Wind and fire as drivers of carbon pool variability in southeastern U.S. forests

by

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Abstract

Forests in the southeastern U.S. play an important role in global climate mitigation via carbon (C) sequestration, yet recurrent disturbances like wind and fire threaten their ability to sequester C. Many southeastern U.S. forests are fire-dependent, and landowners and managers commonly apply low-intensity prescribed fires to maintain and restore these ecosystems. However, severe wind events like hurricanes and tornadoes can create widespread structural damage to forests, potentially increasing fuel loads and modifying fire behavior, thereby adding uncertainties about the re-introduction, effectiveness, and C consequences of prescribed fire. To better understand C dynamics in wind-damaged, fire-managed southeastern U.S. forests, we investigated how forest type and fire history influence C pools and distribution, especially in the forest floor. Understanding forest structural damage following wind events, fuel loads, and C pool dynamics will enhance ability of land managers and forest owners to assess and optimize C sequestration in southeastern U.S. forests, contributing to more effective climate mitigation strategies.

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List of Abbreviations

AL	Alabama
ANOVA	Analysis of Variance
ATV	All-Terrain Vehicle
C	Carbon
CWD	Coarse Woody Debris
DBH	Diameter at Breast Height
DOC	Dissolved Organic Carbon
EF	Enhanced Fujita
FIA	Forest Inventory Analysis
FL	Florida
FWD	Fine Woody Debris
GIS	Geographic Information System
HSD	Honestly Significant Difference
KBDI	Keetch-Bryam Drought Index
MSL	Mean Sea Level
SOC	Soil Organic Carbon
SOL	Soil Organic Layer
U.S.	United States
USDA	United States Department of Agriculture
USFS	United States Forest Service
WFAS	Wildland Fire Assessment System

Chapter 1. Carbon pool dynamics in wind-damaged, fire-managed southeastern U.S. forests

Abstract.

Southeastern U.S. forests are a major regional contributor to the nation's carbon (C) sequestration capacity, yet their C resilience, i.e., forest's capacity to recover C post-disturbance, is often threatened by wind disturbances (e.g., hurricanes and tornadoes). To better understand forest C resilience, this study focused on the temporal dynamics of C pools at four sites varying in stand age and composition that experienced wind damage followed by prescribed fire: two coastal sites (Weeks Bay, AL and Perdido, FL) impacted by hurricanes in 2020, and two inland sites - Oakmulgee, AL (impacted by tornado in 2021) and Flagg Mountain, AL (impacted by straight-line winds in 2020). At each site, we established permanent plots across a gradient of wind damage severity and quantified all aboveground C pools (i.e., live trees, snags, understory vegetation, fine and coarse woody debris) and soil surface C pools (i.e., leaf litter (Oi) and soil organic layer (SOL; Oe + Oa)). We measured C pools within each plot during four sampling periods: after wind damage but before (< 1 month) prescribed fire treatment (i.e., pre-fire) and immediately (within 1-2 weeks), 1-year, and 2-years after prescribed fire treatment. We hypothesized that higher wind damage would lead to higher fuel loading, resulting in higher C consumption as an indicator of severe prescribed burn during re-introduction of fire, and ultimately leading to slower recovery of C pools. Wind damage severity varied across plots within a site, with increasing basal area loss leading to an increase in coarse woody debris and total fuels at two sites (Flagg Mountain: $R^2 = 0.66$, $p < 0.001$ for CWD, Oakmulgee: $R^2 = 0.16$, $p = 0.02$). Overall, however, C loss during fire was mostly driven by the amount of pre-fire fuel load, regardless of whether the fuel loads were related to forest structural changes due to wind damage (e.g., Weeks Bay: $R^2 = 0.33$, $p < 0.001$;

Perdido: $R^2 = 0.87$, $p < 0.001$ for total C loss). Prescribed fires caused only short-term C losses from readily available fuels such as leaf litter, fine woody debris, and understory vegetation, which partially recovered through re-growth and inputs, with little to no impacts on tree and snag C pools during the 2-year study period ($p > 0.05$). Resilience of different C pools varied among sites, with older stands with a long history of fire management showing faster C replenishment through understory regrowth and leaf litter inputs (e.g., Weeks Bay: $R^2 = 0.24$, $p = 0.005$ for total C recovery after one year). This study provides detailed insight into C pool dynamics in wind-damaged, fire-managed forests, informing management practices and enhancing understanding of southeastern U.S. forests' role in long-term C sequestration.

Introduction

Forest carbon (C) sequestration is widely recognized as a pivotal, cost-effective strategy for mitigating climate change impacts in an effort to keep global warming below 2˚ Celsius over the next few decades (Lorenz and Lal, 2010; Fawzy et al., 2020). Forests in the U.S., which sequester approximately 190 $TgCyr^{-1}$, play a vital role as long-term C storage sites and are critical in both national and global climate mitigation efforts (Williams et al., 2016). Notably, forests in the southeastern U.S., which cover 60% of the landscape across a nine-state region (Alabama, Georgia, Florida, Mississippi, Louisiana, North Carolina, South Carolina, Texas, Virginia) represent a significant portion of the nation's C sequestration capacity (United States Department of Agriculture [USDA] Forest Service, 2022). These forests, broadly-distributed across diverse ecoregions, contain ~ 30% of the nation's C stock and play a crucial role in sequestering C and mitigating climate change impacts (Mickler et al., 2002; Zhao et al., 2013). Yet, their C pools and continued ability to act as C sinks are increasingly threatened by common disturbances in the region like severe wind and its interaction with subsequent fire.

Severe wind disturbances like tornadoes and hurricanes regularly occur in southeastern U.S. forests, with potential implications for forest C pools. Recent studies indicate an increasing frequency of these wind events in the region, which can inflict substantial structural damage to forests (Emanuel, 2021; Gensini and Brooks, 2018; Goldenberg et al., 2001; Kupfer et al., 2020; McNulty, 2002; Moore and McGuire, 2019; Smith, 1999). Structural damages include the creation of canopy gaps due to uprooted/snapped trees and conversion of live tree biomass into snags and downed woody debris (Fortuin et al., 2022; Fraver et al., 2017; Rutledge et al., 2021). This damage redistributes forest C pools and can increase C vulnerability to loss, as C pools (e.g. tree C) that took many years to accumulate are now susceptible (e.g. woody debris C) to accelerated decomposition and/or likelihood of combustion during eventual (intentional or unintentional) forest fires due to higher fuel loads and elevated fire hazards (Dahal et al., 2014; McNulty, 2002; Schwartz et al., 2017; Wang et al., 2010).

Fire is another critical natural disturbance in southeastern U.S. forests, often interacting with wind damage to affect C dynamics (Fowler and Konopik, 2007; Kupfer et al., 2020; Mitchell et al., 2014). Many forests in this region are fire-dependent, historically maintained with frequent (2–10-year interval), low-intensity surface fires (Ryan et al., 2013). After a period of fire suppression in the 20th century, prescribed fires became an increasingly common management tool for restoration and maintenance of fire-dependent forests across the region, accounting for 70% of prescribed burns conducted in the U.S. (Addington et al., 2015; Cannon et al., 2019; Kobziar et al., 2015). Studies in various forest types outside the southeastern U.S. have shown that frequent prescribed fires can lead to a temporary loss of C via emissions during fire, although the amount lost is often relatively small. Frequent burning prevents fuel accumulation and high fire severity, and larger, stable C pools (i.e., trees and organic surface soils) are typically left unconsumed (Volkova et al., 2021; Wiedinmyer and Hurteau, 2010). Some research indicates that rapid re-growth of understory vegetation after fire restores most C lost during fire (Carter and Darwin Foster, 2004). Long-term studies in certain forest types have shown positive net ecosystem C balance in fire-managed forests, with C accumulating in stable tree pools (Clark et al., 2024; Gonzalez-Benecke et al., 2015; Samuelson et al., 2014). However, there remain uncertainties and concerns about the C consequences of implementing prescribed fires in southeastern U.S. forests, particularly in wind-damaged stands which have altered fuel loads and types.

Following severe wind disturbance managers are reluctant to reintroduce prescribed fires due to concerns that the fires may burn excessively or have unintended consequences for forest ecosystem services, including C storage and sequestration (Ibanez et al., 2022; Myers and van Lear, 1998; Platt et al., 2002). Even if salvage logging is carried out to reduce large fuels (e.g. tree trunks) from wind disturbed stands, there will be increase in smaller fuels such as small branches (Leverkus et al., 2020). If increased fuel loads lead to higher fuel combustion and fire severity, this may slow down forest C recovery through various means like loss of the soil organic layer (SOL), increased soil erosion, and reduced tree seed availability, especially since the overstory tree C pool may take decades to recover (Abney and Berhe, 2018; Cannon et al., 2017; Pellegrini et al., 2021). In contrast, because coarse woody debris retains moisture, increased inputs may create a discontinuous fuel bed, resulting in decreased fire severity or continuity (Busing et al., 2009; Cannon et al., 2019). Whether wind damage causes increased or decreased fire severity, there will be temporary disruptions in the natural fire regime, which may lead to cascading effects on forest structure and composition, C pools, and C sequestration capacity. Despite the importance of understanding this interaction, few studies have explored interaction of wind and fire disturbances in southeastern U.S. forests.

To address this knowledge gap and better understand the resilience of C pools in wind-damaged, fire-managed forests of the southeastern U.S., we studied four wind-damaged forests of varying age and composition to answer the following questions: 1) How do forest structural changes due to wind (i.e., basal area loss and remaining) affect distribution of C pools that act as fuels (e.g., leaf litter, understory vegetation, woody debris)?; 2) How do variations in these fuel load C pools impact C loss during first prescribed fire after wind events?; 3) How do C loss variations across plots influence C resilience (i.e. ability of forest stand to recover C lost due to disturbances) in the 1- to 2-year interval following the prescribed fire?; and 4) Are there consistent patterns of C loss and recovery across wind-damaged sites with varying forest age and compositional characteristics? We hypothesized that plots with more basal area loss due to wind damage would have more C stored in fine and coarse woody debris (FWD and CWD, respectively) due to inputs from damaged trees, and that plots with less basal area remaining, regardless of the amount of basal area loss, would have more C stored in understory vegetation due to greater light availability and more C in leaf litter fuels due to more canopy cover, and thus, more leaf area. We expected that C loss during fire reintroduction would be greatest in plots with the highest C pools stored in fuels, especially fine fuels (leaf litter, understory vegetation, and FWD), which dry fast and easily ignite (Cannon et al., 2017; Cansler et al., 2019; Sah et al., 2006). We also hypothesized that C recovery rates would be slowest in plots that experienced the most fuel consumption, particularly those with significant loss of slowly replenished fuels like the SOL and CWD (see Appendix table A1 for detailed hypotheses). Ultimately, this study provides detailed insight into C pool dynamics in wind-damaged forests, informing landowners and managers about C implications of prescribed fire treatments and potentially improving their application. Additionally, this work enhances our understanding of the role of southeastern U.S. forests in long-term C sequestration.

Methods

Study description and experimental design

Our study examined four sites across coastal and inland Alabama and Florida, each with distinct wind damage types, fire histories, forest compositions, and ages (Table 1). Two coastal sites experienced hurricane-damage: Weeks Bay National Estuarine Research Reserve (30.4350 °N, 87.8247 °W, AL; hereafter referred to as Weeks Bay) and Betty & Crawford Rainwater –

Perdido River Preserve (30.4655 °N, 87.4094 °W, FL; hereafter referred to as Perdido). The two inland sites experienced tornado and straight-line wind damage, respectively: Oakmulgee, part of the Talladega National Forest, Hale, AL (32.9770 °N, 87.4855 °W) and Flagg Mountain, Coosa County, AL (32.9823 °N, 86.3632 °W).

The two coastal sites, Weeks Bay and Perdido, shared similarities in climate and fire management history (treated with prescribed fire every 2-3 years), but differed in forest composition, stand age, and hurricane impacts. Prior to this study, prescribed fire was last implemented at Weeks Bay in July 2016 before receiving damage from hurricane Sally (category 2) and Zeta (Category 3) in 2020. The hurricane-damaged area (13.4 ha) was a mature stand (60+ years) of coastal slash pine (*Pinus elliottii*). Perdido, 8 km from Perdido Bay, was affected by hurricane Zeta in 2020 (Category 3). The damaged stand (12.3 ha) was young (~20 years), consisting mainly of longleaf pine (*Pinus palustris)*, and prescribed fire was last applied prior to hurricane damage in March 2019. Both Weeks Bay and Perdido are classified within the humid subtropical climate region of the Köppen climate classification system (Kottek et al., 2006) with a mean annual low and high temperatures of 16 °C and 33 °C, respectively, and average annual precipitation of 1700 mm. Weeks Bay and Perdido are ~5 and 7 m, respectively, above mean sea level (MSL) (Google Earth Pro Version 7.3). At Weeks Bay, soils are primarily of Okenee and Hyde series (fine-silty, mixed, active, thermic Typic Umbraquults). At Perdido, soils are primarily of the Hurricane (sandy, siliceous, thermic Oxyaquic Alorthods) and Albany series (siliceous, subactive, thermic Aquic Arenic Paleudults), respectively (https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx, Web Soil Survey, USDA, accessed on 10/14/2024).

The two inland sites, Oakmulgee and Flagg Mountain, shared similarities in climate, forest composition (i.e., mixed pine-hardwood), and age but varied in wind damage type, prescribed fire history and soils. Oakmulgee received EF3 tornado damage in March 2021. This was a mature (~ 60-year-old) longleaf pine mixed hardwood stand (41.3 ha) with white oak (*Quercus alba),* post oak (*Q. stellata*), southern red oak (*Q. falcata*) and hickory (*Carya* spp.) being major hardwoods. Prior to this study, Oakmulgee experienced prescribed fire every 2-3 years for last 20+ years. After the tornado damage, prescribed fire was re-introduced to the stand in February 2023. The site elevation of Oakmulgee is ~ 147 m (Google Earth Pro Version 7.3). For this area, average annual precipitation is 1369 mm with mean annual low temperature 1 °C and mean annual high temperature 27 °C (PRISM 2020). Soils are of Wadley-Smithdale-Boykin complex (sandy, siliceous, thermic), Smithdale sandy loam (fine-loamy, siliceous, thermic Typi Paleudults), Maubila-Smithdale-Boykin complex (fine-loamy, siliceous, thermic) (https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx, Web Soil Survey, USDA, accessed on 10/14/2024). In contrast to the other three sites, Flagg Mountain had (23.8 ha) not been burned for at least the last 60 years but received damage from straight line winds in April 2020. The overstory was dominated by longleaf pine and fire-adapted hardwoods: scarlet oak (*Quercus coccinea*), southern red oak (*Q. falcata*), white oak (*Q. alba*). The site elevation of Flagg Mountain is ~ 220 m (Google Earth Pro Version 7.3). For Flagg Mountain, average annual precipitation is 1397 mm with mean annual low temperature 1 °C and mean annual high temperature 26 °C (PRISM 2020). Soils are of the Bethlehem-Madison complex (fine, kaolinitic, thermic Typic Kanhapludults), consisting of loamy surface horizon, a gravelly sandy clay loam and sandy loam horizons (https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx, Web Soil Survey, USDA, accessed on 10/14/2024).

Fire restoration in the wind-damaged stands

At the two hurricane-damaged sites, the first prescribed fires restored to the forests after receiving wind damage were in spring 2022. At Weeks Bay, the prescribed fire occurred on April

27, 2022, ~1.5 years after wind damage. The fire was ignited by drip torch by hand and All-Terrain Vehicle (ATV) at ~ 1330 hours on the southeastern edge of the unit and was mostly extinguished, except for smoldering dead wood, by 1700 hours. During the burn, winds were out of the north/northwest at 2.2-3.3 m/s. Relative humidity was 25-55%, and air temperature was 25-27 °C. In the week immediately prior to the burn, the Keetch-Bryam Drought Index (KBDI) ranged from 131-212. At Perdido, the burn occurred on March 21, 2022, ~1.5 years after wind damage, and was ignited on the west/northwest side of the unit starting at 1040 hours by hand using drip torches, and fire continued until 1600 hours. Winds were out of the east/southeast at 1.4-2.2 m/s with gusts to 3.3 m/s. Relative humidity was 29-51%, and air temperature was 22-28 °C. KBDI ranged from 98-128 in the week prior to burn.

Prescribed fire was reintroduced at Oakmulgee in spring 2023, ~2 years after wind damage, while prescribed fire was reintroduced after 60+ years at Flagg Mountain in spring 2024, marking its first burn after a long absence of fire. At Oakmulgee, the prescribed fire occurred on February 26, 2023, around 1020 hours and continued until 1345 hours. Ignition began at 1035 hours on the SW corners. The fire was ignited by drip torches by hand. During the burn, the air temperature was 24-27 °C with relative humidity 48-55 %, winds on average of 2.2-3 m/s from north/northeast direction, and KBDI of 100-200 (USFS Wildland Fire Assessment System, WFAS, https://www.wfas.net/data/wfas/, accessed 9/19/2024). At Flagg Mountain, the re-entry prescribed fire occurred on February 15, 2024, nearly 4 years after wind damage. The fire was ignited using drip torch by hand around 1000 hours and continued until 1500 hours with an average southeast wind speed of 1.9-2.8 m/s and air temperature of 10-19 °C to prevent the severe burning of SOL. The relative humidity was 35-45% and KBDI was 100-128 on the day of burn (USFS Wildland Fire Assessment System, WFAS, https://www.wfas.net/data/wfas/, accessed 9/19/2024).

