occurring outside their boundaries. In this region, which generates tremendous volumes of long-lived forest products (e.g., dimensional lumber, manufactured wood) but also large amounts of short-lifetime forest products (e.g., pine litter, bioenergy pellets), whole systems assessments are as needed as insights into how management impacts soils-the dominant C pool within the region's forest ecosystems (Buchholz et al., 2021; Lan et al., 2020). The present synthesis, representing the fourth in a series of ecoregional assessments, is intended to contribute to this progress in the South Atlantic States. It was motivated by four objectives. First, identify baseline controls, land use and management effects on SOC stocks at an ecoregional scale. Second, quantify how forestry and prescribed fire influence SOC stocks by examining ecoregional patterns in greater detail. Third, place management impacts in ecological context, and fourth, discuss how C management can align with forest management at strategic (e.g., policy) to tactical (e.g., best management practices or BMP's) levels.

2. Methods

2.1. Study area

The South Atlantic States of North Carolina (NC) and South Carolina (SC) were the focus of this study, which targets these two states for policy and planning purposes but encompasses a wider ecological definition of the region. We synthesized data from all seven of the ecological sections present in the two states, as extending into adjacent and nearby states with regionally consistent physiography and climate, collectively covering much of Georgia (GA), Virginia (VA), and Delaware (DE), and including portions of Florida (FL), Tennessee (TN), and Maryland (MD; Fig. 1). Ecological Sections tier beneath the Province level in the U.S. Department of Agriculture-Forest Service (USDA-FS) ECOMAP hierarchical ecosystem classification system (Cleland et al., 1997; McNab et al., 2007). Section descriptions are beyond the scope of this paper and are available in McNab et al. (2007).

Briefly, the climate of the study area ranges from warm temperate to subtropical, with short, mild winters, and long, hot summers (mean annual air temperature 12-18°). Precipitation is abundant and evenly distributed throughout the year (mean annual precipitation 1,000–1,500 mm). Forests are the dominant natural vegetation type and consist of mixed mesophytic, oak-hickory, oak-pine, and pine-dominated cover types. These climate and vegetation patterns grossly follow a soil physiographic transition from the cool, wet, topographically rugged interior (mountain and piedmont) ecological sections, where Inceptisols formed in the residuum and colluvium of acid metamorphic rock are dominant, to the increasingly level marine deposits of the coastal plain ecological sections, where Ultisols and Entisols are the dominant soils (McNab et al., 2007; Miller and Robinson, 1994; West, 2000).

2.2. Approach

Our analysis used synthesis methods detailed in prior assessments (Nave et al., 2019b; 2021; 2022). These included: (1) effect size *meta*-analysis of data from published literature; (02) synthesis of soil pedon observations with remote sensing information; (3), analysis of national

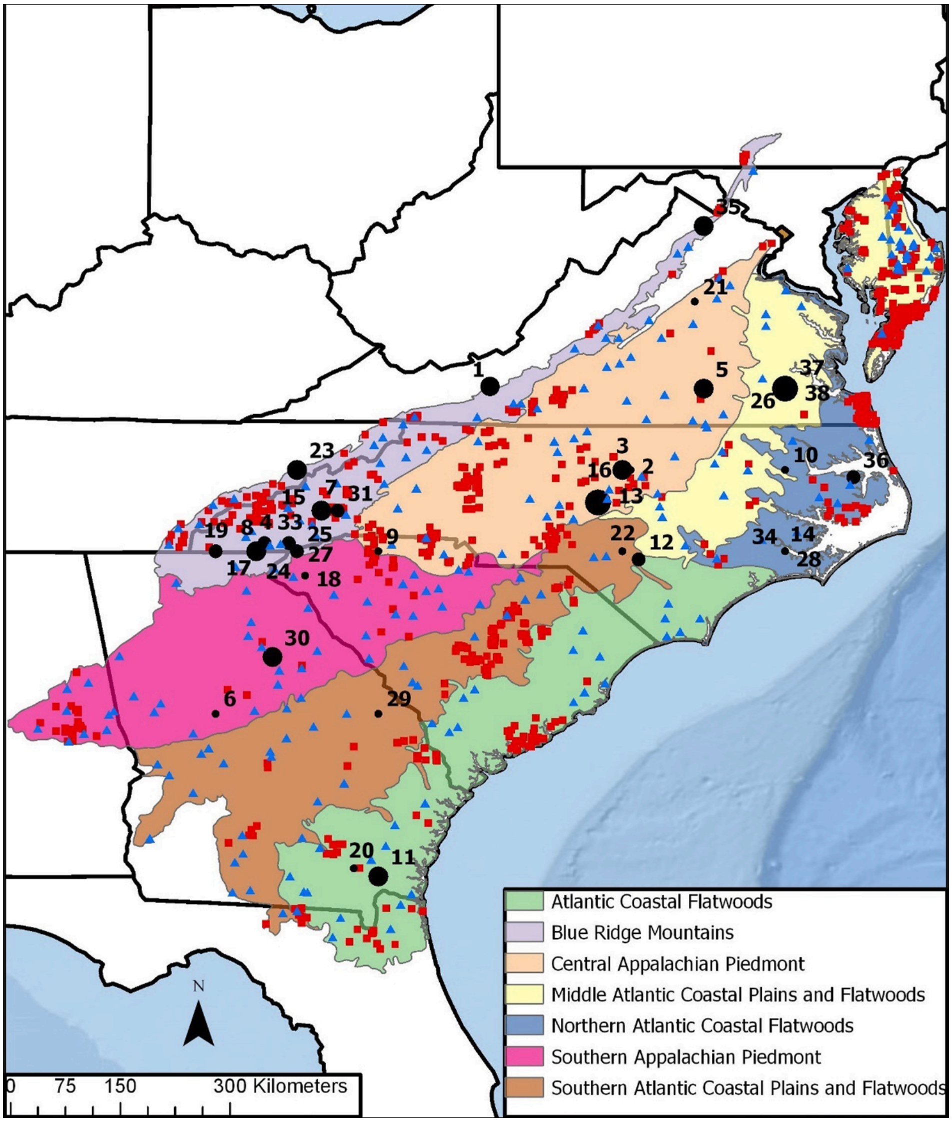

Fig. 1. Map of study area. Shaded polygons are ECOMAP Ecological Sections. Numbered point locations, which are approximate, represent papers reviewed for the *meta*-analysis (see Supplementary material). The two smaller point sizes are papers with ecosystem-specific and landscape-level designs, respectively; the two larger point sizes are papers with sites arrayed across a subregional or regional scale, respectively. Red squares and blue triangles show locations of NRCS pedons (see section 2.4), and NFI plots (approximate; see section 2.5), respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forest inventory (NFI) data from plots in which soils, biomass, and other ecosystem properties were measured. We summarize these methods below.