Sample plot design

Prior to sampling, wind-disturbed areas receiving fire restoration at all four sites were delineated using satellite imagery in Google Earth (Google Earth Pro Version 7.3), and plots were kept within the delineated area. Plot density and number varied between sites due to differences in size, location, and configuration of wind-damaged areas within the prescribed fire units. In all cases, we established a 15-m fixed-radius sampling plot arranged to stratify a range of wind damage severity. To determine sampling plot locations at Weeks Bay, we subdivided the wind-disturbed site into six 70-m wide x 280-m long sections arrayed parallel to the bay, each containing 16 grid cells (35-m x 35-m). Within each of the six sections, five grid cells were randomly selected for plot locations (n = 30 plots), which encompassed an array of wind damage based on visual detection of downed trees from satellite imagery and ground observations. At Perdido, eight plots representing a gradient ranging from no obvious wind damage (no down trees) to high damage (8–10 down trees) were established in the central part of the burn unit that was impacted by hurricane damage and dominated by longleaf pine (6.2 ha). At Oakmulgee, we established two parallel transect lines (470 m) along the tornado path using GIS, with 25 plots spaced ~ 90 m apart. Additionally, we included five randomly selected plots in areas with no tornado damage to capture a gradient of no damage, low damage, medium damage, and high damage. At Flagg Mountain, the tornado-affected area was delineated utilizing satellite imagery following an initial on-site evaluation. The damaged region was subdivided into 35 grid cells, each measuring 90 m in length and width, using ArcGIS Pro software. The centers of these cells were designated as plot centers. Five plots, with their plot centers located within creeks, were subsequently excluded, resulting in a final count of 30 sampling plots.

At all sites, each plot had a 15-m fixed-radius, with plot center marked with metal rebar for re-location (Figure 1). Three transects extended from plot center in the north (0°), southeast (135°), and southwest (225°) directions, and each transect was marked with pin flags at 5, 10, and 15-m intervals to facilitate sampling.

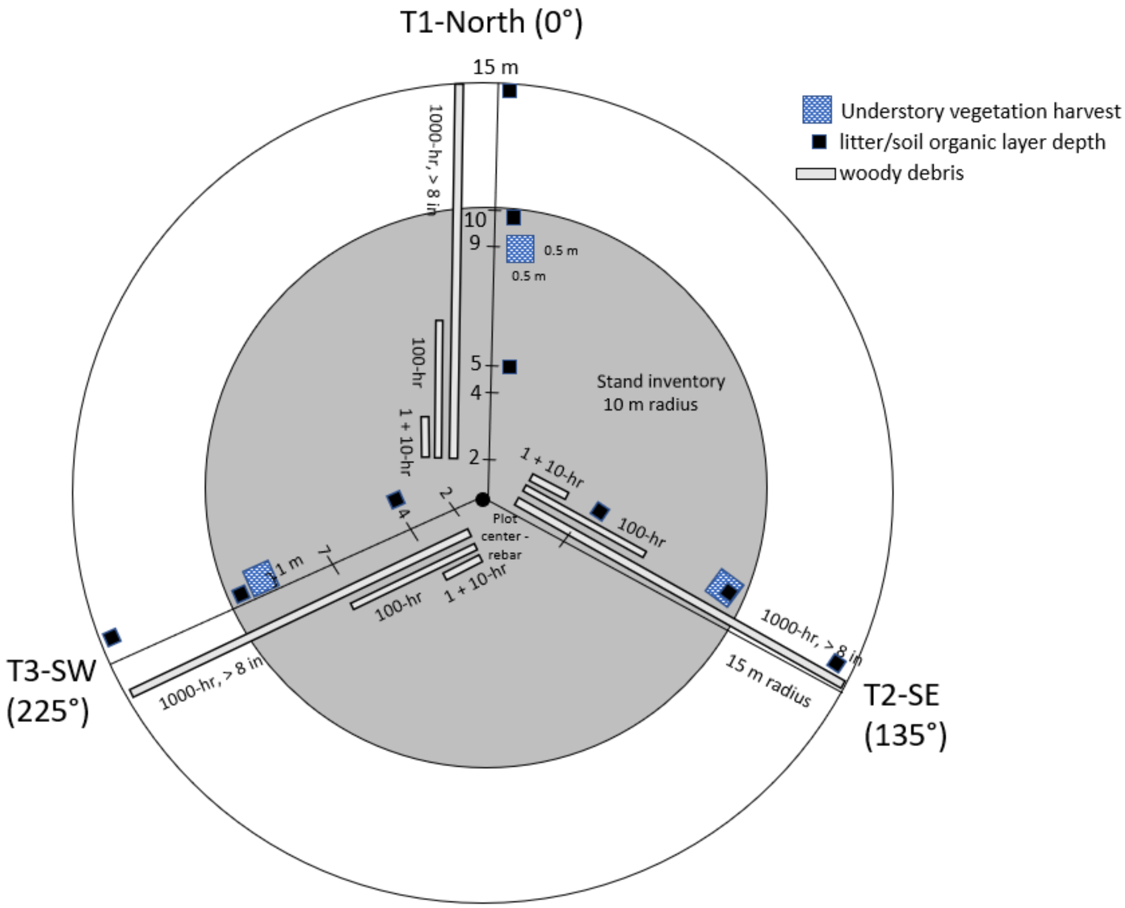

Figure 1: Schematic of fixed radius plots and sampling locations for stand inventory of live trees and snags, understory vegetation via harvest, leaf litter and soil organic layer depth, and downed woody debris (1, 10, 100, and 1000-hour woody fuels) tallies, which were used to calculate carbon pools in wind-damaged, fire-managed forests at four sites in the southeastern U.S.

Pre-wind Damage Stand Reconstructions

To determine the amount of wind damage at each plot, we reconstructed the total basal area of trees that existed prior to wind damage by measuring the basal area of all live (standing and leaning live trees with signs of green leaves and/or live cambium) and dead (both standing and fallen trees, including snags, stumps, and trees that were uprooted completely, snapped along the trunk, or had entire loss of the crown). All live trees and snags originally rooted within the sampling radii of their respective size classes were measured for diameter at breast height (DBH; 1.37 m aboveground). Measurements, which occurred after the burns, were acquired in November 2023 for all sites except Oakmulgee (March 2024). Despite this post-burn sampling, we are confident that damages observed were due to the impact of recent wind events for several reasons: (1) satellite imagery of the stands before and after the wind events indicate few snags or downed trees prior to the wind events; (2) visual inspection of downed trees and stand damage revealed crown loss and branch stripping consistent with wind damage, clean trunk snaps without fire-related charring, uprooted trees with intact, unburned root systems, and directional fall patterns aligning with reported wind events; (3) researchers and land managers of each site confirmed that the majority of downed trees were observed only after the wind events. Basal area (m^2 ha^{-1}) was calculated using the following equation.

$$(1)\ \mathrm{BA} = \left(\pi \times \left(\frac{\mathrm{DBH}}{2}\right)^2\right) \times \left(\frac{10000}{A}\right)$$

Where BA is basal area (m^2 ha^{-1}), DBH (m) is diameter at breast height, and A is area sampled (m^2) for each of three tree size classes based on DBH: sapling (0-10 cm), midstory (10-19.9 cm), and overstory (> 20 cm).

Estimating C Pools and Fuel Loads

Because sites varied in the timing of wind damage and prescribed fire re-introduction, sampling periods differed among the four sites. At Weeks Bay and Perdido, we quantified above- and soil surface C pools in four phases: prior to fire reintroduction (< 1 month), immediately after the fire (within 1-2 weeks), 1-year post-fire, and 2-year post-fire (Table 1). At Oakmulgee, we omitted C pool sampling in 2-years post-fire, and at Flagg Mountain, we omitted C pool sampling both 1- and 2-years post-fire.

We inventoried live trees and snags to estimate biomass within plots before the burn and during the 1- and 2-year post-burn assessments. We did not take tree measurements immediately after the fire because we expected that signs of tree mortality would not be evident so soon after the prescribed burn. We measured the DBH of live trees and snags categorized as overstory, midstory, or saplings within radii of 10 m, 5 m, and 2 m from the plot center, respectively, and identified them to species. For snags, we estimated the height of tree that remained based on surrounding trees that remained to adjust for missing biomass in our snag C pool calculations. We calculated aboveground biomass for trees using the 'allodb' R package, which includes a curated selection of published allometric equations (Gonzalez-Akre et al., 2022). The resulting biomass for live trees was converted to C by applying a standardized conversion factor of 0.5 (Domke et al., 2012). For snags, we adjusted biomass by multiplying it by the percentage of trees remaining and then applied the conversion factor to determine the C pool.

We estimated understory vegetation biomass using 0.5-m x 0.5-m quadrats (0.25 m^2) placed ~ 1 m away from either the 4-m or 9-m mark along each of the three transect lines. To prevent resampling areas that had already been harvested, we changed the sampling locations for each sampling period (4-m mark for immediate postfire sampling period, other side of transect at

9-m mark for 1-year postfire sampling, 8-m mark for 2-year postfire sampling). If a large tree obstructed the quadrat, we slightly adjusted the quadrat's location to ensure unobstructed sampling. Within each quadrat, we clipped and harvested all plant biomass down to the surface of the SOL, and placed in pre-labeled paper bags. In the laboratory, we examined samples for any leaf litter and FWD; if present, we discarded these materials, as we accounted for these C pools using other sampling techniques (see below). We then placed remaining plant biomass in paper bags and dried in an oven at 60 °C for ~48 hours until they reached a constant weight. After removing samples from the oven, we allowed them to cool for ~ 10 minutes to return to room temperature and weighed them immediately. We corrected the sample weights to account for the average weight of the paper bags used during harvesting, which we determined prior to analysis by weighing multiple bags of each bag type used and averaging their weights to establish a standardized bag weight for each type. Finally, we divided the oven-dried biomass values by the sampled area to obtain grams of dry weight per unit area and applied a conversion factor of 0.5 to estimate the C pool from the biomass (Domke et al., 2012).

Dead FWD and CWD C pools were estimated using the Brown's planar intercept method along each of the three transect lines mentioned above (Brown, 1974). Beginning at the 2-m mark of each transect, wood pieces of different sizes and time lag (number of hours for each size class to respond to a certain level of change in relative humidity; Brown, 1974) were tallied in a nested approach, with smaller pieces tallied along a shorter distance than larger pieces. Size class diameters included 0-0.64 cm (1-hour), 0.65-2.54 cm (10-hr), 2.55-7.62 cm (100-hr), >7.62 cm (1,000-hr). The two smallest classes were measured along a 2 m portion of transects (from the 2 m to 4 m position), the 100-hr class along a 5 m portion (from 2 m to 7 m position), and the 1000-hr class along a 13 m portion (from 2 m to 15 m position). 1000-hr fuels were further assessed for diameter and decay class where the log crossed the sampling transect based on five decay classes following Lutes et al (2006). Woody debris biomass was calculated using standard formulas from Brown (1974). Standard specific gravity values for 1-, 10-, and 100- hr fuels were used (Anderson, 1978). Species identification for 1000-hr fuels was not done in the field as species identification based on bark traits was not always possible. Therefore, specific gravity values for 1000-hr fuels were calculated as weighted mean of the specific gravities of overstory trees based on basal area of the respective plot (Miles, 2009; Woodall and Monleon, 2008). The resulting biomass was converted to C pool by applying a standardized conversion factor of 0.5 (Smith et al., 2006).

To quantify leaf litter (Oi) and SOL (Oe + Oa) C pools, we measured leaf litter and SOL depth with a ruler at fixed locations on each transect. During pre-burn and immediate post-burn sampling, litter depth and duff depth were measured at the 4-m and 9-m positions where understory vegetation harvests occurred. During later sampling dates, depths at 5-m, 10-m, and 15-m positions. Leaf litter depths were used along with site-specific bulk density (Weeks Bay = 28 kg m^{-3} , Perdido = 24 kg m^{-3} , Flagg Mountain = 28 kg m^{-3}, Oakmulgee = 27 kg m^{-3}) and site-specific %C (Weeks Bay = 49.8 , Perdido = 50.1 , Flagg Mountain = 49.7, Oakmulgee = 50.0), which were determined using leaf litter samples harvested from various locations at each site during 1-year and 2-year postfire sampling. To calculate leaf litter C pools, following equation was used:

$$\text{C pool (tons ha}^{-1}\text{)} = \text{depth (cm) x bulk density (g cm}^{-3}\text{) x \% C x 100}$$

We also harvested SOL from all sites on the same sampling dates as leaf litter to determine bulk density and %C. Both bulk density and %C exhibited considerable variation with SOL depth, likely due to mineral soil contamination of this portion of the SOL, thereby prohibiting the use of average bulk density and %C values in SOL C pool calculations. Therefore, we calculated SOL C pools using a linear model (C Pool (tons ha^{-1}) = -0.02248 + 6.03108 * SOL Depth (cm)) relating depth to C pools. A single model was fit to data from all four sites, as we found no significant difference in slopes of models fit to sites independently or from samples with different burn histories (Appendix Figure A2 and Table A3).

Data Analysis

Wind damage severity was quantified using basal area loss and basal area remaining. We captured a wide range of basal area loss across plots at Weeks Bay, Perdido and Flagg Mountain, while we had intentionally sampled five plots without wind damage at Oakmulgee. One-way ANOVA revealed significant differences in basal area loss among sites ($F(3, 95) = 11.01$, $p < 0.001$), with Weeks Bay experiencing significantly higher basal area loss (mean basal area loss = 16.0 ± 11.7 m^2 ha^{-1}) than all other sites ($p < 0.05$ for all comparisons). Flagg Mountain retained most of its basal area with 21 out of 30 plots losing < 5 m^2 ha^{-1} of basal area (mean basal area loss = 4.29 ± 5.02 m^2 ha^{-1}; Figure 2A and 2B). Because both basal area loss and pre-wind event total basal area were not uniform across plots, we also anticipated an effect of remaining basal area on fuel load distribution, fuel condition and subsequent C loss during re-introduction of fire. Thus, we assessed both basal area loss and basal area remaining as metrics of wind damage.

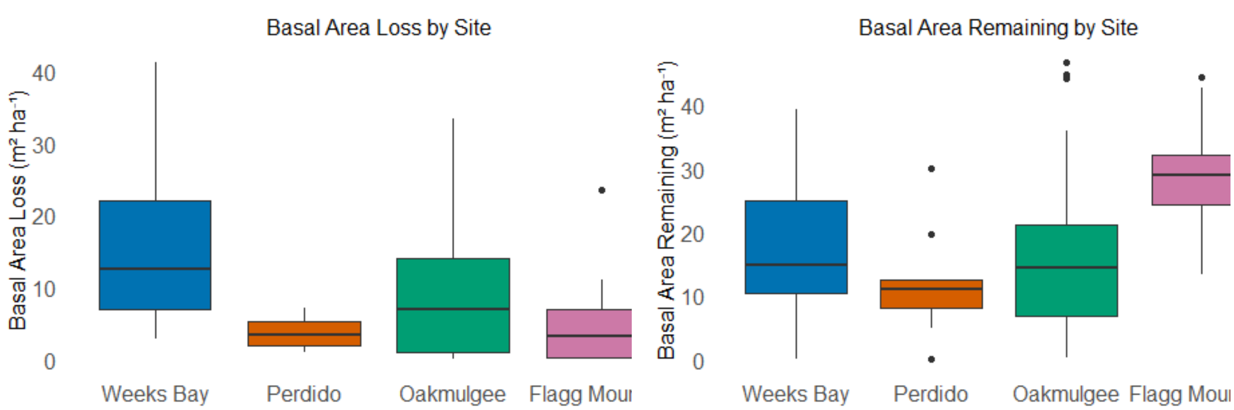

Figure 2: Mean basal area loss (A) and remaining (B) following wind events across plots at wind-damaged, fire-managed forests at four sites in the southeastern U.S. based on stand reconstruction surveys.

To calculate fuel loads for each plot at each site, we summed C pools that could contribute as fuel during prescribed fire re-introductions (CWD, FWD, understory vegetation, SOL, and leaf litter), thereby excluding live trees and snags. To examine the relationship between wind damage and fuel load C pools, we used linear regression focusing on the association between basal area loss or basal area remaining with fuel load C pool components and total C pool fuel loads.

Carbon loss for each plot at each site during prescribed fire was estimated by subtracting the immediately post-fire C pool from the pre-fire C pool for all individual C pools. We excluded trees and snags in the total C loss calculation as we did not measure them immediately post-fire since we did not expect them to change due to low-intensity surface fires. We acknowledge that estimating C loss based on C estimation before and after burn could result in underestimation of C loss during fire due to inputs of FWD and CWD during fire. Sites were sampled immediately after the burn, as soon as conditions were safe for sampling, assuming that comparing the pre-fire C and post-fire C was the best way to estimate C loss (consumption). The loss in each C pool (CWD, FWD, understory vegetation, SOL, and leaf litter) was summed to calculate the total C loss (C tons ha^{-1}). We also explored the impact of basal area loss and basal area remaining on C resilience observed for 1-year post fire period and 2-year post fire period and found correlations for only understory vegetation C, which were very weak (Appendices Figure A8-A11). To assess post-fire C resilience, we divided C recovered during the 1-year or 2-year post-fire time point measurements by pre-fire C. Positive resilience value below 1 meant recovery of C but not yet the pre-fire level, value more than 1 means C recovered post fire exceeded the pre-fire level, while negative values meant there was loss of C post-fire. We then used linear regression to examine the relationship between C resilience and C loss during fire.

Initially, we used simple linear regression to examine potential linear relationships between (C) loss and wind damage indicators (basal area loss and basal area remaining; Appendices Figure A6 and Figure A7). Few C pools exhibited significant linear relationships with wind damage. Further analysis of the relationship between C loss during fire and pre-fire fuel loads (measured in C tons ha^{-1}, hereafter referred to as pre-fire fuel load C pools for consistency) revealed more pronounced associations compared to those with basal area loss and remaining. Similarly, the relationship between C recovery after fire reintroduction and C loss during fire was more pronounced than the relationship between C recovery and basal area loss or remaining. Consequently, we focused our analysis on the relationship between C loss during fire and pre-fire fuel load C pools, as well as the relationship between C recovery and C loss during fire.

Data availability varied across sites due to different study initiation times, necessitating two separate analysis approaches. Pre-fire, immediate post-fire, one-year post-fire, and two-year post-fire period data were available for Weeks Bay and Perdido. Data up to one-year post-fire was available for Oakmulgee, while Flagg Mountain had data only up to the immediate post-fire period. Consequently, we used repeated measures ANOVA to analyze the data, accounting for correlations between repeated measurements over time within each site. We analyzed total and individual C pools across different sampling periods both within and across sites, with additional site-specific analyses to explore temporal variations in C pools

All statistical analyses were performed using R software (version 4.4.1, R Core Team, 2024), with a significance level of $\alpha = 0.05$ applied to all statistical tests. We checked for normality of residuals using the Shapiro-Wilk test and Q-Q plots, and homogeneity of variances using Levene's test. When necessary, data were log-transformed to meet assumptions of normality and homoscedasticity.