2.3. Meta-analysis

We synthesized data from 38 papers identified through literature review, published between 1970 and 2019 (identified with a corresponding superscript in the References). As with our prior *meta*-analyses, we followed a predetermined protocol for assessing each publication to determine suitability. To be included, each paper had to: 1) report control and treatment values for SOC stocks or concentrations for at least one treatment of interest, 2) provide adequate metadata to constrain locations and use as potential predictor variables, 3) present response data not included in previous studies, and 4) be located within the study footprint. We extracted control and treatment SOC values from all 38 papers and used these to calculate effect sizes (as the ln-transformed response ratio *R*). As in our other published *meta*-analyses, these response ratios span a wide range of forest types, soil depths, amount of time elapsed since experimental treatments, and other sources of variation, both known and unknown. Additionally, it is important to note that response ratios calculated for effect size *meta*-analysis are sensitive to how the control condition is defined. For example, published papers comparing SOC stocks from harvested vs. non-harvested forests span a wide range of experimental treatments, and also a wide range in what is defined as the “control” or non-harvested forest: in some cases, the control may be a plantation that has not been harvested in 40 years, in other, a forest that has not been harvested in 100, and still another, a forest whose management or disturbance history is unknown but includes no recent harvest. We generated effect sizes and bootstrapped 95% confidence intervals (Hedges et al., 1999) using MetaWin software (Sinauer Associates, Sunderland MA, USA). We chose unweighted *meta*-analysis to maximize data availability (weighted *meta*-analyses require sample size and variance statistics that are often not reported), and because we did not assume that the data met the parametric preconditions of a weighted *meta*-analysis. Treatments of interest included fire management (all publications in this region reported prescribed fire), silvicultural operations (harvesting, site preparation, stand management treatments), and land use change (i.e., reforestation, deforestation, wetland restoration).

SOC stock (Mg C ha^{-1}) was our response variable of interest. When data were not reported in those units we converted them, as needed, using the same approach as other recent assessments (Nave et al., 2019b, 2021, 2022). We converted loss on ignition values to %SOC using a fixed factor (0.5; 26 of 328 total response ratios). For studies that reported SOC concentration (%SOC; 78 of 328 total) rather than SOC stock, we used prediction equations to derive bulk density (Db) from horizon designation or %SOC, in order to calculate SOC stocks. Identically to other published assessments, we used data from the Natural Resources Conservation Service (NRCS) National Cooperative Soil Survey (NCSS) Database to predict missing Db values. We gap-filled missing Db values for O horizons based on subhorizon designation (0.11, 0.14, and 0.18 g cm^{-3} for Oi, Oe, and Oa horizons, respectively), or if not specified, 0.28 g cm^{-3} for the O horizon as a whole, based on n = 233O horizons drawn from the database. Importantly, this expression of Db was db_fmst (oven-dry sample mass / field-moist sample volume). For mineral soils, we used only samples drawn from our study area possessing both %SOC and Db (db_od; g cm^{-3} of the fine earth fraction; (n = 2,887). We tested a variety of model forms, ultimately selecting the exponential decay model, which had the best fit: (Db = 0.4503*exp(14.0316/(%SOC + 10.6286), $P < 0.0001$; $r^2 = 0.43$; range 0.42 – 2.46 g cm^{-3}; standard error of estimate 0.186 g cm^{-3}).

We extracted predictor variables from each paper to test factors potentially influencing treatment effects on SOC stocks. We looked up missing information (e.g., study site characteristics) in other publications from the same sites, or using information about the soil series reported from those study sites, via the USDA-Natural Resources Conservation Service (USDA-NRCS) online Official Soil Series Descriptions. Given the lack of standardization across studies in details such as soil sampling depth and parent material, it was necessary to create categories for many attributes. Our strategy for categorizing reporting depths requires explanation. First, we recorded the genetic horizon (e.g., Oe, Oa, A, Bw1) or sampling increment (as depth range in cm) for each SOC value. Next, for soils reported as depth increments, we correlated each specified depth increment to its probable genetic horizon, based upon associated methods descriptions or USDA-NRCS soil series descriptions. Last, we aggregated these into master horizons (i.e., O, A, or B horizons), which we used as the categorical variable for sample depth and discuss as organic horizons, upper mineral soils, and lower mineral soils, respectively. When SOC was reported for increments greater than 50 cm total depth, we summed them and categorized them as "whole profiles.".

As in prior published assessments, we used *meta*-analysis to identify significant predictors of variation in SOC responses to management, which is done statistically by parsing variation into within-group (Q_w) and between-group heterogeneity (Q_b), and inspecting corresponding P values. Grouping variables that have large Q_b relative to Q_w are significant ($P < 0.05$) and explain a larger share of total variation among all studies (Q_t). However, the statistical significance of P values is only one way to assess significance of *meta*-analysis results. In our *meta*-analysis, we were as interested in identifying groups that are significantly different from zero percent change (e.g., in response to harvest), in terms of their 95% confidence intervals, as we were interested in groups that were significantly different from each other (e.g., soil orders differing in their responses to harvest).

2.4. Synthesis of pedon and remote sensing data

We complemented the experimental strength of *meta*-analysis, which generates strong inferences for a limited number of sites, with a synthesis of soil pedon data from across the study area. These were data for geo-located soil pedons from the NCSS Database, including latitude, longitude, soil taxonomy, and physical and chemical properties of individual genetic horizons according to Schoeneberger et al. (2012) and Burt and Staff (2014). Data from the NCSS Database span decades of soil survey; to harmonize geo-located pedons with complementary remote sensing information, we only used pedons from 1989-present in the results presented herein, as in prior papers (Nave et al., 2018; 2019b; 2021; 2022). We extracted the following attributes for each geo-located NRCS pedon: land cover from the most closely coincident version of the National Land Cover Dataset (Vogelmann et al., 2001; Homer et al., 2004; Fry et al., 2011; Homer et al., 2015; Dewitz 2019), aboveground biomass C density from the National Biomass Carbon Dataset (NBCD2000; only for pedons sampled 1997–2006; Kellndorfer et al., 2013), mean annual temperature (MAT) and precipitation (MAP) from PRISM's United States Annual Precipitation and Mean Temperature datasets (PRISM Climate Group 2015). In addition to these attributes extracted from GIS products, we also created a 30 m DEM from the National Elevation Dataset (USGS, 2013) and from it derived each pedon's elevation, slope, and aspect, and landform index according to McNab (1993). We converted slope aspects in degrees into 4 cardinal aspects (N, S, E, W).

In order to assess land use and management with higher confidence than possible using remotely sensed NLCD land cover, we manually inspected a wide array of aerial and satellite imagery from public sources ranging from 1984 to 2019 for each pedon. Our intent in this step was twofold: (1) to evaluate whether the NLCD land cover classification at the time of pedon sampling was accurate; (2) to identify pedons where land use changes or management activities occurred within 10 years prior to pedon sampling. Similar to prior publications in which we critically assessed this approach, it was accurate approximately three-fourths of the time. Namely, 73% (732 of 1,048) of pedons had NLCD land cover classifications that reflected dominant land cover at the time of pedon sampling. For the remaining pedon locations, due to limited imagery, we were unable to confirm actual land use at time of sampling for 58 (6%) and we were unable to confirm whether or not any land use changes or management activities had occurred within the 10 years prior to the sampling date for 62 pedons (6%). Land cover classes defined by NLCD were inaccurate for the remaining 15% of pedons. For these 198 pedons, we manually corrected their land cover to represent what we observed for the pedon location using aerial imagery. We report this information in the interest of transparency, noting here that the number of pedons used for eventual statistical analyses was much smaller, per several stringent criteria. Specifically, pedons included in analyses were limited to confirmed, correctly classified, or manually corrected pedons from forested land uses, with horizon-level information available for greater than 90% of their reported sampling depths (n = 101 pedons comprised of n = 645 horizons).