Table 1:General site information, wind event descriptions, prescribed fire history, details of prescribed fire reintroduction, and sampling dates for study sites: Weeks Bay, Perdido, Oakmulgee, and Flagg Mountain of southeastern U.S.

Characteristics	**Weeks Bay**	**Perdido**	**Oakmulgee**	**Flagg Mountain**
General Information				
Location	Fairhope, AL	Escambia, FL	Hale, AL	Coosa, AL
Lat/Long	30.4350 N, 87.8247 W	30.4655 N, 87.4094 W	32.9770 N, 87.4855 W	32.9823 N, 86.3632 W
Landscape Position	Coastal	Coastal	Inland	Inland
Stand type	Slash Pine	Coastal Longleaf Pine	Mixed Longleaf Pine - Hardwood	Mixed Longleaf Pine - Hardwood
~ Stand Age (yr)	60	20	60	70
Wind Event				
Type	Hurricane (Sally, Zeta)	Hurricane (Sally, Zeta)	Tornado	Straight Line Wind
Dates(s)	Sep/Oct 2020	Sep/Oct 2020	Mar 2021	Apr 2020
Intensity	Category 2 & 3	Category 2 & 3	EF 3	-
Mean BA Loss (m^2 ha^{-1})	15.9	3.5	8.9	4.3
BA Loss Range (m^2 ha^{-1})	0-41.2	1-7.5	0-33.4	0-23.5
Prescribed Fire				
Pre-Wind Event History	Burned every 2-3 years (20+ years)	Burned every 2-3 years (20+ years)	Burned 2-4 years (20+ years)	Unburned for last 60 years
Prescribed fire Date	Apr 2022	Mar 2022	Feb 2023	Feb 2024
Relative Humidity (%)	25-55	29-51	48-55	35-45
Wind Speed (m/s)	2.2-3.3	1.4-2.2	2.2-3	1.9-2.8
Air Temperature (°C)	25-27	22-28	24-27	10-19
Keetch-Bryam Drought Index (KBDI)	131-212	98-128	100-200	100-128
Sampling Dates				
Pre-Fire	Mar 2022	Mar 2022	Feb 2023	Feb 2023
Immed-Post Fire	Apr 2022	Apr 2022	Mar 2023	Feb 2024
1-year post-fire	Mar 2023	Mar 2023	Mar 2024	*NA*
2-year post-fire	Mar 2024	Mar 2024	*NA*	*NA*
Stand Reconstruction Survey	Nov 2023	Nov 2023	Mar 2024	Nov 2023

(*NA = not applicable, indicating sites that were not sampled during specific periods due to timing of wind events and prescribed fire re-introduction; BA = basal area; EF = Enhanced Fujita, a scale rating for Tornado).*

Results

Wind damage and C pool distribution

Wind damage severity significantly influenced some fuel load C pools such as CWD and total fuel load C across study sites, with CWD showing the strongest response to basal area loss. As basal area loss increased, CWD C pools increased at all sites except Weeks Bay (Figure 3A). Perdido and Flagg Mountain had the strongest CWD-basal area loss relationships ($R^2 = 0.734$ and 0.664 $p = 0.003$ and < 0.001, respectively), with weaker correlations at Oakmulgee ($R^2 = 0.159$, $p = 0.029$) (Figure 3A). While the linear relationship between total fuel load C pools was not significant at Weeks Bay and Perdido, total fuel load C pools exhibited weak positive linear relationships with increased basal area loss at Flagg Mountain ($R^2 = 0.228$, $p = 0.008$) and Oakmulgee ($R^2 = 0.173$, $p = 0.022$), which were primarily driven by CWD (Figure 3B). All other fuel load C pools showed no significant relationships with basal area loss (Appendix Figure A4) or basal area remaining (Appendix Figure A5), exclusive of a weak positive linear correlation between basal area remaining and leaf litter C pools at Oakmulgee ($R^2 = 0.14$, $p = 0.04$, Figure 3C).

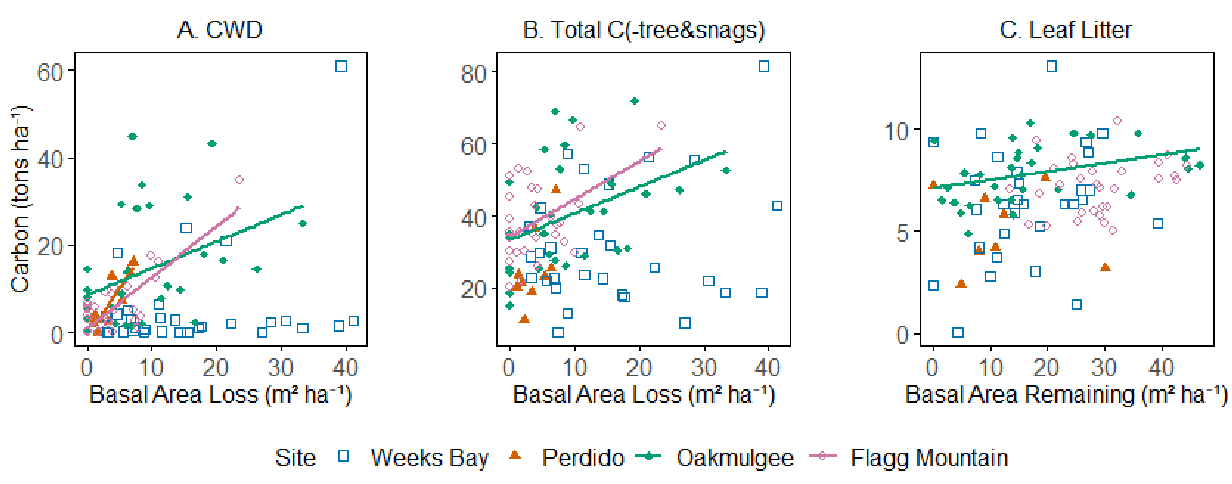

Figure 3: Post-wind event (but prior to prescribed fire reintroduction) (A) coarse woody debris (CWD) and (B) total carbon in fuels (excludes live trees and snags) as a function of basal area loss;

and (C) leaf litter C pool as a function of basal area remaining at wind-damaged, fire-managed forests at four sites in the southeastern U.S.

C loss during prescribed fire

Individual fuel load C pool loss and total fuel load C loss during prescribed fire were highly correlated with total fuel load C pools (excludes trees and snags) present before fire at all sites (Figure 4). Coarse woody debris (CWD) C loss exhibited significant positive relationships with pre-fire fuel load C pools at Weeks Bay ($R^2 = 0.17$, $p = 0.025$), Perdido ($R^2 = 0.54$, $p = 0.024$), and Flagg Mountain ($R^2 = 0.15$, $p = 0.035$), but not at Oakmulgee ($R^2 = 0.02$, $p = 0.47$; Figure 4A). Fine woody debris (FWD) C loss demonstrated a strong positive linear relationship with pre-fire fuel load C pools only at Perdido ($R^2 = 0.82$, $p < 0.001$), with other sites showing no significant correlations (Figure 4B). Leaf litter C loss was notably linked to pre-fire fuel load C pools at Weeks Bay ($R^2 = 0.26$, $p = 0.004$), but this trend was not observed at other sites (Figure 4C). The SOL C loss had significant positive relationships with pre-fire SOL C at Weeks Bay ($R^2 = 0.15$, $p = 0.036$) and Flagg Mountain ($R^2 = 0.17$, $p = 0.026$), while Perdido ($R^2 =0.02$, $p = 0.69$) and Oakmulgee ($R^2 = 0.07$, $p = 0.15$) showed no significant correlations (Figure 4D). Understory vegetation C loss showed correlation with pre-fire C pool at Weeks Bay ($R^2 = 0.26$, $p = 0.004$), with other sites showing no significant relationships (Figure 4E). Total fuel load C loss (excludes trees and snags) showed the most consistent trends across sites. Weeks Bay exhibited a significant relationship ($R^2 = 0.33$, $p < 0.001$) with C loss increasing by 0.581 tons ha^{-1} for every 1-ton ha^{-1} increase in total fuels. Perdido demonstrated an even stronger correlation ($R^2 = 0.87$, $p < 0.001$), where total C loss increased by 0.575 tons ha^{-1} per unit increase in total fuels. Oakmulgee showed no significant relationship, while Flagg Mountain displayed a weaker but still significant correlation ($R^2 = 0.26$, $p = 0.004$) (Figure 4F).

Only CWD C, leaf litter C, and total fuel load C (excludes tree and snags) loss during fire correlated with basal area loss (Appendix Figure A4). There was an increase in CWD loss with increase in basal area loss at Perdido and Flagg Mountain, while total fuel load C loss Flagg Mountain was driven by CWD loss. Leaf litter C loss decreased with increased basal area loss, but increased with increased basal area remaining, while all other C pool losses showed no relationship with basal area loss or remaining (Appendix Figure A4 and A5).

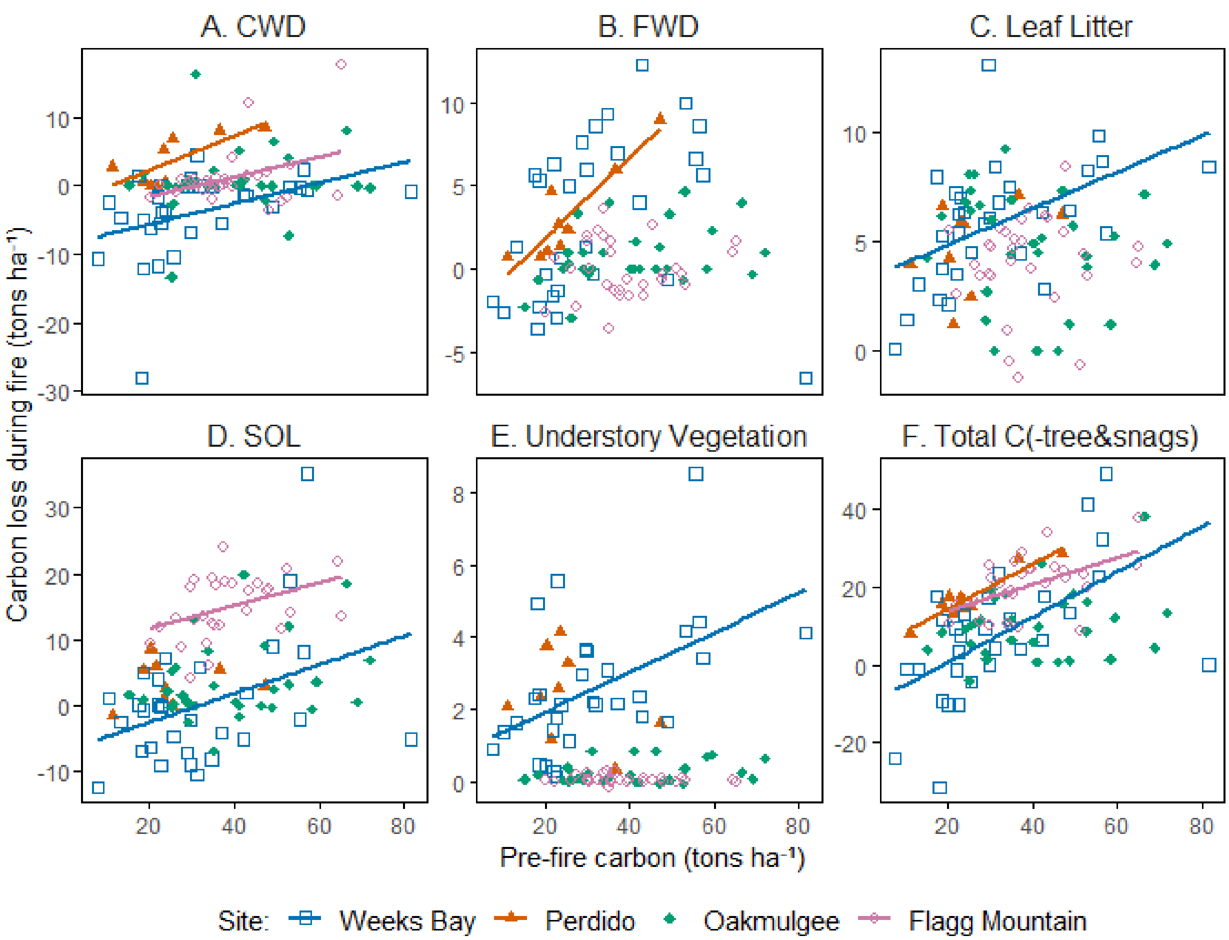

Figure 4: Carbon loss during prescribed fire as a function of pre-fire carbon as fuel load (i.e., all carbon pools that could serve as fuels) for (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total fuel load C pools (excludes live trees and snags). Note: C = carbon, + values = loss, - values = gain) at wind-damaged, fire-managed forests at four sites in the southeastern U.S.

C resilience

C resilience observed one year after fire

For one year period after fire, the resilience of C pools (C recovered / initial C) following prescribed fire did not exhibit linear trend with total C loss apart from few C pools at Weeks Bay (Figure 5). Coarse woody debris showed linear trends with total C loss and CWD C only at Weeks Bay ($R^2 = 0.32$, $p = 0.005$) but CWD C was not resilient at all sites (Weeks Bay= -1.76, Perdido = -0.16, and Oak = -0.003; Figure 5A). FWD C pool also showed linear relationship with total C loss during fire at Weeks Bay ($R^2 = 0.20$, $p = 0.013$, mean resilience = -0.43; Figure 6B). For all other individual C pools at all sites and Oakmulgee, no significant relationships were observed between total C loss and resilience for any C pool (all $p > 0.05$), but positive mean resilience was observed apart from SOL C at Oakmulgee (-0.08) site indicating decrease for one year recovery period after fire (Figure 6B-6D). For Weeks Bay and Perdido, the highest mean resilience was observed for SOL C with 1.43 and 1.27 respectively, while litter C showed the highest mean resilience (0.99) at Oakmulgee. Although the resilience of total C (excluding tree and snags) correlated with total C loss during fire for only Weeks Bay ($R^2 = 0.24$, $p < 0.007$), positive mean resilience less than 1 was observed at all sites (Weeks Bay = 0.14, Perdido = 0.36, and Oakmulgee = 0.10), indicating sites have yet to recover these C pools.

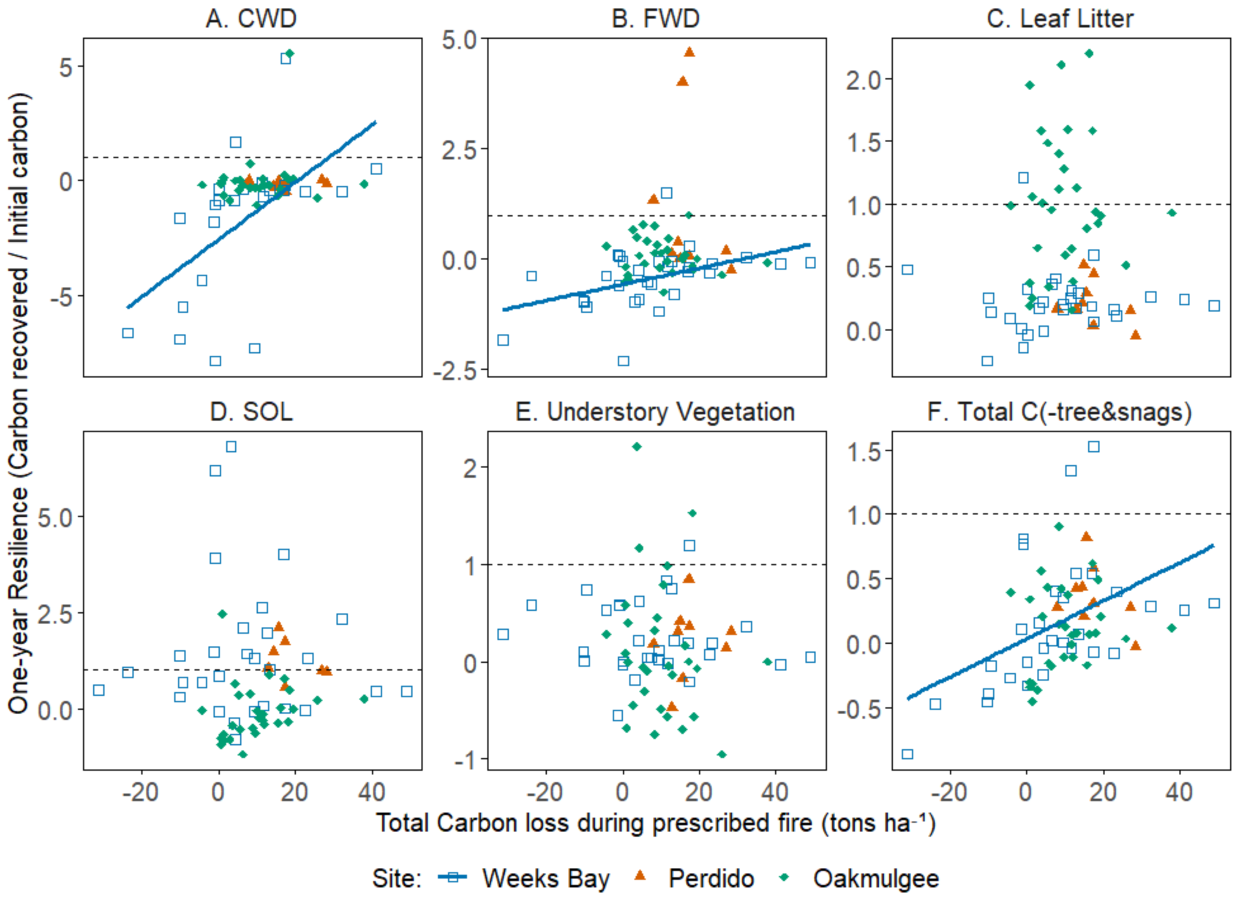

Figure 5: Carbon resilience (C recovered during 1-year period / initial carbon) observed during the 1-year period following prescribed fire re-introduction as a function of carbon loss during prescribed fire for (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total C pool (excludes trees and snags) at three wind-damaged, fire-managed forests at four sites in the southeastern U.S. Note: C = carbon, for y-axis: + values = gain, - values = loss; 1-year postfire sampling is yet to take place at Flagg Mountain at the time of this writing.

C resilience observed two years after fire

The resilience of C pools (C recovered / initial C) observed after two years following prescribed fire showed notable patterns across sites and among C pools (Figure 6). A significant relationship was found between total C loss and CWD C resilience ($R^2 = 0.37$, $p = 0.003$; Figure 6A) as CWD C loss decreased with increase in total C loss during fire. But the resilience for CWD was not observed for Weeks Bay (mean = -1.66) and Perdido (mean = -0.21), indicating continued CWD C loss during the 2-year recovery period following the fire (Figure 6A). FWD C resilience at Weeks Bay showed significant positive relationship with total C loss during fire ($R^2 = 0.23$, $p = 0.008$, slope = 0.02; Figure 6B), with mean resilience of -0.4, while positive resilience was observed at Perdido (mean resilience = 1.59). The resilience of all other individual C pools (leaf litter, SOL, and understory vegetation) was not related with total C loss during fire, with highest resilience of 1.34 observed for SOL at Weeks Bay (Figure 6C-6E). Total C resilience (excluding trees and snags) showed contrasting trends: a significant positive relationship at Weeks Bay ($R^2 = 0.16$, $p = 0.031$) and a significant negative relationship at Perdido ($R^2 = 0.60$, $p = 0.014$). Both Weeks Bay and Perdido had positive mean resilience for total C (Weeks Bay: 0.17, Perdido: 0.44), indicating partial but incomplete C recovery post-fire.

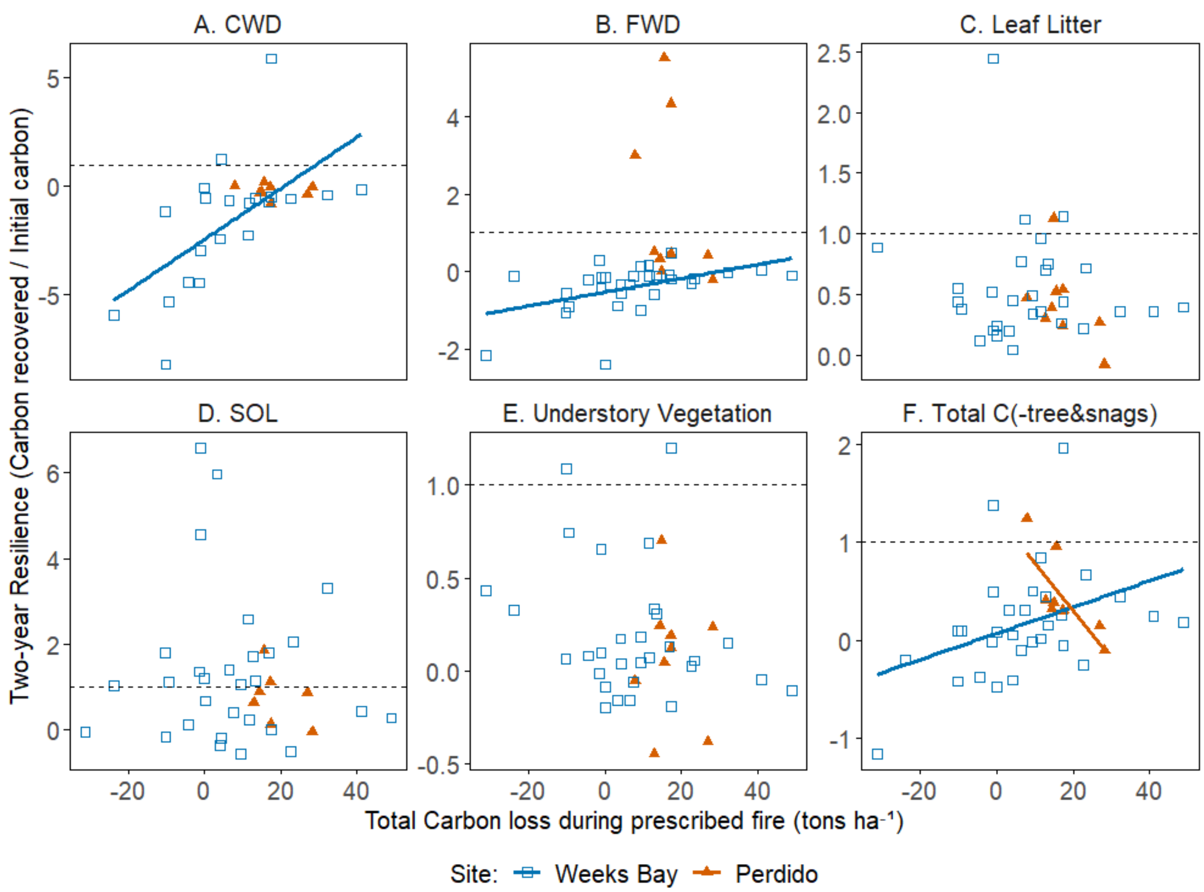

Figure 6: Carbon resilience (C recovered during 2-year period / initial carbon) observed during the 2-year period following prescribed fire re-introduction as a function of carbon loss during the prescribed fire for (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total C pool (excluding trees and snags) at wind-damaged, fire-managed forests at four sites in the southeastern U.S. Note: C = carbon, for y-axis: + values = gain, - values = loss) 2-year postfire sampling is yet to take place at Oakmulgee and Flagg Mountain at the time of this writing.

C pools over time

Woody debris C pools exhibited varied responses to prescribed fire across the study sites. Notably, CWD C increased by 67% at Weeks Bay immediately post-fire, while it decreased at other sites. This increase at Weeks Bay was significant compared to Oakmulgee ($p = 0.02$). Over time, CWD declined further during the recovery phase, with Weeks Bay and Perdido reaching 86% and 27% of pre-fire levels two years post-fire, respectively (Figure 7A).

Fine fuels, including FWD, leaf litter, and understory vegetation, experienced significant reductions immediately post-fire across all sites. FWD decreased significantly at Weeks Bay, Perdido, and Oakmulgee ($p < 0.05$). Recovery was observed over time, with Weeks Bay reaching 44% and Perdido reaching 77% of pre-fire FWD levels two years post-fire (Figure 7B). Understory vegetation also showed recovery one-year post-fire but slowed by the second year (Figure 7E). Leaf litter C exhibited consistent losses at Weeks Bay (92%) and Perdido (92%), remaining significantly lower than pre-fire levels even two years post-fire ($p < 0.001$). In contrast, Oakmulgee showed a notable recovery to 136% of pre-fire levels (Figure 7C). The soil organic layer (SOL) C displayed minimal change at Weeks Bay immediately post-fire (+1%) but varied significantly at other sites, with a reduction of 72% at Perdido and a decrease of 71% at Flagg Mountain. SOL C increased one-year post-fire at Weeks Bay (188%) and Perdido (159%) but stabilized by the second year (Figure 7D).

The total C pool excluding trees and snags decreased significantly immediately post-fire at all sites ($p < 0.001$). Recovery varied, with Weeks Bay achieving 85% of pre-fire levels two years post-fire and Perdido recovering to 63% (Figure 7H). The total C pool, including trees and snags, remained relatively stable across sites, with no significant changes observed at Perdido and Weeks Bay over the two-year period ($p > 0.05$). Overall, total C pool changes ranged from a minor decrease of 4% at Perdido to a more significant reduction of 15% at Flagg Mountain, with intermediate decreases observed at Weeks Bay and Oakmulgee (Figure 7I)

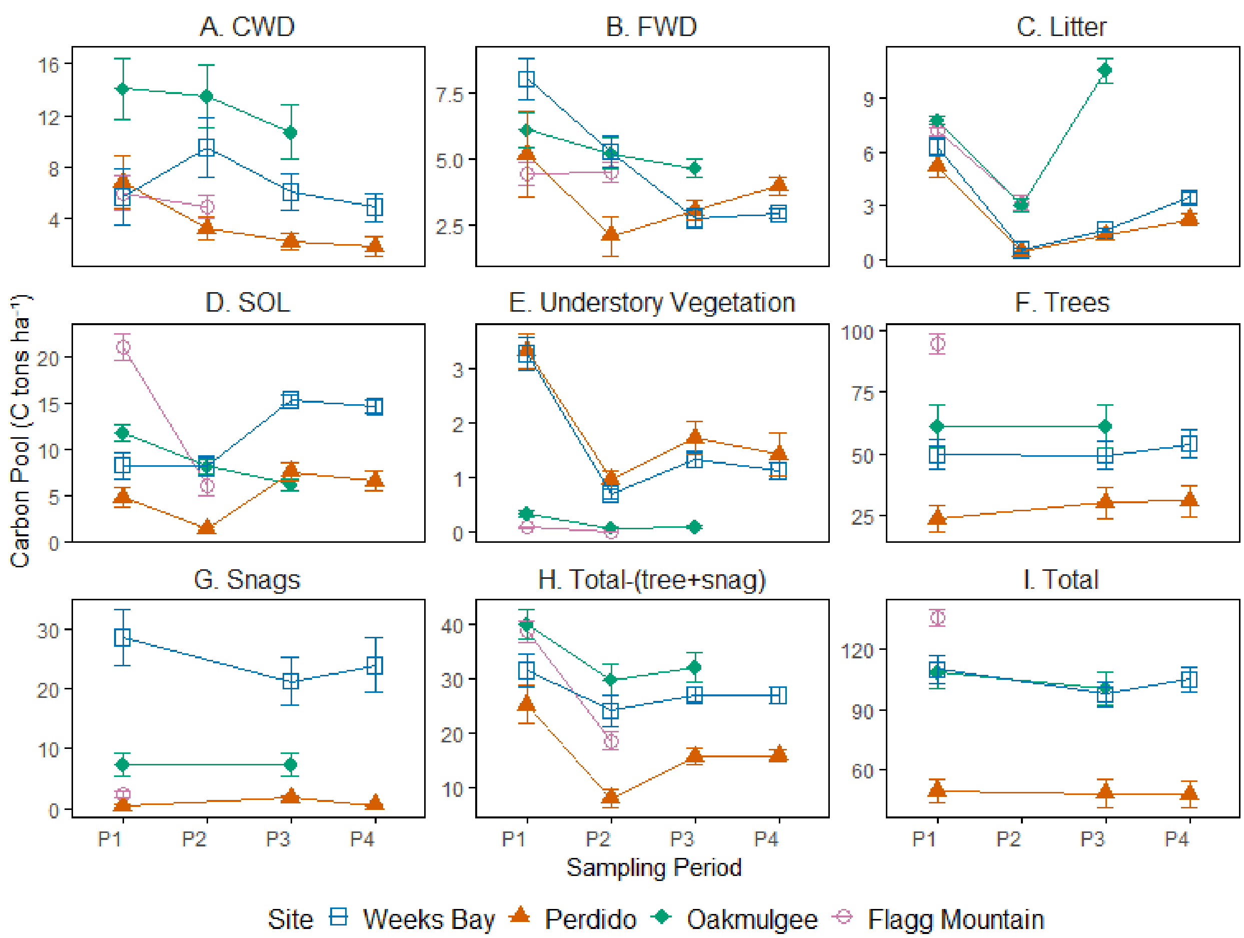

Figure 7: Mean (± SE) C pools during the course of study for (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) trees, (G) snags, (H) total C pool (excluding trees and snags); at wind-damaged, fire-managed forests at four sites in the southeastern U.S. Note: P1= pre-fire sampling

period, P2 = Immediate post-fire sampling period, P3 = One year post-fire sampling period, P4 = two year post fire sampling period.

Discussion

Our findings indicate that C loss during prescribed fire re-introduction into wind-damaged stands is primarily driven by the amount of C stored in fuels prior to the fire, regardless of whether the fuel load distribution was affected by wind events. Different magnitudes of C loss were observed, likely due to different stand age, tree species composition, site characteristics and the fire history of the stand. Leaf litter, understory vegetation, and FWD were often consumed during fire re-introduction, but they recovered quickly through re-growth and inputs post-fire. Coarse woody debris exhibited did not show resilience for all sites, likely due to accelerated decomposition and disintegration after exposure to fire. The one long-unburned site lost a significant amount of SOL C during fire, where frequently burned sites recovered SOL C through replenishment, sometimes exceeding pre-fire levels. This complex interplay between wind damage, fuel loading, fire behavior, and C dynamics underscores the importance of site-specific management strategies in maintaining forest C resilience and storage.

Wind damage effects on C pool fuel distribution

Wind damage severity only appeared to directly influence the distribution of some C pools that act as fuels. Only CWD C pools positively correlated with increased wind damage severity (i.e., basal area loss) at three of the four sites, a finding comparable to several other studies

(Bradford et al., 2012; Pile-Knapp et al., 2022). Strong wind events result in uprooting, snapping and breaking of branches and tree boles, putting large pieces of wood on the ground (Sah et al., 2006). In contrast, Weeks Bay did not exhibit a relationship between CWD C pools and basal area loss as most of the snags (counted as basal area loss) remained standing as snags, rather than falling to the ground as CWD. Overall, distribution of total fuels was primarily driven by CWD distribution at two of the four sites. Carbon pools of other fuels such as FWD, leaf litter, and understory vegetation did not show a significant relationship with basal area loss, most likely due to heterogeneity in spatial structure of fuel loading fine fuels like leaf litter and FWD are concentration beneath the crowns of live or downed trees (Cannon et al., 2014). Lack of correlation between understory vegetation C and basal area loss/remaining suggests that the wind damage did not impact the light availability significantly to influence the response of vegetation or our study period was not enough to see such impacts. In contrast, only leaf litter C positively correlated with basal area remaining likely due to more leaf litter input in areas with more live trees. As expected, SOL C pools were not related to wind events, likely due to the formation of SOL being a gradual long-term process through decomposition of organic materials (Cotrufo and Lavallee, 2022). Thus, the immediate effects of forest structural changes due to wind on C pools that act as fuels appeared mainly due to increases in CWD C pools.

Pre-fire fuel load C pools and C loss during fire re-introduction

The impact of fuel load distribution on C loss during prescribed fire re-introduction was statistically significant, but the weak correlations suggests that the C loss during prescribed fire reintroduction to wind-damaged stands is driven by other things in addition to pre-fire fuel loads, such as intensity of prescribed fire, moisture content of fuel loads, and composition of fuel bed (Atchley et al., 2021; Ritter et al., 2020). The increase in CWD C at Weeks Bay after fire indicated that standing trees damaged by wind events fell down during fire and were counted as CWD. This finding is similar to previous studies which reported two to eight times greater tree mortality in wind damaged stand for two decades after wind events (Hanula et al., 2012; Sharma et al., 2021). Understory vegetation, FWD and leaf litter, which are considered fine fuels, were significantly consumed as they are easily combustible. Overall, significant correlations observed between total C (excluding trees and snags) loss and pre-fire C for 3 out of 4 sites support our hypothesis that increased fuel load leads to more fuel consumption and, thus, greater C loss due to fire. Such findings have been well documented by past studies (Clark et al., 2020; Loudermilk et al., 2012).

Carbon resilience observed after fire re-introduction

The influence of C loss variations across plots on C recovery rates in the 1- and 2-year period following prescribed fire was complex and often counterintuitive. Our findings are similar to the previous studies suggesting impact and magnitude of disturbance, recovery patterns and resilience varies by forest C pools (Peneva-Reed et al., 2021; Rothstein et al., 2004; Vargas et al., 2010). The lack of resilience of CWD C during study period was due to accelerated decay of woody debris due to exposure to fire, and more sunlight due to canopy openings as the most of the CWD had higher decay class in 1-year and 2-year post fire sampling (Garrett et al., 2006; Hanula et al., 2012; Palmero-Iniesta et al., 2017; Zhou et al., 2007). However, the linear trend of loss with total C loss meant more CWD in the ground resulted in higher CWD C loss. FWD C did not exhibit resilience at Weeks Bay, while positive mean resilience of below 1 for all other individual C pools hinted recovery, but not at pre-fire level yet. However, the resilience did not correlate with total C loss during fire indicating that C loss may not be the only factor influencing the resilience of C pools (Falk et al., 2022; Nikinmaa et al., 2020; Thompson et al., 2009). Some plots have shown high resilience with recovery of C up to 5 times of the initial C, likely due to increase in minerals and nutrients in topsoil, greater light availability due to canopy openings contributing to understory vegetation regrowth, which resulted in FWD input and leaf litter input (Borden et al., 2021; Oakman et al., 2019; Odland et al., 2021; Starr et al., 2015; Wang and Kemball, 2005). The high resilience of SOL might be due to increase in the SOL C pool immediately after fire due to our inability to differentiate SOL from mineral soil layer and the deposition of partially burned organic matter from incomplete combustion of fuel load (Cotrufo and Lavallee, 2022; Michelotti and Miesel, 2015). Another possible reason for higher SOL C pool at plots with higher C loss might be the higher deposition of partially burned organic material i.e. Black Carbon (BC) (González-Pérez et al., 2004). The positive relationship shown by total C (excluding trees and snags) resilience with C loss at Weeks Bay suggests that mature stands are more resilient to higher C loss compared to young stand (i.e. Perdido). Overall, individual C pools and total C (excluding trees and snags) showed resilience as expected, apart from CWD and FWD, which were supposed to decrease naturally (Fraver et al., 2013; Schmid et al., 2016).