2.5. NFI dataset

We complemented our *meta*-analysis and NRCS pedon + remote sensing datasets with independent observational data from the USDA-FS NFI. The NFI plots that are the basis for data from the Forest Inventory and Analysis (FIA) program obtained from an equal-probability sample of forests across the CONUS. There is one permanent plot on approximately every 2,400 ha across the U.S., with each plot placed randomly within a systematic hexagonal grid (McRoberts et al., 2005). All NFI plots with at least one forest land condition are measured every 5–7 years in the eastern US and soils are sampled from a subset of these plots, according to a protocol in which the organic horizon is first removed, and mineral soils are then sampled as depth increments of 0–10 and 10–20 cm (USDA, 2011). The NFI plot design ensures that FIA data have no systematic bias with regard to location, ownership, composition, soil, physiographic or other factors. Data for this analysis were obtained from an April 2017 query of the FIA Database for records of aboveground biomass, organic horizon, upper and lower mineral soil C stocks (all in Mg C ha^{-1}) for all single-condition plots in the ECOMAP ecological sections comprising the study area. We set the single-condition criterion in order to exclude plots divided along sharp boundaries into conditions of different stand age, slope, wetness, etc, such that local variation in such factors would misrepresent conditions at the actual location of soil sampling. As an additional constraint, we only utilized the most recent observation of each long-term NFI plot, and only plots observed since 2000, in order to make FIA data reasonably concurrent with the NRCS pedon and remote sensing data. Altogether, our NFI datasets included n = 6,918 plots for aboveground biomass (Phase 2 or P2 plots), n = 219 organic horizons and n = 175 for mineral soils (Phase 3 or P3 plots).

2.6. Statistical analysis of NRCS and FIA data

To complement the non-parametric *meta*-analysis of experimental data from published papers, we used parametric and nonparametric statistics (SigmaPlot, SYSTAT Software, San Jose, CA US) to analyze observational NRCS and FIA data. To identify factors influencing baseline SOC stocks in (1) upper mineral soils vs. (2) whole soil profiles (to 1 m or refusal), we analyzed NRCS data using best subsets regressions to identify variables with statistically significant categorical (coded as dummy variables) or continuous (standardized by subtracting the mean and dividing by the standard deviation) relationships with SOC stocks. Before model selection, we set the criteria for the optimal model (for each depth) as the one with the highest adjusted R^2, and comprised entirely of variables with significant partial P values. We set these criteria in order to identify the largest possible suite of factors influencing SOC stocks in each depth, while protecting against over-fitting by including variables that increased total proportion of variance explained, but themselves lacked significant relationships with SOC stocks. We used variance inflation factors to assess the degree of multicollinearity between predictor variables. To examine ecosystem C pools and accumulation rates (biomass, organic horizon, upper and lower mineral soil) across a range of forest types, management regimes, and physiographic conditions, we analyzed NFI data using simple linear regressions with stand age as the independent variable. We also used histograms to visualize differences in stand age distribution across forest types, management regimes, and physiographic conditions, and made nonparametric pairwise comparisons of median stand ages using the Mann-Whitney test. For parametric analyses, we used ln-transformations as necessary to normalize response variables, and in all analyses, we set $P < 0.05$ as the *a priori* threshold for accepting test results as statistically significant.

3. Results

3.1. Regional forest SOC stocks: Baseline drivers, land use and management effects

At the regional scale, variation in baseline SOC stocks was more related to inherent soil factors than land use change or management (Table 1). Climatic relationships with SOC stocks were evident for upper mineral soils and the soil profile as a whole; SOC increased with MAP and decreased with MAT (see also Fig. S1). However, other factors overshadowed climate in both upper mineral soils and whole soil profiles. In upper mineral soils, pedogenic relationships with upper mineral soil SOC stocks emerged through the large, positive categorical variable coefficient for Inceptisols (vs. Ultisols, which were the reference group; see also Fig. S2). Silt (range: 5–65%) and sand (range: 11–91%) contents were negatively associated with SOC stocks in upper mineral soils, and steeper slopes also had significantly smaller upper mineral soil SOC stocks. In terms of forest management patterns at a regional scale, unmanaged deciduous forests (i.e., not subject to fire, harvest, or other activities within 10 years before sampling) had significantly more upper mineral soil and whole profile SOC than the more frequently managed conifer plantations (which were the reference group). SOC stocks in whole soil profiles were also related to topography. The single strongest effect size predicting profile SOC stocks to 1 m was a strong negative influence of south-facing exposure (compared to north-facing slopes, which were the reference group), and in a pattern similar to upper mineral soils, steeper slopes also held less SOC. Variance inflation factors indicated moderate autocorrelation between silt and sand contents in the upper mineral soil model, weak autocorrelation between Inceptisols, slope gradient, and MAP in upper mineral soils, and weak autocorrelation between MAT and MAP in whole profiles.

Meta-analysis of published experiments across the region suggested that harvesting resulted in statistically significant SOC stock increases (soils across all depths compared to unharvested controls), while fires (all of which were prescribed in the experiments synthesized here) resulted in statistically significant SOC stock decreases (Fig. 2). Soil carbon impacts of land use changes involving forests varied widely depending on the specific change. Reforestation on previously cultivated land showed strongly positive SOC changes, while reforestation on lands managed for forage production (but not cultivated) was not associated with any significant SOC change. Forests growing on formerly cultivated land had SOC stocks not significantly different from forests that had never been cleared or cultivated. Deforestation, i.e., the comparison of native forest soils to paired treatment soils that had been deforested for cultivation, was associated with a significant loss of SOC. Lastly, comparing wetlands that had been restored on previously cultivated land to never-cultivated ("natural") wetlands indicated significantly larger SOC stocks for the never-cultivated, natural wetlands.

According to *meta*-analysis, the distinct overall impacts of harvest, fire, and reforestation on SOC stocks were associated with differing depth distributions of SOC change (Fig. 3). Harvesting had no significant effect on O horizon or upper mineral soil (A horizon) SOC stocks, but

Table 1
Statistically significant predictors of SOC storage in upper mineral soils (top) vs. whole soil profiles (bottom) for forest lands across the study region, based on analysis of NRCS pedon and harmonized geospatial data. The number of observations and adjusted R^2 are reported for each model. Parameters are sorted by effect size, with the coefficient, standard error, P value, and variance inflation factor presented for each.