Carbon pool dynamics across pools and sites

Prescribed fire after wind events induced diverse temporal changes in C pools across the four study sites based on available data. The patterns of C loss and recovery varied inconsistently among wind-damaged sites, likely due to differences in stand-age, species composition, forest composition and site quality (Anderson-Teixeira et al., 2013; Reinikainen et al., 2014). Different C pools responded differently to wind and fire disturbances, reflecting their distinct C storage and loss mechanisms. Weeks Bay, Perdido and Oakmulgee showed similar trends of C loss and recovery due to re-introduction of fire into the wind damaged stand. However, the magnitude of change was smaller at Perdido, likely because it is a young planted longleaf pine stand with smaller overall C pools, and a more open stand to begin with, factors known to influence disturbance impacts (Rich et al., 2007; Wales et al., 2020; Whelan et al., 2024). At Flagg Mountain, pre-fire SOL C pool per unit area was two times higher than SOL C compared to other sites likely due to long absence of fire (60+ years), and SOL C lost during fire was relatively large, driving the overall C loss of that site. This finding is supported by past studies, which reported high consumption of SOL during re-entry fires in longleaf and other southeastern forests, conducted after a long absence of fire, resulting in loss of C accumulated over decades (Clabo and Campbell, 2020; Kreye et al., 2014a; Miyanishi, 2001; Zhao et al., 2019). Live tree and snag C pools remained relatively stable throughout study period as low-intensity surface fire did not cause significant changes to live tree and snags C pools at all sites (Bennett et al., 2017; Vaillant et al., 2013). Overall, Weeks Bay and Oakmulgee shared similar patterns of C loss and recovery throughout the study period, which is likely due to the stands having similar age, structure, and fire history. Although some individual C pools like understory vegetation, leaf litter, and SOL started to recover, they were not yet at pre-fire C levels, suggesting that forests require decades to recover some C pools such as aboveground tree biomass, which were mainly lost in the form of CWD C (McNulty, 2002; Peneva-Reed et al., 2021; Tumber-Dávila et al., 2024; Uriarte and Papaik, 2007).

Management Implications

Our findings challenge some preconceptions about disturbance effects on forest C pools, which has important implications for management in wind-damaged, fire-managed ecosystems of the southeastern U.S. Contrary to expectations, wind damage severity did not consistently influence the distribution of all C pools, with only CWD showing a positive correlation with basal area loss across plots at most sites. This suggests that managers should not assume uniform increases in fuel loads across all C pools following wind disturbance. Additionally, the lack of correlation between understory vegetation C and basal area loss/remaining indicates that light availability changes from wind damage may not always lead to significant understory responses.

As the C loss was often driven by pre-fire C pools that act as fuels rather than wind damage severity for most C pools, the focus should be on careful assessment of fuel loading and distribution to monitor prescribed fire behavior and minimize C loss during reintroduction of fire into wind-damaged stands. This emphasizes the importance of site-specific fuel assessments rather than relying on general assumptions about post-wind disturbance fuel dynamics. More importantly, recent studies have also reported that the use of prescribed fire in wind-damaged stands enhanced post-disturbance recovery of pine woodlands (Kleinman et al., 2020).

The loss of C from larger stable C pools like trees, snags, coarse wood, and SOL in some cases could be concerning, such as heavy loss of SOL C in long-unburned stands. Such significant losses of C from forest ecosystem due to wind and fire disturbances necessitates careful use of prescribed fire to minimize C loss from certain C pools (Bradford et al., 2012). However, delaying re-introduction of fire might only have negative effects as it creates a fire hazard from fuels resulted from wind damage while preventing short-term C recovery from re-growth of understory vegetation.

Furthermore, the complex and sometimes counterintuitive C recovery patterns observed across different pools and sites highlight the need for adaptive management approaches. Although studies have reported slower decomposition rate of large woody debris following fire due to high charcoal content (Mackensen et al., 2003), decomposition and subsequent loss of CWD C within a short period of two years after fire necessitates proper monitoring such C pools. Managers should be aware that C recovery trajectories after disturbance will be heterogenous, and may vary depending on stand age, species composition, and site characteristics, and that short-term observations may not accurately reflect long-term recovery trends (Goetz et al., 2012). This underscores the importance of ongoing monitoring and flexible management strategies to optimize C sequestration and fire hazard reduction goals in wind-damaged, fire-managed forests.

Conclusion

This study sheds light on the intricate complex relationships between wind damage, prescribed fire, and C dynamics in fire-managed forests of the southeastern U.S. Our findings challenge some preconceptions about disturbance effects on forest C pools and provide detailed insight such as loss of C from CWD over time but minimal to no changes in tree C pool in these ecosystems. The research highlights the need for nuanced, site-specific management approaches that consider the unique characteristics of each forest stand such as higher amount of SOL C in long unburned stands compared to frequently burned stands. By carefully assessing fuel loads and tailoring prescribed fire treatments, managers can better balance the goals of fire hazard reduction and C sequestration. This work contributes to our understanding of forest C cycling following multiple disturbances and provides a foundation for developing more effective, C-conscious management practices in fire-prone ecosystems. Future research should focus on long-term C recovery patterns and the potential for adaptive management strategies to enhance forest resilience in the face of changing disturbance regimes.

References:

Abney, R.B., Berhe, A.A., 2018. Pyrogenic Carbon Erosion: Implications for Stock and Persistence of Pyrogenic Carbon in Soil. Front. Earth Sci. 6.

Addington, R.N., Hudson, S.J., Hiers, J.K., Hurteau, M.D., Hutcherson, T.F., Matusick, G., Parker, J.M., 2015. Relationships among wildfire, prescribed fire, and drought in a fire-prone landscape in the south-eastern United States. Int. J. Wildland Fire 24, 778–783. https://doi.org/10.1071/WF14187

Anderson, H.E., 1978. Graphic Aids for Field Calculation of Dead, Down Forest Fuels. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., DeLucia, E.H., 2013. Altered dynamics of forest recovery under a changing climate. Glob. Change Biol. 19, 2001–2021. https://doi.org/10.1111/gcb.12194

Atchley, A.L., Linn, R., Jonko, A., Hoffman, C., Hyman, J.D., Pimont, F., Sieg, C., Middleton, R.S., 2021. Effects of fuel spatial distribution on wildland fire behaviour. Int. J. Wildland Fire 30, 179–189. https://doi.org/10.1071/WF20096

Bennett, L.T., Bruce, M.J., Machunter, J., Kohout, M., Krishnaraj, S.J., Aponte, C., 2017. Assessing fire impacts on the carbon stability of fire-tolerant forests. Ecol. Appl. 27, 2497–2513.

Borden, C.G., Duguid, M.C., Ashton, M.S., 2021. The legacy of fire: long-term changes to the forest understory from periodic burns in a New England oak-hickory forest. Fire Ecol. 17, 24. https://doi.org/10.1186/s42408-021-00115-2

Bradford, J.B., Fraver, S., Milo, A.M., D’Amato, A.W., Palik, B., Shinneman, D.J., 2012. Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. For. Ecol. Manag. 267, 209–214. https://doi.org/10.1016/j.foreco.2011.12.010

Brown, J.K., 1974. Handbook for inventorying downed woody material. Gen Tech Rep INT-16 Ogden UT US Dep. Agric. For. Serv. Intermt. For. Range Exp. Stn. 24 P 016.

Busing, R.T., White, R.D., Harmon, M.E., White, P.S., 2009. Hurricane disturbance in a temperate deciduous forest: patch dynamics, tree mortality, and coarse woody detritus, in: Van der Valk, A.G. (Ed.), Forest Ecology: Recent Advances in Plant Ecology. Springer Netherlands, Dordrecht, pp. 351–363. https://doi.org/10.1007/978-90-481-2795-5_26

Cannon, J.B., Henderson, S.K., Bailey, M.H., Peterson, C.J., 2019. Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. For. Ecol. Manag. 436, 117–128. https://doi.org/10.1016/j.foreco.2019.01.015

Cannon, J.B., O'Brien, J.J., Loudermilk, E.L., Dickinson, M.B., Peterson, C.J., 2014. The influence of experimental wind disturbance on forest fuels and fire characteristics. For. Ecol. Manag. 330, 294–303. https://doi.org/10.1016/j.foreco.2014.07.021

Cannon, J.B., Peterson, C.J., O'Brien, J.J., Brewer, J.S., 2017. A review and classification of interactions between forest disturbance from wind and fire. For. Ecol. Manag. 406, 381–390. https://doi.org/10.1016/j.foreco.2017.07.035

Cansler, C.A., Swanson, M.E., Furniss, T.J., Larson, A.J., Lutz, J.A., 2019. Fuel dynamics after reintroduced fire in an old-growth Sierra Nevada mixed-conifer forest. Fire Ecol. 15, 16. https://doi.org/10.1186/s42408-019-0035-y

Carter, M.C., Darwin Foster, C., 2004. Prescribed burning and productivity in southern pine forests: a review. For. Ecol. Manag. 191, 93–109. https://doi.org/10.1016/j.foreco.2003.11.006

Clabo, D., Campbell, H., 2020. Restoring Fire to Long-Unburned Pine-Dominated Stands on Georgia Private Lands.

Clark, K.L., Heilman, W.E., Skowronski, N.S., Gallagher, M.R., Mueller, E., Hadden, R.M., Simeoni, A., 2020. Fire Behavior, Fuel Consumption, and Turbulence and Energy Exchange during Prescribed Fires in Pitch Pine Forests. Atmosphere 11, 242. https://doi.org/10.3390/atmos11030242

Clark, K.L., Skowronski, N.S., Gallagher, M.R., 2024. Carbon dynamics of prescribed fire in pine- and oak-dominated forests on the mid-Atlantic coastal plain, USA. For. Ecol. Manag. 553, 121589. https://doi.org/10.1016/j.foreco.2023.121589

Cotrufo, M.F., Lavallee, J.M., 2022. Chapter One - Soil organic matter formation, persistence, and functioning: A synthesis of current understanding to inform its conservation and regeneration, in: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 1–66. https://doi.org/10.1016/bs.agron.2021.11.002

Dahal, D., Liu, S., Oeding, J., 2014. The Carbon Cycle and Hurricanes in the United States between 1900 and 2011. Sci. Rep. 4, 5197. https://doi.org/10.1038/srep05197

Domke, G.M., Woodall, C.W., Smith, J.E., Westfall, J.A., McRoberts, R.E., 2012. Consequences of alternative tree-level biomass estimation procedures on U.S. forest carbon stock estimates. For. Ecol. Manag. 270, 108–116. https://doi.org/10.1016/j.foreco.2012.01.022

Emanuel, K., 2021. Atlantic tropical cyclones downscaled from climate reanalyses show increasing activity over past 150 years. Nat. Commun. 12, 7027. https://doi.org/10.1038/s41467-021-27364-8

Falk, D.A., van Mantgem, P.J., Keeley, J.E., Gregg, R.M., Guiterman, C.H., Tepley, A.J., JN Young, D., Marshall, L.A., 2022. Mechanisms of forest resilience. For. Ecol. Manag. 512, 120129. https://doi.org/10.1016/j.foreco.2022.120129

Fawzy, S., Osman, A.I., Doran, J., Rooney, D.W., 2020. Strategies for mitigation of climate change: a review. Environ. Chem. Lett. 18, 2069–2094. https://doi.org/10.1007/s10311-020-01059-w

Fortuin, C.C., Montes, C.R., Vogt, J.T., Gandhi, K.J.K., 2022. Predicting risks of tornado and severe thunderstorm damage to southeastern U.S. forests. Landsc. Ecol. 37, 1905–1919. https://doi.org/10.1007/s10980-022-01451-7

Fowler, C., Konopik, E., 2007. The History of Fire in the Southern United States. Hum. Ecol. Rev. 14, 165–176.

Fraver, S., Dodds, K.J., Kenefic, L.S., Morrill, R., Seymour, R.S., Sypitkowski, E., 2017. Forest structure following tornado damage and salvage logging in northern Maine, USA. Can. J. For. Res. 47, 560–564. https://doi.org/10.1139/cjfr-2016-0395

Fraver, S., Milo, A.M., Bradford, J.B., D'Amato, A.W., Kenefic, L., Palik, B.J., Woodall, C.W., Brissette, J., 2013. Woody Debris Volume Depletion Through Decay: Implications for Biomass and Carbon Accounting. Ecosystems 16, 1262–1272. https://doi.org/10.1007/s10021-013-9682-z

Garrett, L., Davis, M., Oliver, G., 2006. DECOMPOSITION OF COARSE WOODY DEBRIS, AND METHODS FOR DETERMINING DECAY RATES.

Gensini, V.A., Brooks, H.E., 2018. Spatial trends in United States tornado frequency. Npj Clim. Atmospheric Sci. 1, 1–5. https://doi.org/10.1038/s41612-018-0048-2

Goetz, S.J., Bond-Lamberty, B., Law, B.E., Hicke, J.A., Huang, C., Houghton, R.A., McNulty, S., O'Halloran, T., Harmon, M., Meddens, A.J.H., Pfeifer, E.M., Mildrexler, D., Kasischke, E.S., 2012. Observations and assessment of forest carbon dynamics following disturbance in North America. J. Geophys. Res. Biogeosciences 117. https://doi.org/10.1029/2011JG001733

Goldenberg, S.B., Landsea, C.W., Mestas-Nuñez, A.M., Gray, W.M., 2001. The Recent Increase in Atlantic Hurricane Activity: Causes and Implications. Science 293, 474–479. https://doi.org/10.1126/science.1060040

Gonzalez-Akre, E., Piponiot, C., Lepore, M., Herrmann, V., Lutz, J.A., Baltzer, J.L., Dick, C.W., Gilbert, G.S., He, F., Heym, M., Huerta, A.I., Jansen, P.A., Johnson, D.J., Knapp, N., Král, K., Lin, D., Malhi, Y., McMahon, S.M., Myers, J.A., Orwig, D., Rodríguez-Hernández, D.I., Russo, S.E., Shue, J., Wang, X., Wolf, A., Yang, T., Davies, S.J., Anderson-Teixeira, K.J., 2022. allodb: An R package for biomass estimation at globally distributed extratropical forest plots. Methods Ecol. Evol. 13, 330–338. https://doi.org/10.1111/2041-210X.13756

Gonzalez-Benecke, C.A., Samuelson, L.J., Stokes, T.A., Cropper, W.P., Martin, T.A., Johnsen, K.H., 2015. Understory plant biomass dynamics of prescribed burned *Pinus palustris* stands. For. Ecol. Manag. 344, 84–94. https://doi.org/10.1016/j.foreco.2015.02.018

González-Pérez, J.A., González-Vila, F.J., Almendros, G., Knicker, H., 2004. The effect of fire on soil organic matter—a review. Environ. Int. 30, 855–870. https://doi.org/10.1016/j.envint.2004.02.003

Hanula, J.L., Ulyshen, M.D., Wade, D.D., 2012. Impacts of Prescribed Fire Frequency on Coarse Woody Debris Volume, Decomposition and Termite Activity in the Longleaf Pine Flatwoods of Florida. Forests 3, 317–331. https://doi.org/10.3390/f3020317

Ibanez, T., Platt, W.J., Bellingham, P.J., Vieilledent, G., Franklin, J., Martin, P.H., Menkes, C., Pérez-Salicrup, D.R., Russell-Smith, J., Keppel, G., 2022. Altered cyclone–fire interactions are changing ecosystems. Trends Plant Sci. 27, 1218–1230. https://doi.org/10.1016/j.tplants.2022.08.005

Kleinman, J.S., Goode, J.D., Hart, J.L., Dey, D.C., 2020. Prescribed fire effects on *Pinus palustris* woodland development after catastrophic wind disturbance and salvage logging. For. Ecol. Manag. 468, 118173. https://doi.org/10.1016/j.foreco.2020.118173

Kobziar, L.N., Godwin, D., Taylor, L., Watts, A.C., 2015. Perspectives on Trends, Effectiveness, and Impediments to Prescribed Burning in the Southern U.S. Forests 6, 561–580. https://doi.org/10.3390/f6030561

Kreye, J.K., Varner, J.M., Dugaw, C.J., 2014. Spatial and temporal variability of forest floor duff characteristics in long-unburned Pinus palustris forests. Can. J. For. Res. 44, 1477–1486. https://doi.org/10.1139/cjfr-2014-0223

Kupfer, J.A., Terando, A.J., Gao, P., Teske, C., Hiers, J.K., 2020. Climate change projected to reduce prescribed burning opportunities in the south-eastern United States. Int. J. Wildland Fire 29, 764–778. https://doi.org/10.1071/WF19198

Leverkus, A.B., Gustafsson, L., Lindenmayer, D.B., Castro, J., Rey Benayas, J.M., Ranius, T., Thorn, S., 2020. Salvage logging effects on regulating ecosystem services and fuel loads. Front. Ecol. Environ. 18, 391–400. https://doi.org/10.1002/fee.2219

Lorenz, K., Lal, R., 2010. The Importance of Carbon Sequestration in Forest Ecosystems, in: Lorenz, K., Lal, R. (Eds.), Carbon Sequestration in Forest Ecosystems. Springer Netherlands, Dordrecht, pp. 241–270. https://doi.org/10.1007/978-90-481-3266-9_6

Loudermilk, E.L., O’Brien, J.J., Mitchell, R.J., Cropper, W.P., Hiers, J.K., Grunwald, S., Grego, J., Fernandez-Diaz, J.C., 2012. Linking complex forest fuel structure and fire behaviour at fine scales. Int. J. Wildland Fire 21, 882–893. https://doi.org/10.1071/WF10116

Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris—A review with particular emphasis on Australian tree species. Aust. J. Bot. 51, 27–37. https://doi.org/10.1071/bt02014

McNulty, S.G., 2002. Hurricane impacts on US forest carbon sequestration. Environ. Pollut. 116, S17–S24. https://doi.org/10.1016/S0269-7491(01)00242-1

Michelotti, L.A., Miesel, J.R., 2015. Source Material and Concentration of Wildfire-Produced Pyrogenic Carbon Influence Post-Fire Soil Nutrient Dynamics. Forests 6, 1325–1342. https://doi.org/10.3390/f6041325

Mickler, R.A., Earnhardt, T.S., Moore, J.A., 2002. Regional estimation of current and future forest biomass. Environ. Pollut. 116, S7–S16. https://doi.org/10.1016/S0269-7491(01)00241-X

Miles, P.D., 2009. Specific Gravity and Other Properties of Wood and Bark for 156 Tree Species Found in North America. U.S. Department of Agriculture, Forest Service, Northern Research Station.