Upper mineral soils (n = 129, R^2 = 0.51)				
Variable	**Coef.**	**SE**	**P**	**VIF**
Constant	3.50	0.09	<0.001	0.00
Inceptisol	0.56	0.15	<0.001	2.14
% silt	−0.43	0.12	<0.001	5.38
Unmanaged deciduous	0.37	0.13	0.005	1.53
% slope	−0.32	0.07	<0.001	2.16
MAP	0.32	0.08	<0.001	2.23
% sand	−0.31	0.12	0.015	5.61
MAT	−0.30	0.07	<0.001	1.90
Profile to 1 m (n = 101, R^2 = 0.48)				
Variable	**Coef.**	**SE**	**P**	**VIF**
Constant	4.62	0.10	<0.001	0.00
South-facing slope	−0.44	0.17	0.012	1.02
MAT	−0.41	0.12	<0.001	2.31
Unmanaged deciduous	0.38	0.17	0.028	1.23
MAP	0.35	0.12	0.004	2.73
% slope	−0.24	0.09	0.012	1.76

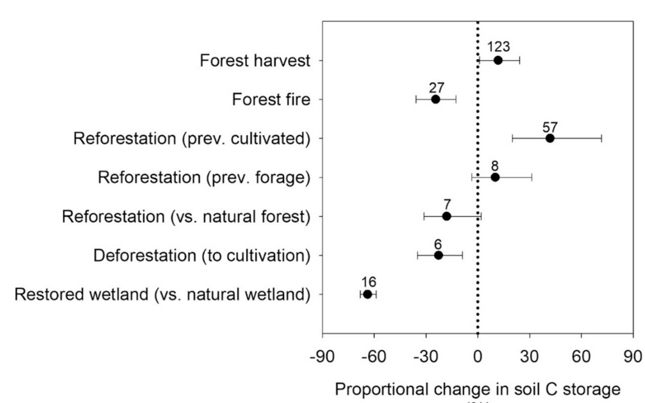

Fig. 2. Changes in soil C storage associated with forest management activities and land use changes across the region. Points are means, bars are bootstrapped 95% CIs, numbers indicate sample sizes, and the dotted reference line indicates no net change in SOC.

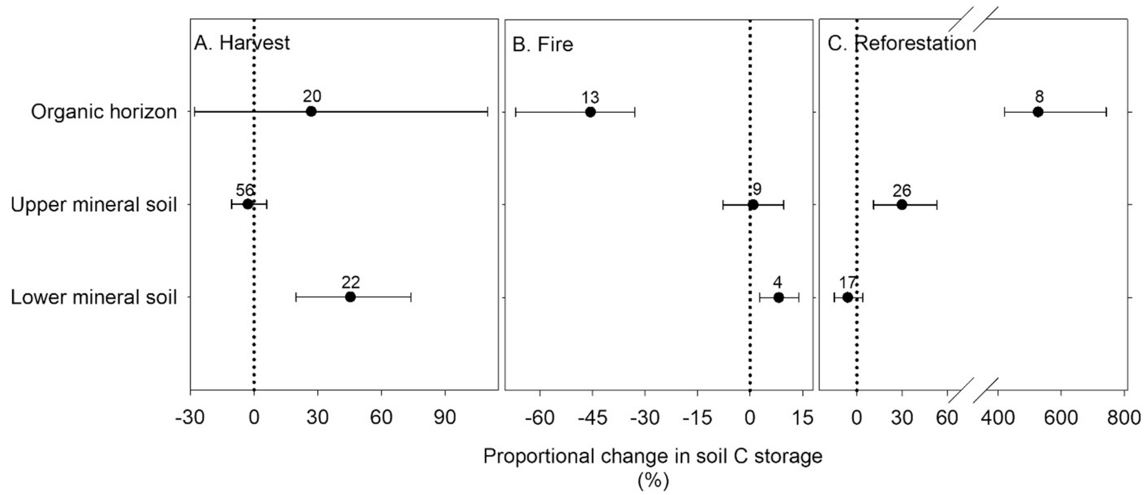

Fig. 3. Depth distribution of changes in soil C storage associated with harvesting (A), fire (B), and reforestation (C) across the region. Points are means, bars are bootstrapped 95% CIs, numbers indicate sample sizes, and the dotted reference lines indicate no net change in SOC.

was associated with significant but variable increases in lower mineral soil (E and B horizon) SOC storage. Fires diminished O horizon C stocks, had no effect on upper mineral soils, and a small sample size suggested a significant increase in lower mineral soil SOC stocks. Reforestation on formerly cultivated land was associated with large and variable increases in O horizon C stocks, more modest and less variable (but still statistically significant) increases in upper mineral soil SOC, and had no detectable effect on lower mineral soils.

3.2. A closer look: Harvest and fire impacts on soil carbon storage

Setting aside depth distributions for a look at other sources of variation in *meta*-analytic responses, overall SOC responses to forest harvesting and fire varied according to soil taxonomy (Fig. 4). On Ultisols, harvesting was associated with statistically significant increases in SOC stocks, while on Inceptisols, harvesting was associated with statistically significant decreases in SOC storage. The pattern was similar for fire, with Ultisols exhibiting a significantly less negative effect of fire on SOC storage than Inceptisols (*meta*-analysis, $P = 0.019$).

Examining harvest impacts specifically for upper mineral soils, which were the most extensively reported soil depth across the study region, revealed several patterns with respect to the ecological context of forestry in the South Atlantic States (Fig. 5). Namely, while *meta*-analysis revealed no significant harvest impacts in conifer-dominated or mixed forests, upper mineral soil SOC stocks declined significantly when broadleaved deciduous (i.e., hardwood) forests were harvested. In terms of wetness, hydric sites were associated with significant upper mineral soil SOC increases following harvest, while mesic sites were associated with significant declines. Physiographic trends also emerged, with the topographically rugged interior (mountain and piedmont ecological sections) showing significant SOC declines, and the Northern Atlantic Coastal Flatwoods ecological section showing no change.

Upper mineral soil SOC changes with harvesting also revealed significant *meta*-analytic patterns with respect to harvest practices (Fig. 6). Harvests that retained little to no residual basal area were associated with no significant change in upper mineral soil SOC; in contrast, harvests that retained large proportions of residual basal area were associated with significant declines in upper mineral soil SOC. Harvests that removed logs and harvest residues were associated with significant increases in upper mineral soil SOC stocks, while harvests that removed only logs were associated with significant SOC decreases.

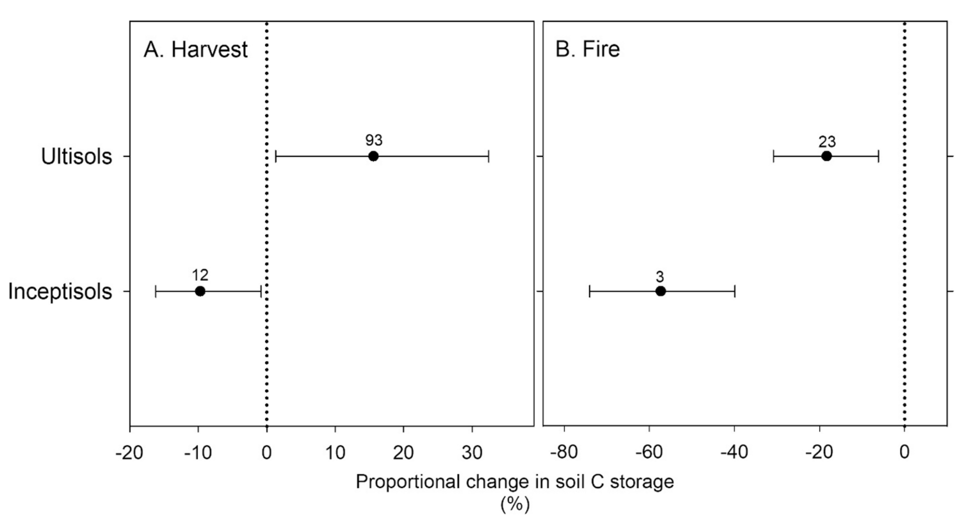

Fig. 4. Changes in soil C storage with forest harvesting (A) and fire (B), by soil taxonomic order. Points are means, bars are bootstrapped 95% CIs, numbers indicate sample sizes, and the dotted reference lines indicate no net change in SOC.

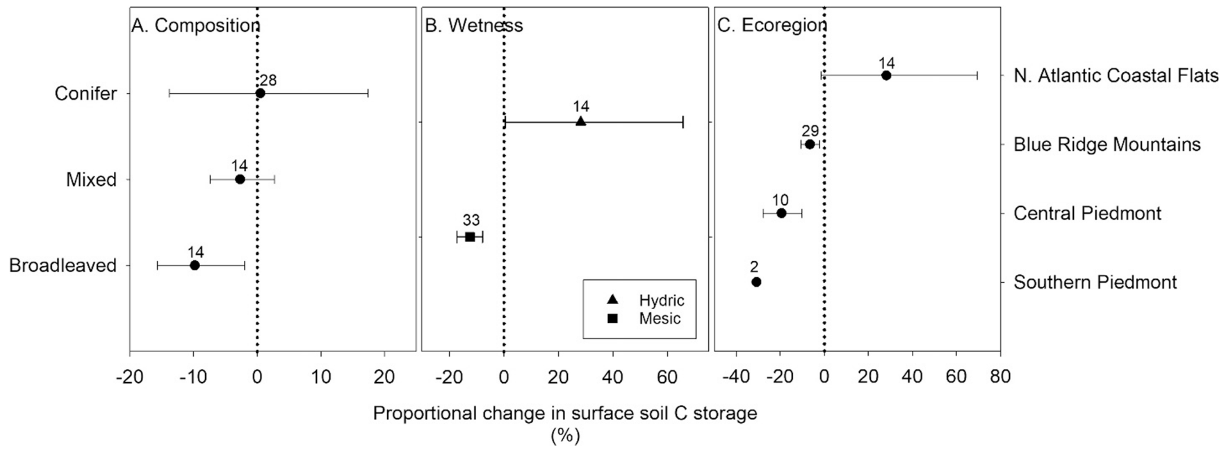

Fig. 5. Harvest impacts on upper mineral soil C storage as a function of forest composition (A), site wetness (B), and ecoregion (C). Points are means, bars are bootstrapped 95% CIs, numbers indicate sample sizes, and the dotted reference lines indicate no net change in SOC.

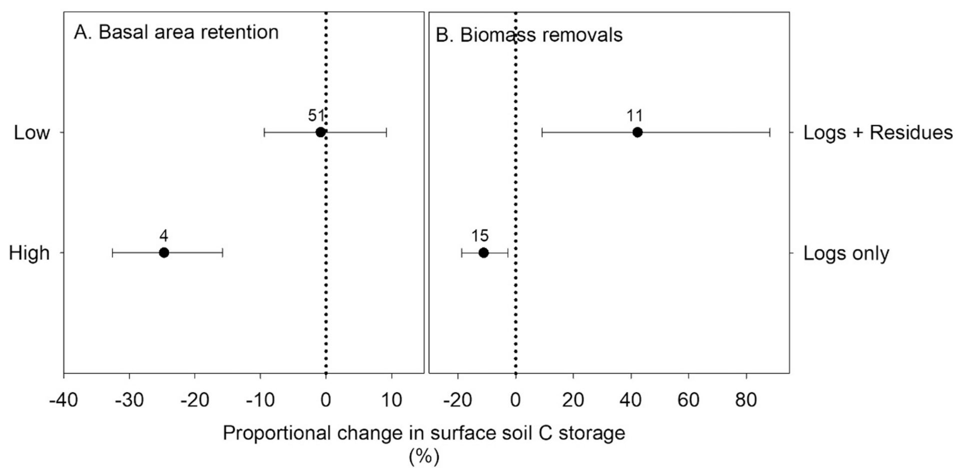

Fig. 6. Harvest impacts on upper mineral soil C storage as a function of residual basal area retention (A) and type of biomass removals (B). Points are means, bars are bootstrapped 95% CIs, numbers indicate sample sizes, and the dotted reference lines indicate no net change in SOC.

3.3. Harvest regimes and practices in ecological context

Regional data from the NFI program (FIA data) revealed physiographic and management patterns that contextualized and supported the NRCS pedon and *meta*-analysis results (Table 2). Expressed as a function of stand age, aboveground biomass showed larger initial standing stocks, but slower accumulation rates in natural forests (hardwood or pine) than plantation pines throughout the South Atlantic States. Subregionally, the topographically rugged interior (i.e., the mountain and piedmont ecological sections) had larger initial standing stocks and slower accumulation rates than the coastal plains and flatwoods, for two of three forest types (natural hardwood and plantation pine). The exception was natural pine forests, which had lower initial aboveground biomass stocks and faster rates of accumulation in the mountain and piedmont subregion than the coastal plains and flatwoods subregion.

Organic horizon C stocks showed similar trends to aboveground biomass in terms of management regimes. Plantation pines had smaller initial C stocks, but unlike unmanaged forests (natural hardwoods, natural pines), showed significant increases as a function of stand age in both physiographic subregions ($P = 0.01$ and $P = 0.02$; $r^2 = 0.19$ and 0.33 for plains/flatwoods and piedmont/mountain subregions, respectively). Modeled relationships with stand age (slope coefficients from linear regression) suggested O horizon accumulation rates between 0.2 and 0.3 Mg C ha^{-1} yr^{-1} for plantation pines.

SOC stocks in upper mineral soils showed significant relationships with stand age in only two cases, both of which were in the coastal plains and flatwoods physiographic subregion. Specifically, upper mineral SOC stocks in natural hardwoods vs. plantation pines showed contrasting patterns as a function of stand age, with the former exhibiting large initial stocks and relatively slow accumulation, and the latter showing small initial stocks and rapid accumulation. These modeled relationships were weaker than those observed for aboveground biomass and organic horizons (P = 0.04 for both, $r^2 = 0.12$ and 0.14, respectively).

SOC stocks in lower mineral soils showed a range of relationships across forest types and subregions. In the coastal plains and flatwoods subregion, lower mineral soil SOC was significantly related to stand age only in plantation pines, which had small initial stocks, but rapid accumulation (modeled at 1.25 Mg C ha^{-1} yr^{-1}; $r^2 = 0.20$, $P < 0.001$). In the piedmont and mountain subregion, lower mineral soil SOC stocks were significantly related to stand age in both natural forest types, but not in plantation pines. Accumulation rates in the natural forest types were in the 0.15–0.21 Mg C ha^{-1} yr^{-1} range ($P = 0.02$ and $P = 0.03$, $r^2 =$ 0.11 and 0.24, respectively).

Stand age distributions from NFI plots revealed how management regimes differ subregionally, as a function of physiography, and as a function of forest type (Fig. 7). Overall, the most evident pattern was the dominance of long-rotation, naturally regenerated hardwood forestry in the mountain and piedmont subregion vs. short-rotation plantation pines in the coastal plains and flatwoods subregion. The divergence

Table 2
Carbon stocks (Mg C ha^{-1}) as a function of stand age (in years) in aboveground biomass, organic horizon, upper mineral soil, and lower mineral soil for the two physiographic subregions comprising the study area. In each subregion, C accumulation equations are presented for three forest types: naturally regenerated hardwoods, naturally regenerated pines, and plantation pines. Accumulation equations are best-fit linear models based on NFI data, with statistically significant linear models ($P < 0.05$) highlighted in bold text.