Mitchell, R.J., Liu, Y., O'Brien, J.J., Elliott, K.J., Starr, G., Miniat, C.F., Hiers, J.K., 2014. Future climate and fire interactions in the southeastern region of the United States. For. Ecol. Manag. 327, 316–326. https://doi.org/10.1016/j.foreco.2013.12.003

Miyanishi, K., 2001. Chapter 13 - Duff Consumption, in: Johnson, E.A., Miyanishi, Kiyoko (Eds.), Forest Fires. Academic Press, San Diego, pp. 437–475. https://doi.org/10.1016/B978-012386660-8/50015-5

Moore, T.W., McGuire, M.P., 2019. Using the standard deviational ellipse to document changes to the spatial dispersion of seasonal tornado activity in the United States. Npj Clim. Atmospheric Sci. 2, 1–8. https://doi.org/10.1038/s41612-019-0078-4

Myers, R.K., van Lear, D.H., 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. For. Ecol. Manag. 103, 265–276. https://doi.org/10.1016/S0378-1127(97)00223-5

Nikinmaa, L., Lindner, M., Cantarello, E., Jump, A.S., Seidl, R., Winkel, G., Muys, B., 2020. Reviewing the Use of Resilience Concepts in Forest Sciences. Curr. For. Rep. 6, 61–80. https://doi.org/10.1007/s40725-020-00110-x

Oakman, E.C., Hagan, D.L., Waldrop, T.A., Barrett, K., 2019. Understory Vegetation Responses to 15 Years of Repeated Fuel Reduction Treatments in the Southern Appalachian Mountains, USA. Forests 10, 350. https://doi.org/10.3390/f10040350

Odland, M.C., Goodwin, M.J., Smithers, B.V., Hurteau, M.D., North, M.P., 2021. Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. For. Ecol. Manag. 495, 119361. https://doi.org/10.1016/j.foreco.2021.119361

Palmero-Iniesta, M., Domènech, R., Molina-Terrén, D., Espelta, J.M., 2017. Fire behavior in *Pinus halepensis* thickets: Effects of thinning and woody debris decomposition in two rainfall scenarios. For. Ecol. Manag. 404, 230–240. https://doi.org/10.1016/j.foreco.2017.08.043

Pellegrini, A.F.A., Caprio, A.C., Georgiou, K., Finnegan, C., Hobbie, S.E., Hatten, J.A., Jackson, R.B., 2021. Low-intensity frequent fires in coniferous forests transform soil organic matter in ways that may offset ecosystem carbon losses. Glob. Change Biol. 27, 3810–3823. https://doi.org/10.1111/gcb.15648

Peneva-Reed, E.I., Krauss, K.W., Bullock, E.L., Zhu, Z., Woltz, V.L., Drexler, J.Z., Conrad, J.R., Stehman, S.V., 2021. Carbon stock losses and recovery observed for a mangrove ecosystem following a major hurricane in Southwest Florida. Estuar. Coast. Shelf Sci., Mangroves and People: Impacts and Interactions 248, 106750. https://doi.org/10.1016/j.ecss.2020.106750

Pile-Knapp, L.S., Guan, S., Song, B., Wang, G.G., 2022. Temporal effects of hurricanes and prescribed fire on fuel loading and pine reproduction in the Southeastern United States. Willis John Self Andrew B Siegert Court. M Eds Proc. 21st Bienn. South. Silvic. Res. Conf. Gen Tech Rep SRS-268 Asheville NC US Dep. Agric. For. Serv. South. Res. Stn. 268, 21–31.

Platt, W.J., Beckage, B., Doren, R.F., Slater, H.H., 2002. Interactions of Large-Scale Disturbances: Prior Fire Regimes and Hurricane Mortality of Savanna Pines. Ecology 83, 1566–1572. https://doi.org/10.1890/0012-9658(2002)083[1566:IOLSDP]2.0.CO;2

Reinikainen, M., D'Amato, A.W., Bradford, J.B., Fraver, S., 2014. Influence of stocking, site quality, stand age, low-severity canopy disturbance, and forest composition on sub-boreal aspen mixedwood carbon stocks. Can. J. For. Res. 44, 230–242. https://doi.org/10.1139/cjfr-2013-0165

Rich, R.L., Frelich, L.E., Reich, P.B., 2007. Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. J. Ecol. 95, 1261–1273. https://doi.org/10.1111/j.1365-2745.2007.01301.x

Ritter, S.M., Hoffman, C.M., Battaglia, M.A., Stevens-Rumann, C.S., Mell, W.E., 2020. Fine-scale fire patterns mediate forest structure in frequent-fire ecosystems. Ecosphere 11, e03177. https://doi.org/10.1002/ecs2.3177

Rothstein, D.E., Yermakov, Z., Buell, A.L., 2004. Loss and recovery of ecosystem carbon pools following stand-replacing wildfire in Michigan jack pine forests. Can. J. For. Res. 34, 1908–1918. https://doi.org/10.1139/x04-063

Rutledge, B.T., Cannon, J.B., McIntyre, R.K., Holland, A.M., Jack, S.B., 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. For. Ecol. Manag. 481, 118724. https://doi.org/10.1016/j.foreco.2020.118724

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11, e15–e24. https://doi.org/10.1890/120329

Sah, J.P., Ross, M.S., Snyder, J.R., Koptur, S., Cooley, H.C., 2006. Fuel loads, fire regimes, and post-fire fuel dynamics in Florida Keys pine forests. Int. J. Wildland Fire 15, 463–478. https://doi.org/10.1071/WF05100

Samuelson, L.J., Stokes, T.A., Butnor, J.R., Johnsen, K.H., Gonzalez-Benecke, C.A., Anderson, P., Jackson, J., Ferrari, L., Martin, T.A., Cropper, W.P., 2014. Ecosystem carbon stocks in

Pinus palustris forests. Can. J. For. Res. 44, 476–486. https://doi.org/10.1139/cjfr-2013-0446

Schmid, A.V., Vogel, C.S., Liebman, E., Curtis, P.S., Gough, C.M., 2016. Coarse woody debris and the carbon balance of a moderately disturbed forest. For. Ecol. Manag. 361, 38–45. https://doi.org/10.1016/j.foreco.2015.11.001

Schwartz, N.B., Uriarte, M., DeFries, R., Gutierrez-Velez, V.H., Pinedo-Vasquez, M.A., 2017. Land-use dynamics influence estimates of carbon sequestration potential in tropical second-growth forest. Environ. Res. Lett. 12, 074023. https://doi.org/10.1088/1748-9326/aa708b

Sharma, A., Ojha, S.K., Dimov, L.D., Vogel, J.G., Nowak, J., 2021. Long-term effects of catastrophic wind on southern US coastal forests: Lessons from a major hurricane. PLOS ONE 16, e0243362. https://doi.org/10.1371/journal.pone.0243362

Smith, E., 1999. Atlantic and East Coast Hurricanes 1900–98: A Frequency and Intensity Study for the Twenty-First Century.

Smith, J.E., Heath, L.S., Skog, K.E., Birdsey, R.A., 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. Gen Tech Rep NE-343 Newtown Sq. PA US Dep. Agric. For. Serv. Northeast. Res. Stn. 216 P 343. https://doi.org/10.2737/NE-GTR-343

Starr, G., Staudhammer, C.L., Loescher, H.W., Mitchell, R., Whelan, A., Hiers, J.K., O'Brien, J.J., 2015. Time series analysis of forest carbon dynamics: recovery of Pinus palustris physiology following a prescribed fire. New For. 46, 63–90. https://doi.org/10.1007/s11056-014-9447-3

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change. Secr. Conv. Biol. Divers. Montr. Tech. Ser. No 43 1-67 43, 1–67.

Tumber-Dávila, S.J., Lucey, T., Boose, E.R., Laflower, D., León-Sáenz, A., Wilson, B.T., MacLean, M.G., Thompson, J.R., 2024. Hurricanes pose a substantial risk to New England forest carbon stocks. https://doi.org/10.1111/gcb.17259

Uriarte, M., Papaik, M., 2007. Hurricane impacts on dynamics, structure and carbon sequestration potential of forest ecosystems in Southern New England, USA. Tellus Dyn. Meteorol. Oceanogr. 59, 519–528. https://doi.org/10.1111/j.1600-0870.2007.00243.x

Vaillant, N.M., Reiner, A.L., Noonan-Wright, E.K., 2013. Prescribed fire effects on field-derived and simulated forest carbon stocks over time. For. Ecol. Manag. 310, 711–719. https://doi.org/10.1016/j.foreco.2013.09.016

Vargas, R., Hasselquist, N., Allen, E.B., Allen, M.F., 2010. Effects of a Hurricane Disturbance on Aboveground Forest Structure, Arbuscular Mycorrhizae and Belowground Carbon in a Restored Tropical Forest. Ecosystems 13, 118–128. https://doi.org/10.1007/s10021-009-9305-x

Volkova, L., Roxburgh, S.H., Weston, C.J., 2021. Effects of prescribed fire frequency on wildfire emissions and carbon sequestration in a fire adapted ecosystem using a comprehensive carbon model. J. Environ. Manage. 290, 112673. https://doi.org/10.1016/j.jenvman.2021.112673

Wales, S.B., Kreider, M.R., Atkins, J., Hulshof, C.M., Fahey, R.T., Nave, L.E., Nadelhoffer, K.J., Gough, C.M., 2020. Stand age, disturbance history and the temporal stability of forest production. For. Ecol. Manag. 460, 117865. https://doi.org/10.1016/j.foreco.2020.117865

Wang, G.G., Kemball, K.J., 2005. Effects of fire severity on early development of understory vegetation. Can. J. For. Res. 35, 254–262. https://doi.org/10.1139/x04-177

Wang, W., Qu, J.J., Hao, X., Liu, Y., Stanturf, J.A., 2010. Post-hurricane forest damage assessment using satellite remote sensing. Agric. For. Meteorol. 150, 122–132. https://doi.org/10.1016/j.agrformet.2009.09.009

Whelan, A.W., Bigelow, S.W., Staudhammer, C.L., Starr, G., Cannon, J.B., 2024. Damage prediction for planted longleaf pine in extreme winds. For. Ecol. Manag. 560, 121828. https://doi.org/10.1016/j.foreco.2024.121828

Wiedinmyer, C., Hurteau, M.D., 2010. Prescribed Fire As a Means of Reducing Forest Carbon Emissions in the Western United States. Environ. Sci. Technol. 44, 1926–1932. https://doi.org/10.1021/es902455e

Williams, C.A., Gu, H., MacLean, R., Masek, J.G., Collatz, G.J., 2016. Disturbance and the carbon balance of US forests: A quantitative review of impacts from harvests, fires, insects, and droughts. Glob. Planet. Change 143, 66–80. https://doi.org/10.1016/j.gloplacha.2016.06.002

Woodall, C., Monleon, V., 2008. Sampling Protocol, Estimation, and Analysis Procedures for the Down Woody Materials Indicator of the FIA Program.

Zhao, F., Liu, Y., Goodrick, S., Hornsby, B., Schardt, J., 2019. The contribution of duff consumption to fire emissions and air pollution of the Rough Ridge Fire. Int. J. Wildland Fire 28, 993–1004. https://doi.org/10.1071/WF18205

Zhao, S., Liu, S., Sohl, T., Young, C., Werner, J., 2013. Land use and carbon dynamics in the southeastern United States from 1992 to 2050. Environ. Res. Lett. 8, 044022. https://doi.org/10.1088/1748-9326/8/4/044022

Zhou, L., Dai, L., Gu, H., Zhong, L., 2007. Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. J. For. Res. 18, 48–54. https://doi.org/10.1007/s11676-007-0009-9

Appendices

Table A1: Hypothesized carbon (C) loss during prescribed burns and subsequent recovery rates for various carbon pools in wind-damaged southeastern U.S. forests, with rationale for each prediction

C pool	**C Loss During Prescribed Burn**	**C Recovery After Prescribed Burn**	**Rationale**
Live Trees	Low	Slow	Most prescribed fires are low-intensity surface fires that do not kill large diameter (i.e., overstory/midstory trees); thus, loss is minimal. However, if/when large trees are killed, recovery is very slow.
Snags	Low/ Medium	Slow	While prescribed fires likely do not consume snags, repeated fires can destabilize snags, causing them to fall to the forest floor, thereby decreasing the snag C pool and increasing the woody debris C pool. Snags are slow to recover because their creation requires mortality of large trees.
Coarse Woody Debris	Low/ Medium	Slow	Prescribed fires with low intensity do not typically consume whole coarse woody debris, as decaying wood often holds moisture; however, increased canopy openness due to wind damage may increase temperature, thereby increasing decomposition rates.
Leaf litter (fine fuel)	High	Fast	Leaf litter is a primary fuel in surface fires so most of this pool is consumed; recovery rates are generally fast but will be relatively slower in areas with more wind damage as there are fewer trees to supply leaves to the litter pool.
Soil organic layer	Low/ Medium	Slow	The moisture content at the time of prescribed burn determines the consumption as higher moisture content leads to less damage to organic soil. Recovery rates will decline in areas with more wind damage, as there will be less deposition of tree derived leaf litter.
Understory Vegetation (fine fuel)	High	Fast	Understory vegetation is also an important fuel, especially with more canopy openness. With more wind damage, drying rates should be higher, making consumption of this pool higher. Increased mineral nutrient cycling from fire and light availability due to canopy openness will help this pool recover quickly.
Fine Woody Debris (fine fuel)	High	Fast	Fine woody debris become more drier due to open canopy and burns easily during prescribed fire but will recover slowly afterwards due to fewer live trees in more wind damaged areas.

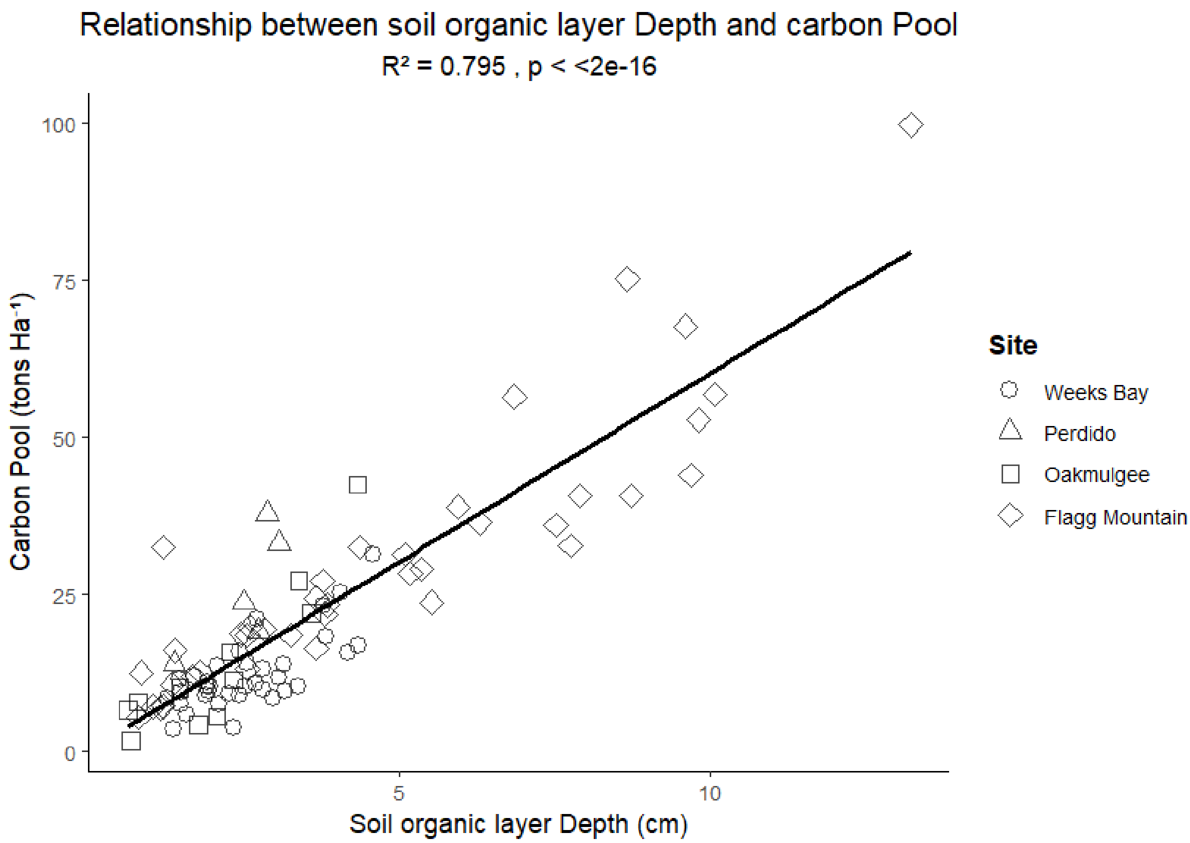

Figure A2: Linear model used to calculate soil organic layer (SOL) carbon pool, which was developed based on SOL samples from all four sites: Weeks Bay, Perdido, Oakmulgee, and Flagg Mountain.

Table A3: Percent carbon, depth, bulk density of soil organic layer (SOL) samples used to develop the model of figure A2.