	Aboveground Biomass		
Physiographic Subregion	**Natural Hardwood**	**Natural Pine**	**Plantation Pine**
Coastal Plains and Flatwoods	**C = 4.1 + 1.07*Age**	C = 41.7 + 0.67*Age	**C = 0.0 + 2.26*Age**
Piedmont and Blue Ridge	**C = 18.3 + 0.75*Age**	**C = 13.9 + 1.28*Age**	**C = 3.8 + 1.50*Age**
	Organic Horizon		
	Natural Hardwood	**Natural Pine**	**Plantation Pine**
Coastal Plains and Flatwoods	C = 10.1 + 0.10*Age	C = 10.7 + 0.03*Age	**C = 3.5 + 0.28*Age**
Piedmont and Blue Ridge	C = 9.2 + 0.03*Age	C = 6.9 + 0.05*Age	**C = 2.9 + 0.20*Age**
	Upper Mineral Soil		
	Natural Hardwood	**Natural Pine**	**Plantation Pine**
Coastal Plains and Flatwoods	**C = 27.8 + 0.27*Age**	C = 23.3 + 0.11*Age	**C = 9.4 + 0.83*Age**
Piedmont and Blue Ridge	C = 24.7 + 0.07*Age	C = 16.9 + 0.12*Age	C = 21.6–0.18*Age
	Lower Mineral Soil		
	Natural Hardwood	**Natural Pine**	**Plantation Pine**
Coastal Plains and Flatwoods	C = 19.6 + 0.21*Age	C = 8.4 + 0.08*Age	**C = 6.3 + 1.25*Age**
Piedmont and Blue Ridge	**C = 9.9 + 0.15*Age**	**C = 5.0 + 0.21*Age**	C = 10.7–0.14*Age

between these management regimes was indicated by a large and statistically significant difference in median stand ages for the two groups, with natural mountain/piedmont hardwoods being managed on significantly longer timescales (median stand age: 66 years; 75th percentile: 81 years) than coastal plantation pines (median: 19 years; 75th percentile: 28 years). Other notable patterns were the older age-class distributions of naturally regenerated forests (hardwood and pine) compared to plantation pines in both subregions, and the larger number of plantation pine plots in the coastal / flatwood subregion (vs. the mountain/piedmont subregion), despite its smaller overall area (170,000 vs. 208,000 km^2).

Meta-analysis of published experiments (all soil depths collectively) provided insight into specific postharvest and stand management practices commonly employed in coastal plain pine plantation forestry (Fig. 8). These results indicate that post-harvest residue burning and herbicide application were associated with SOC stock declines, when compared to plantation pines not subjected to these treatments. Most practices appeared to have no effect on SOC stocks in coastal plain plantation pines; neither fertilization alone, fertilization + herbicide application, tillage, bedding, fertilization, and herbicide application, or bedding, fertilization, and herbicide application were associated with any significant effects compared to plantation pines lacking these additional treatments. In terms of SOC-positive management, only the tillage + bedding treatment was associated with a significant increase in SOC stocks.

4. Discussion

4.1. Patterns and drivers of SOC stocks and stock change

Our analysis of forest soils across the South Atlantic States indicates that as in other ecoregions, spatial patterns in SOC stocks are related more to geographic and inherent soil factors than management practices (Nave et al., 2019b; 2021; 2022). Baseline patterns in forest SOC storage are largely a function of the same driving factors whether considering upper mineral soils alone or the entire soil profile, with climatic, topographic, and soil physical and pedogenic properties emerging as important controls. Across the region, larger forest SOC stocks were associated with higher precipitation and lower temperature. This macroclimatic pattern is congruent with the apparent effect of topoclimate, which indicated significantly larger profile SOC stocks on north-facing slopes than south-facing slopes, which are typically warmer and drier. Forest SOC stocks were negatively related to soil silt and sand contents, and by difference, positively related to soil clay content. Overall, these climatic, topographic, and textural controls are readily explained by pedogenesis and soil taxonomy, as results also showed that Inceptisols had significantly larger upper mineral soil SOC stocks than Ultisols. Regionally, Inceptisols are characteristic of the cooler, wetter, finer-textured residual and colluvial soils of the Blue Ridge Mountains, whereas Ultisols are extensive throughout the warmer, effectively drier piedmont and coastal plain ecological sections (Miller and Robinson, 1994; West, 2000). Here, Ultisols form in a wide range of parent materials and textures, most notably including coarser marine deposits.

Although consistent with climatic, topographic, and pedogenic expectations, physiographic and pedogenic control of forest SOC stocks does not mean human activities have no impact. Meta-analysis of published experiments designed to test for SOC stock changes revealed a range of land use changes and management practices with significant impacts on SOC storage. Regionally, reforestation increases SOC only when trees establish on soils with a history of cultivation (vs. no change with reforestation on non-tilled lands used for forage production). Conversely, forest clearing for cultivation decreases SOC stocks, a result mirrored by the SOC deficit of wetlands restored on formerly cultivated lands vs. natural wetlands without past cultivation. Overall, these land use change results largely follow patterns described in larger-scale syntheses (Guo and Gifford, 2002; Laganiere et al., 2010; Nave et al., 2013; 2018; 2019c). Although subtler than land use changes, forest management practices also impact SOC at a regional scale, with prescribed fires driving SOC loss (Nave et al., 2011) and harvest associated with SOC gains.

Investigating the depth distribution of SOC change improves our understanding of how land use change and management impact SOC storage. Regionally, the apparently positive effect of harvesting was driven by high-variability, large-magnitude SOC increases in lower mineral soil horizons, potentially indicating a role of altered litter sources, quantity, or quality in these soils, where organic matter is principally root-derived (Heckman et al., 2021). Conversely, the apparently negative impact of fire is an artifact of its superficial impacts and a literature focused on organic horizons: significant decreases in O horizons drive the overall trend, and likely reflect the intent of prescribed fire to reduce surface fuels and litter (Knoepp et al., 2009). Reforestation produced large and variable increases in O horizons, which usually do not exist after cultivation, and comprise a small fraction of whole profile SOC (an average of 9% of whole-profile SOC stocks for the studies included in the *meta*-analysis). Modest upper mineral soil SOC increases with reforestation are consistent with prior regionalized assessment of reforestation impacts on SOC (Nave et al., 2018). Lastly, while we detected no significant change in lower mineral soil SOC with reforestation at a regional level, this does not preclude specific cases, perhaps driven by unique site histories, which clearly show negative trends (Mobley et al., 2015; Richter et al., 1999).