Site	Status	Percent carbon (%)	Depth (cm)	Bulk density (g cm^{-3})	Carbon pool (tons ha^{-1})
Weeks Bay	Fire-managed	20.17	2.82	0.23	13.08
Weeks Bay	Fire-managed	27.75	3.78	0.22	23.08
Weeks Bay	Fire-managed	22.06	2.82	0.16	9.95
Weeks Bay	Fire-managed	34.27	2.45	0.19	15.95
Weeks Bay	Fire-managed	12.12	2.72	0.33	10.88
Weeks Bay	Fire-managed	20.35	4.36	0.19	16.86
Weeks Bay	Fire-managed	34.30	3.83	0.14	18.39
Weeks Bay	Fire-managed	11.47	2.09	0.57	13.66
Weeks Bay	Fire-managed	35.82	4.60	0.19	31.31
Weeks Bay	Fire-managed	13.32	1.94	0.43	11.11
Weeks Bay	Fire-managed	34.01	3.15	0.13	13.93
Weeks Bay	Fire-managed	19.20	1.99	0.27	10.32
Weeks Bay	Fire-managed	34.39	4.18	0.11	15.81
Weeks Bay	Fire-managed	18.29	1.94	0.29	10.29
Weeks Bay	Fire-managed	12.64	1.50	0.50	9.48
Weeks Bay	Fire-managed	10.20	1.96	0.48	9.60
Weeks Bay	Fire-managed	11.02	1.72	0.63	11.94
Weeks Bay	Fire-managed	10.22	1.49	0.76	11.57
Weeks Bay	Fire-managed	32.52	4.08	0.19	25.21
Weeks Bay	Fire-managed	12.67	2.74	0.61	21.18
Flagg Mountain	Fire-excluded	22.31	2.58	0.23	13.24
Flagg Mountain	Fire-excluded	15.76	0.84	0.41	5.43
Flagg Mountain	Fire-excluded	38.18	3.82	0.15	21.88
Flagg Mountain	Fire-excluded	20.17	1.23	0.29	7.19
Flagg Mountain	Fire-excluded	18.45	0.88	0.77	12.50
Flagg Mountain	Fire-excluded	36.03	2.84	0.19	19.44
Flagg Mountain	Fire-excluded	28.61	5.53	0.15	23.73
Flagg Mountain	Fire-excluded	44.61	2.61	0.17	19.79
Flagg Mountain	Fire-excluded	12.34	2.48	0.61	18.67
Flagg Mountain	Fire-excluded	21.95	1.71	0.32	12.01
Flagg Mountain	Fire-excluded	37.05	1.07	0.18	7.14
Flagg Mountain	Fire-excluded	44.87	9.80	0.12	52.77
Flagg Mountain	Fire-excluded	36.70	1.23	0.72	32.50
Flagg Mountain	Fire-excluded	39.13	1.42	0.29	16.11
Flagg Mountain	Fire-excluded	15.61	1.18	0.38	7.00
Flagg Mountain	Fire-excluded	32.72	2.58	0.22	18.57
Flagg Mountain	Fire-excluded	39.05	3.68	0.17	24.43

Site	Status	Percent carbon (%)	Depth (cm)	Bulk density (g cm^{-3})	Carbon pool (tons ha^{-1})
Flagg Mountain	Fire-excluded	19.33	3.68	0.23	16.36
Flagg Mountain	Fire-excluded	31.23	3.78	0.23	27.15
Oakmulgee	Fire-managed	4.43	2.09	0.60	5.56
Oakmulgee	Fire-managed	27.27	2.47	0.82	55.23
Oakmulgee	Fire-managed	11.41	3.40	0.70	27.16
Oakmulgee	Fire-managed	4.62	1.79	0.52	4.30
Oakmulgee	Fire-managed	18.09	2.30	0.38	15.81
Oakmulgee	Fire-managed	15.82	0.83	0.60	7.88
Oakmulgee	Fire-managed	20.08	0.66	0.50	6.63
Oakmulgee	Fire-managed	10.24	0.72	0.23	1.70
Oakmulgee	Fire-managed	15.05	4.34	0.65	42.46
Oakmulgee	Fire-managed	17.91	2.35	0.27	11.36
Oakmulgee	Fire-managed	14.97	3.60	0.41	22.10
Oakmulgee	Fire-managed	16.54	1.50	0.41	10.17
Perdido	Fire-managed	24.19	1.41	0.41	14.07
Perdido	Fire-managed	27.67	2.52	0.34	23.74
Perdido	Fire-managed	37.89	2.90	0.34	37.82
Perdido	Fire-managed	42.69	3.09	0.25	33.16
Perdido	Fire-managed	25.44	2.75	0.27	19.21
Weeks Bay	Fire-excluded	16.29	2.29	0.25	9.13
Weeks Bay	Fire-excluded	33.91	1.40	0.07	3.52
Weeks Bay	Fire-excluded	35.73	2.57	0.15	14.11
Weeks Bay	Fire-excluded	28.47	2.46	0.13	8.92
Weeks Bay	Fire-excluded	27.98	1.51	0.18	7.52
Weeks Bay	Fire-excluded	31.85	1.30	0.21	8.51
Weeks Bay	Fire-excluded	19.19	1.60	0.19	5.92
Weeks Bay	Fire-excluded	21.16	2.35	0.08	3.75
Weeks Bay	Fire-excluded	27.08	3.00	0.10	8.38
Weeks Bay	Fire-excluded	34.84	3.09	0.11	11.84
Weeks Bay	Fire-excluded	25.42	2.12	0.14	7.56
Weeks Bay	Fire-excluded	18.86	3.38	0.16	10.32
Weeks Bay	Fire-excluded	33.42	2.54	0.12	10.28
Weeks Bay	Fire-excluded	22.92	1.92	0.20	8.96
Weeks Bay	Fire-excluded	26.40	3.19	0.11	9.56
Flagg Mountain	Fire-managed	39.29	8.72	0.12	40.73
Flagg Mountain	Fire-managed	54.39	8.66	0.16	75.24
Flagg Mountain	Fire-managed	20.83	5.36	0.26	29.04
Flagg Mountain	Fire-managed	38.24	9.59	0.18	67.66
Flagg Mountain	Fire-managed	37.65	5.95	0.17	38.96
Flagg Mountain	Fire-managed	47.27	13.20	0.16	99.75
Flagg Mountain	Fire-managed	32.42	10.06	0.17	56.88

Site	Status	Percent carbon (%)	Depth (cm)	Bulk density (g cm^{-3})	Carbon pool (tons ha^{-1})
Flagg Mountain	Fire-managed	38.15	6.30	0.15	36.44
Flagg Mountain	Fire-managed	30.17	5.19	0.18	28.34
Flagg Mountain	Fire-managed	36.05	6.85	0.23	56.48
Flagg Mountain	Fire-managed	27.64	7.52	0.17	36.01
Flagg Mountain	Fire-managed	45.61	4.38	0.16	32.57
Flagg Mountain	Fire-managed	50.07	7.90	0.10	40.67
Flagg Mountain	Fire-managed	18.27	1.83	0.38	12.68
Flagg Mountain	Fire-managed	24.53	1.38	0.32	10.67
Flagg Mountain	Fire-managed	37.51	5.10	0.16	31.43
Flagg Mountain	Fire-managed	29.37	7.75	0.14	32.72
Flagg Mountain	Fire-managed	46.12	9.68	0.10	44.02
Flagg Mountain	Fire-managed	23.45	3.85	0.26	23.34
Flagg Mountain	Fire-managed	30.50	3.26	0.19	18.51

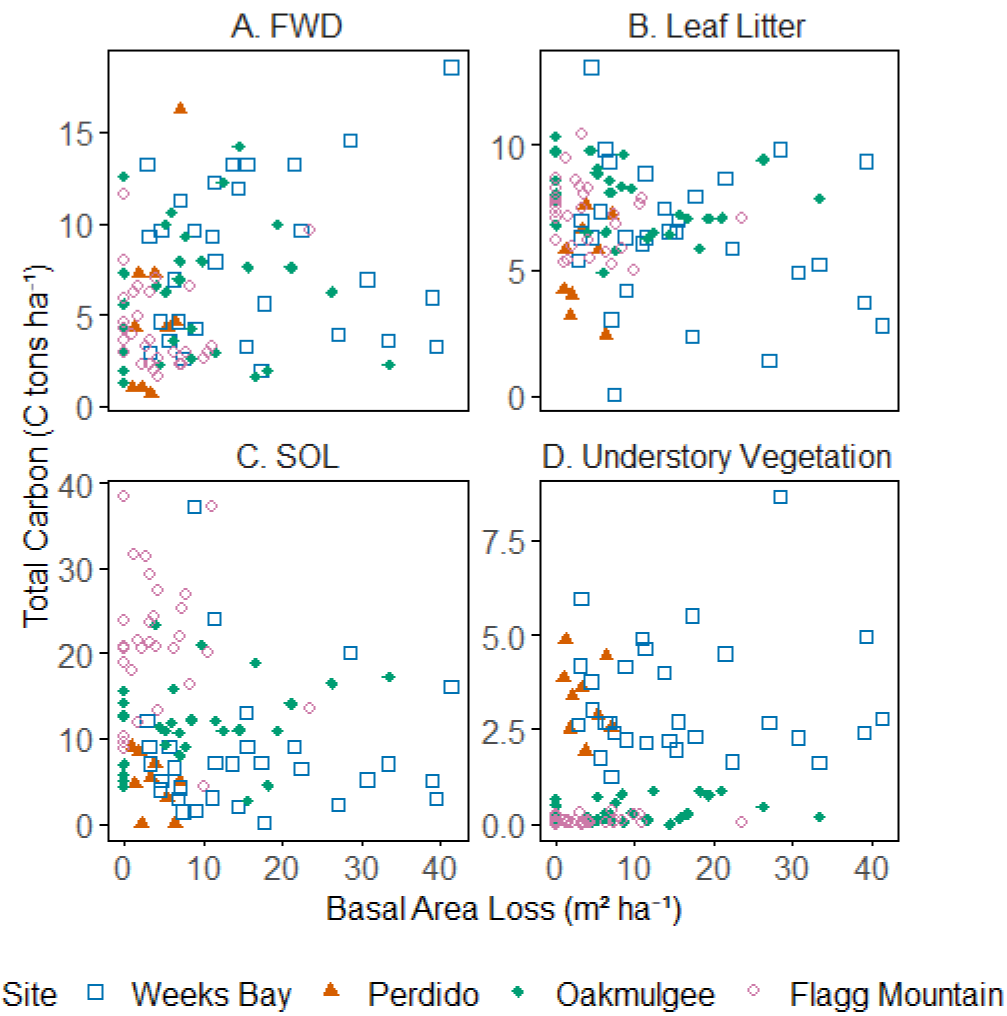

Figure A4. Post-wind event (but prior to prescribed fire reintroduction) (A) fine woody debris (CWD), (B) leaf litter, (C) soil organic layer (SOL), (D) understory vegetation C pools as a function of basal area loss across two inland and two coastal sites in southeastern U.S.

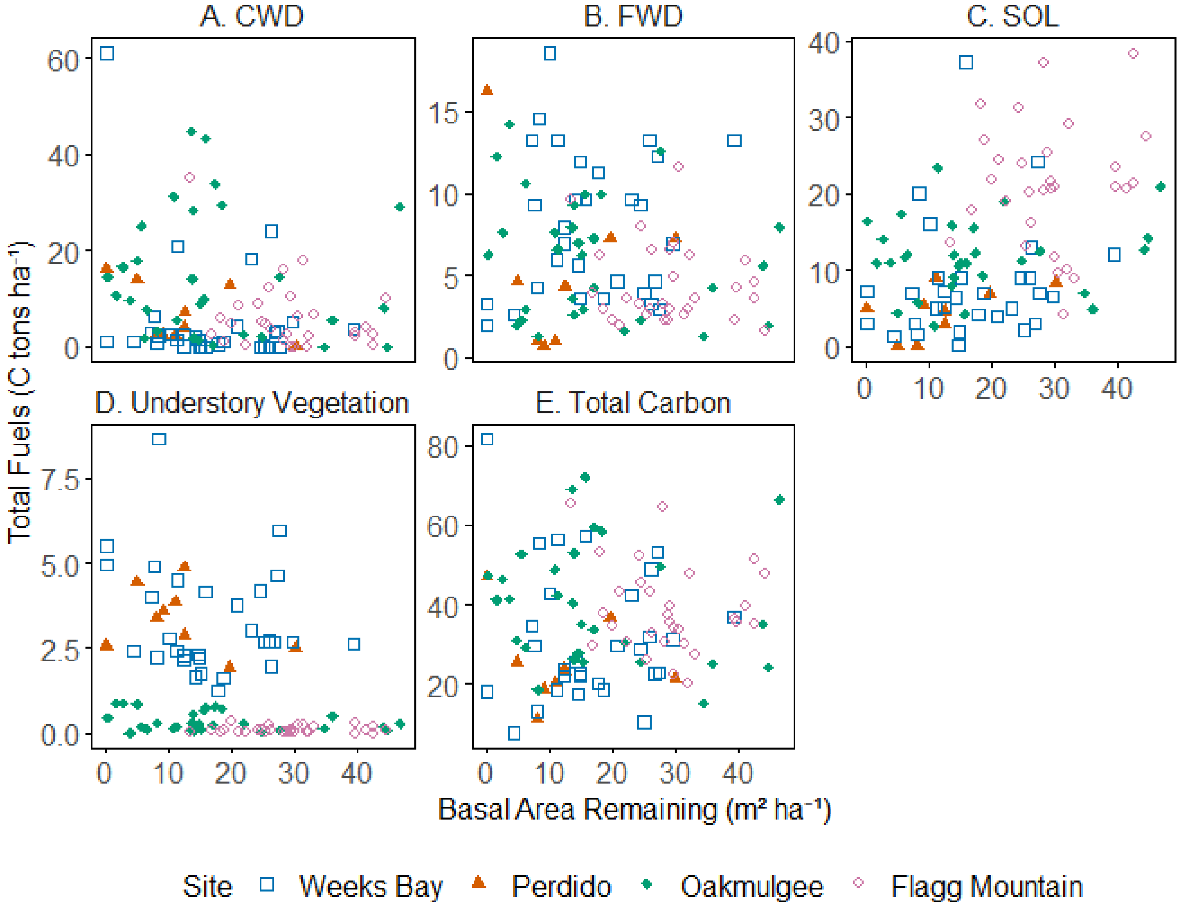

Figure A5. Post-wind event (but prior to prescribed fire reintroduction) (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) soil organic layer (SOL), (D) understory vegetation, and (E) total carbon pool as a function of basal area loss remaining at two inland and two coastal sites in southeastern U.S.

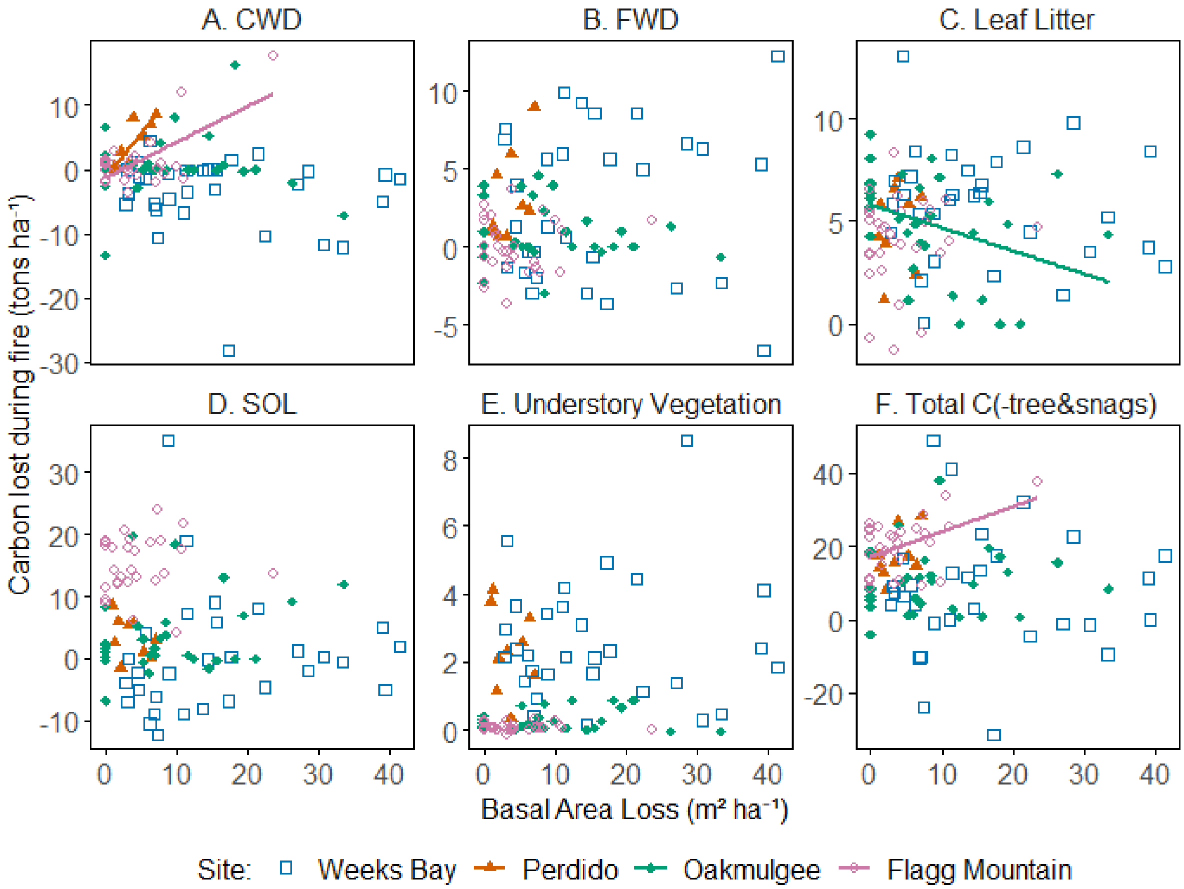

Figure A6. Carbon loss during prescribed fire reintroduction as a function of basal area loss at two inland and two coastal sites in southeastern U.S. Note: (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total carbon pool (excluding trees and snags) during prescribed fire reintroduction as a function of basal area loss at two inland and two coastal sites in southeastern U.S.