Setting aside the depth distribution of SOC stock changes to focus on a broader pattern, management impacts on SOC in the South Atlantic States emerge as trends that covary with physiography, forest type, and soil properties. For example, harvest and fire impacts on SOC depend on soil type, with Inceptisols showing generally more negative impacts than Ultisols. This result may indicate that forest soils in mountainous areas, which are more frequently Inceptisols, are simply less resistant to

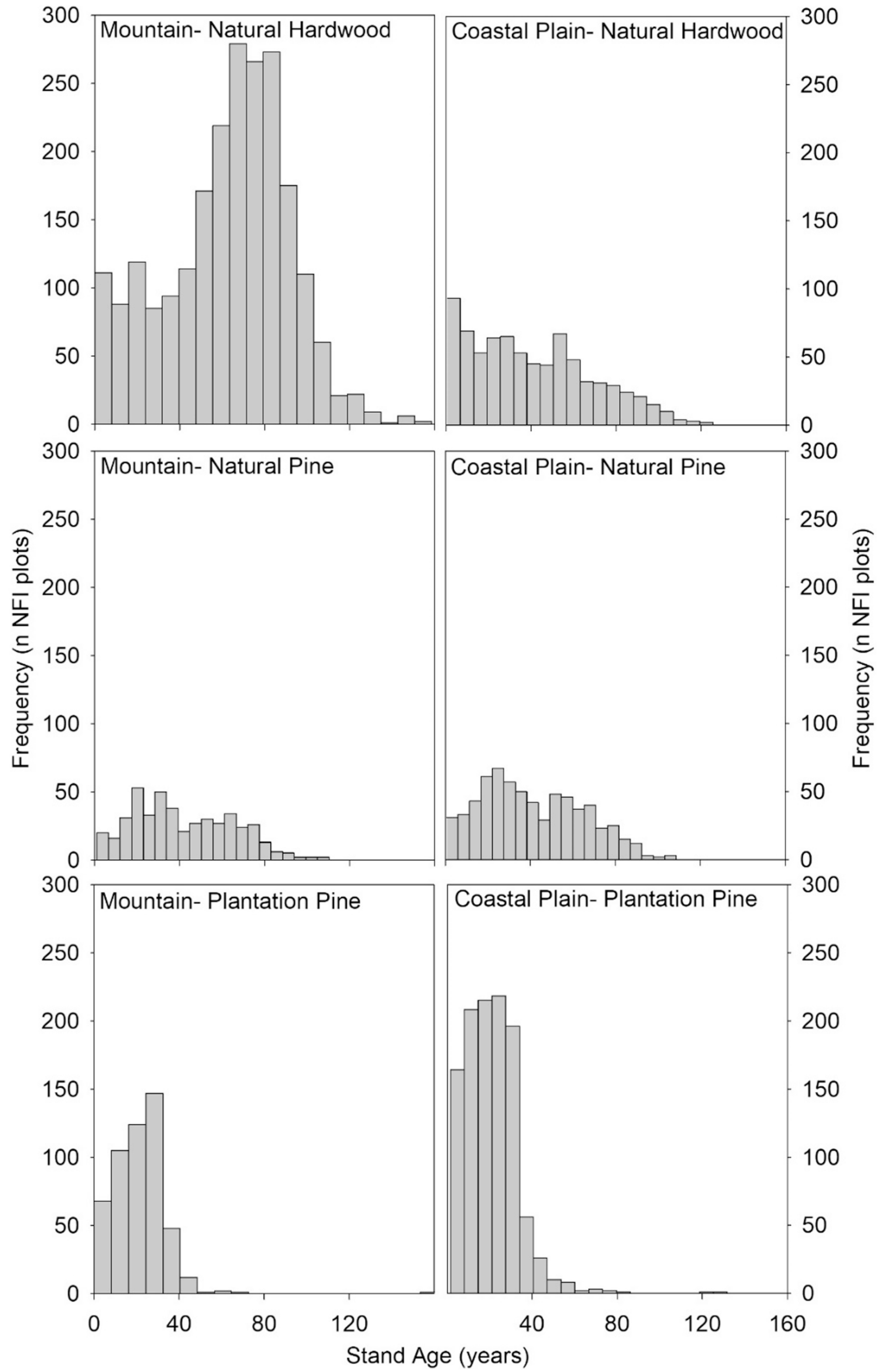

Fig. 7. Stand age distributions for three generalized forest types in the piedmont and mountain (left column panels) vs. coastal plains and flatwoods (right column panels) physiographic subregions. All axes share common scaling to aid in visualizing differences by forest type and subregion. Data represent the number of P2 plot NFI plots, as described in section 2.5.

disturbances that alter microclimate, litter inputs, or soil stability than the Ultisols that predominate on coastal plains and flatwoods. Similarly, the forests that grow on mountain Inceptisols vs. coastal plain Ultisols are characterized by different disturbance regimes. In mountain hardwoods, where soils are more often Inceptisols, the generally modest natural disturbance regime is one of small canopy gaps and, in xeric settings, low-frequency surface fires (Schafale and Weakley 1990; Xi et al., 2008). In contrast, on coastal plain Ultisols, natural disturbances such as hurricanes and larger and more frequent surface fires result in more extensive areas of periodic stand replacement (Ojha et al., 2019; Sharma et al., 2021). The net result of these geographic relationships between soil and forest types is the emergence of two broad, covarying, divergent forest type - management regimes: long-lived hardwoods in the mountain/piedmont interior vs. short-rotation plantation pines on

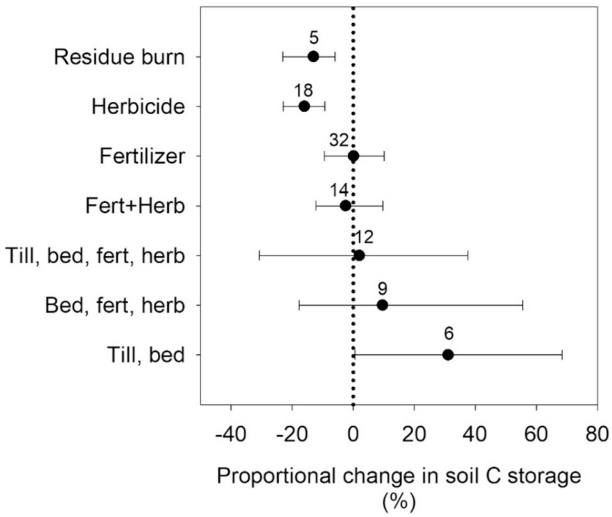

Fig. 8. Changes in soil C storage associated with specific post-harvest and stand management practices in coastal plain pine plantations. Points are means, bars are bootstrapped 95% CIs, numbers indicate sample sizes, and the dotted reference line indicates no net change in SOC.

the coastal plain. These patterns may be described as two distinct forest ecology-management syndromes: geographically distinct forest / soil types with different natural disturbance regimes, which are customarily managed differently. The larger initial SOC stocks and greater potential for loss in mountain hardwood Inceptisols encompasses trends illustrated in Figs. 5 and 6: SOC losses in mesic, broadleaved deciduous hardwoods, associated with mountain and piedmont ecoregions, where retention of residual basal area and harvest residues is typically greater. Conversely, forestry on the coastal plains and flatwoods largely consists of conifer-dominated systems on Ultisols, more often hydric, which are characterized by lower residual basal area retention and more frequent removal of harvest residues. Ultimately, these patterns indicate how at the regional scale, place and practice go hand in hand, and SOC impacts co-vary with site factors. The net result is seemingly counter-intuitive patterns—e.g., SOC losses when residues are retained, gains when they are removed—that come into focus when considering the two types of systems in which either practice is more common. Because *meta*-analysis cannot reveal mechanisms, the underlying reasons for SOC gains under the more intensive management regimes of coastal plain pine plantations are unknown. In this regard the main contribution of this finding is in documenting a previously unknown link between place, management regime, and SOC response.

4.2. Ecological context and carbon management

The wide extent and high density of NFI data across the South Atlantic States permit keen insights into how divergent management regimes produce distinct C impacts, through the filters of physiography and forest type. At establishment, pine plantations begin with small whole ecosystem C stocks (little C in biomass, organic horizons, or mineral soils) compared to C stocks in the less intensively managed, naturally regenerated forest types (Table 2). Subsequently, during the short rotation period—typically no more than three decades—C gains in all pools are rapid and clearly tied to biomass aggradation as the plantations develop. This overall pattern for pine plantations, which is consistent across mountainous and coastal subregions, indicates that management can override physiography through how and when C enters or is removed from the system. In this regard, whole system assessments of plantation forests, including the fate of C removed during precommercial thinning, final harvest, and litter raking, are critical for determining the wider role of these important forestlands in land sector C budgets (Gonzalez-Benecke et al., 2010; Vance 2018). Model-based assessments of C within and outside of the ecosystem boundary also have much to contribute to this accounting of forest C, particularly in light of the low initial C stocks, rapid C accumulation rates, and short rotation lengths of plantation forests. Where these C accounting exercises are possible for plantation forests, accounting for physiographic differences will be important, as initial mineral soil SOC stocks are substantially smaller in coastal (typically Ultisols) vs. mountainous (Inceptisols) systems.

Longer-rotation, naturally regenerated forests, particularly hardwoods, provide a strong counterpoint to pine plantations in terms of C management. In these longer-rotation systems, C stocks in early stand ages are larger than in plantation systems for nearly all ecosystem pools, but accumulation rates are slower, or in many cases, not detectable. In these systems, which as described previously are more likely to lose SOC with harvesting or fire, more conservative C management may be appropriate. The larger initial C stocks reflect typically greater retention of basal area, harvest residues, and biological legacies in general (e.g., snags). Given their SOC vulnerability, despite less intensive management, actions intended to increase aboveground C sequestration (e.g., longer rotations, increased reserve areas, greater residual basal area retention) may carry SOC management co-benefits in these longer-lived, deciduous forests (Littlefield and D'Amato, 2022; Ontl et al., 2020). Additionally, because these systems are part of a syndrome with the steeper topography and shallower, finer-textured soils of mountainous ecoregions, judicious implementation of existing best management practices (BMPs) aimed at minimizing the extent of soil disturbance and protecting soils in sensitive sites, which otherwise could result in SOC losses, is critical to protecting SOC (Fox et al., 2004; Hawks et al., 2022).

Forest, soil, and C management plans that consider the physiographic, ecological and soil factors identified as important in this paper can minimize the potential for SOC losses during management. Existing BMPs provide many guidelines for actions that are often justified for reasons not distinctly related to SOC (e.g., soil or water quality protection), but which may also provide SOC benefits. For example, mechanical site preparation is often needed to support management objectives related to residue management or replanting in coastal plain pine plantations, but following specific BMPs can allow site preparation with little to no mineral soil exposure or erosion (NCFS, 2021). For example, judicious control of bulldozer blade height, or use of toothed bulldozer blades, can allow harvest residues to be manipulated without displacing O-horizons or exposing mineral soils. Our results suggest that as practiced, mechanical site preparation techniques have either no effects, or slightly positive effects on SOC (Fig. 8). Where mineral soils are exposed, direct additions of organic matter as soil amendments (e.g., wood chips) protect the soil surface from erosion while also directly increasing organic matter stocks (NCFS, 2021). Recognizing that a large proportion of the potential soil impacts from forestry operations are associated with a small proportion of harvested areas, detailed guidelines govern where, how, and when features such as roads, landings, and water body crossings are constructed and how they are repaired after operations. These BMPs include actions intended to prevent the water-borne transport of soil and organic matter, and to retain slope-stabilizing, large-diameter harvest debris when residues are burned prior to replanting (NCASI, 2009, 2012). Even where practices that apparently diminish SOC are employed (e.g., residue burning; Fig. 8), they may still be justifiable in terms of C if their net C impact at the ecosystem or land sector scale is ultimately positive, such as through increased production of durable wood products. Overall, adoption of existing BMPs is already very high in the southeastern U.S. (>90%; Schilling et al., 2021), and evidence shows that when followed, they are highly effective in meeting their soil and water quality objectives (NCASI, 2004, Cristan et al., 2015). Quantifying the SOC co-benefits of these BMPs is an area in need of continued research; at present, our findings suggest that they have a generally positive influence on SOC, even if the magnitude of their impacts is unknown. We summarize a handful of such practices, drawn from existing BMPs, climate adaptation and C mitigation literature, in

Table 3
Example management practices with SOC co-benefits, in the context of the two forest ecology – management regimes summarized in the discussion.

Management Regime	Practice	Intent	Additional considerations	References
Mountain hardwoods	Restrict harvesting to slopes < 16%	Minimize risk of detrimental soil disturbance	SOC benefit is assumed; risk still exists on level ground	NCASI, 2004; North Carolina Forest Service, 2021
Mountain hardwoods	Extend rotation length	Increase woody biomass (and debris) C stocks	Increasing rotation length only delays eventual SOC loss	Ontl et al., 2020
Coastal pine plantations	Restrict litter raking	Accumulate organic horizon C, mix into soil during site prep	Litter straw demand displacement; cost:benefit of site preparation	Butnor et al., 2006; Sanchez et al., 2008
Coastal pine plantations	Decrease herbicide use	Allow competing vegetation to grow and input C to soil	Competing vegetation may diminish wood yield; SOC gains may be transient	Laiho et al., 2001; Sartori et al., 2006; Shan et al., 2001

Table 3, in the context of the two forest ecology – management syndromes that we have articulated in this paper. Each of these practices emerges from trends revealed through our synthesis, as supported by relevant literature.

There are potentially many SOC-positive management practices that align with existing BMPs, climate adaptation or C mitigation literature; those provided in Table 3 illustrate three key points. First, the relevant practices for the longer-rotation interior hardwood soil systems are quite different than those relevant in the intensive, short-rotation coastal plain pine plantations. In keeping with this simplified bifurcation of place and practice come the second and third points. Namely, in the cooler, wetter, topographically rugged, more disturbance-sensitive hardwoods of the mountains and piedmont, soils are more vulnerable to physical disturbance, and rates of C accumulation in soils and biomass are slower. As a result, moving management in a less impactful direction—e.g., through increased slope restrictions or longer rotations—is in keeping with ecological context. On the other hand, in coastal plain pine plantations—which are economically optimized, highly productive systems—changes in management to promote SOC have more to do with the nature of the management inputs and material removals from the system. There is at present little question that the principal goals of pine plantations will continue to be the rapid production of woody biomass, but through modest adjustments to how those goals are pursued, SOC may be encouraged to accrue as a co-benefit. Ultimately, none of these practices are recommendations so much as they are examples of how SOC may be introduced as a consideration into existing BMP, C management, and climate adaptation frameworks. Implementation, monitoring, C accounting, and continued research will determine the extent to which they are feasible within the context of other ecological and economic goals in the forests of the South Atlantic States.

All authors have approved the revised version of this manuscript, which is not under consideration for publication elsewhere.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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