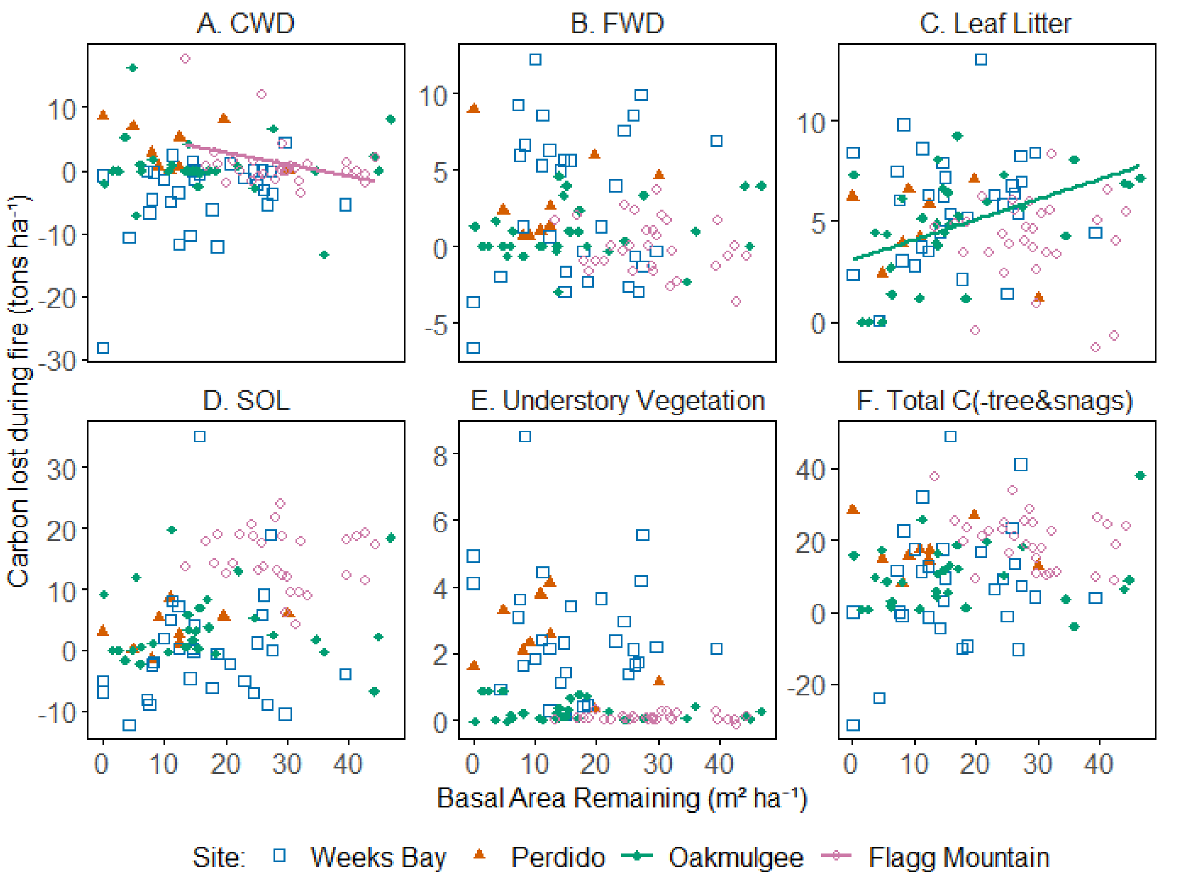

Figure A7. Carbon loss during prescribed fire reintroduction as a function of basal area remaining at two inland and two coastal sites in southeastern U.S. Note: (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total carbon pool (excluding trees and snags)

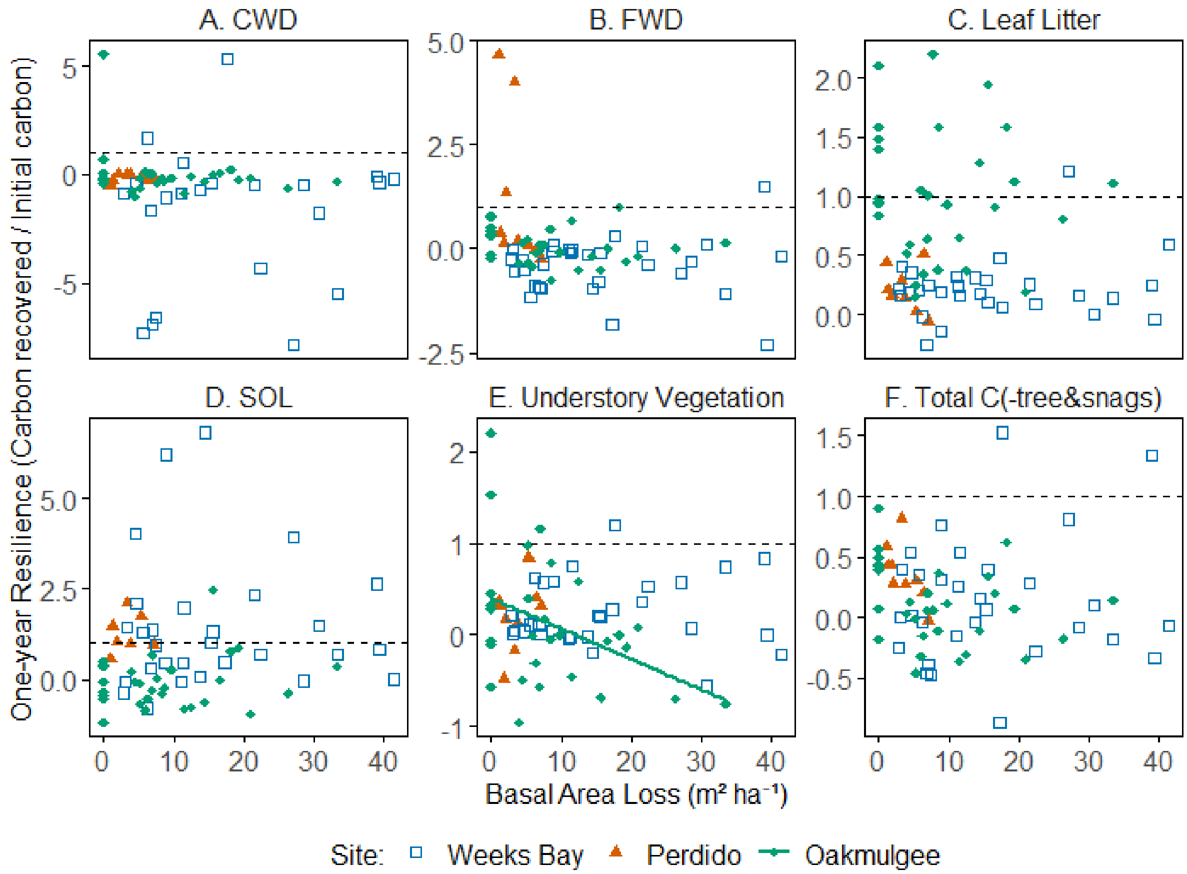

Figure A8. Carbon resilience observed for one-year period after reintroduction of prescribed fire as a function of basal area loss at one inland and two coastal sites in southeastern U.S. Note: (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total carbon pool (excluding trees and snags).

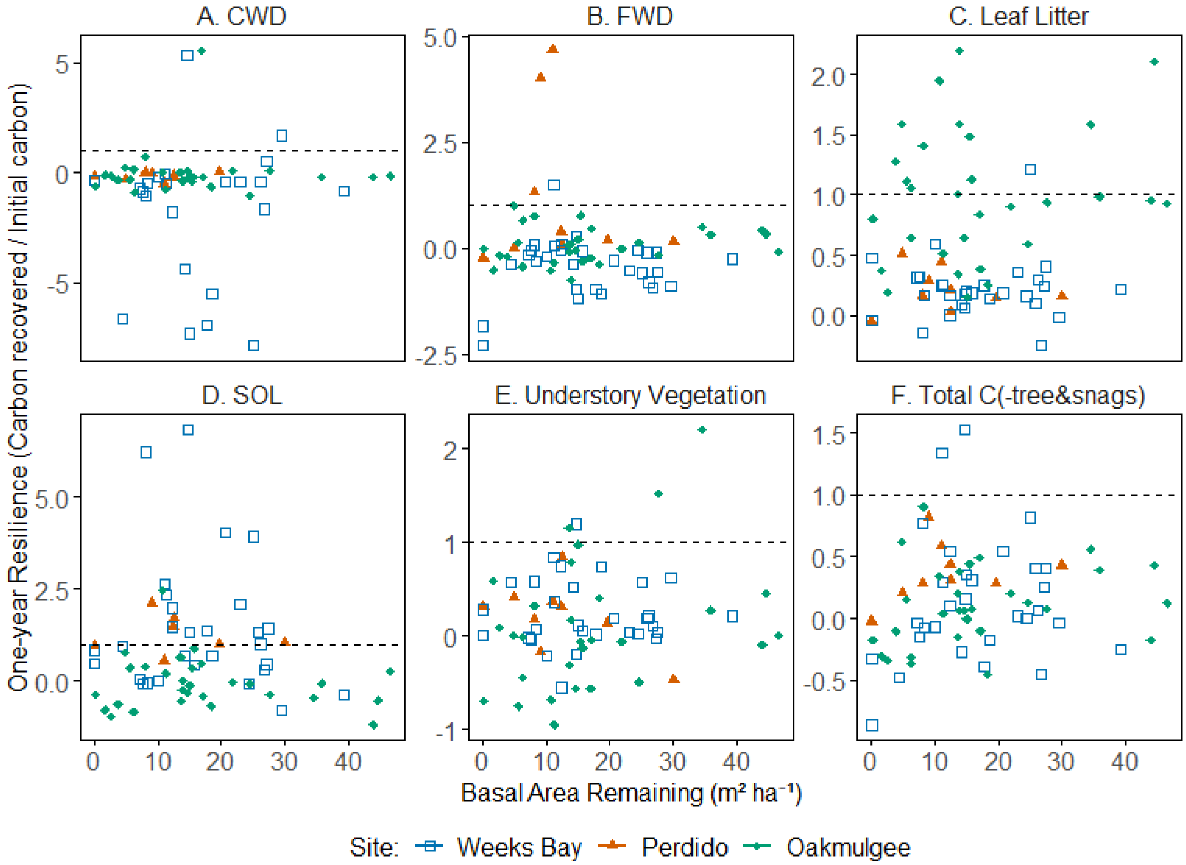

Figure A9. Carbon resilience observed for one-year period after reintroduction of prescribed fire as a function of basal area remaining at one inland and two coastal sites in southeastern U.S. Note: (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total carbon pool (excluding trees and snags).

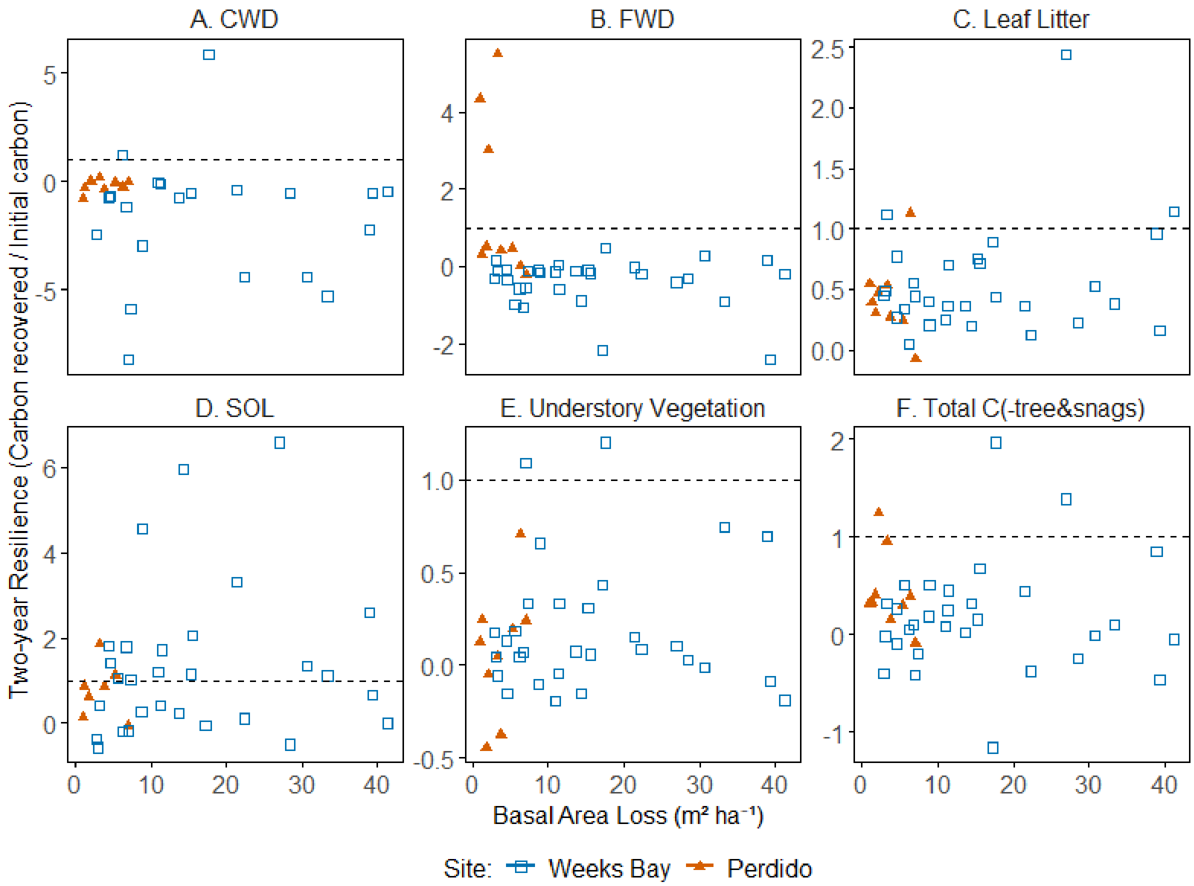

Figure A10. Carbon resilience observed for two-year period after reintroduction of prescribed fire as a function of basal area loss at two coastal sites in southeastern U.S. Note: (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total carbon pool (excluding trees and snags)..

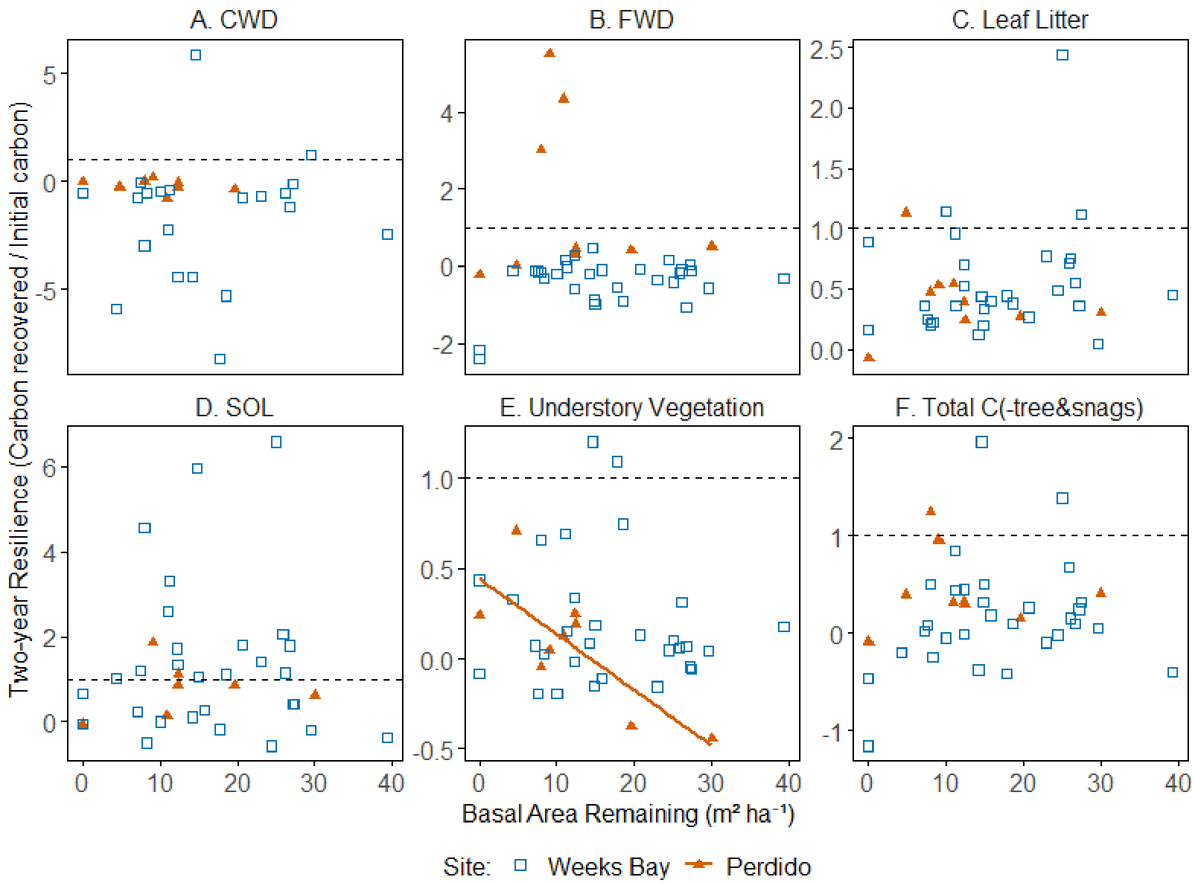

Figure A11. Carbon resilience observed for two-year period after reintroduction of prescribed fire as a function of basal area remaining at two coastal sites in southeastern U.S. Note: (A) coarse woody debris (CWD), (B) fine woody debris (FWD), (C) leaf litter, (D) soil organic layer (SOL), (E) understory vegetation, and (F) total carbon pool (excluding trees and snags).

Chapter 2: Evaluating forest floor characteristics across fire-dependent southeastern U.S. forests to simplify biomass and carbon pool estimation using depth and bulk density

Abstract:

The forest floor, which encompasses organic material in various stages of decomposition above the mineral soil, plays a crucial role in fire behavior, and impacts carbon (C) storage and sequestration in fire-dependent forests of the southeastern U.S., yet adequate characterization and accurate estimation of forest floor mass and C pools remain challenging. Here, we aim to address this knowledge gap by characterizing bulk density, and % C of leaf litter and the underlying soil organic layer (SOL) from 14 sites representing seven forest types with varying fire histories (i.e., fire-excluded vs. fire-managed). Frequent burning in most sites resulted in higher SOL bulk density (fire-managed = 360 kg m^{-3}, fire-excluded = 243 kg m^{-3}) and lower % C of SOL (fire-managed = 19%, fire-excluded = 23%). Across most forest types, % C was relatively consistent in leaf litter (~50 %) but varied significantly in the SOL (4-54 %). Strong positive linear relationships were found between forest floor depth and C pools, particularly for the SOL due to trade-offs between increasing % C with decreasing bulk density (R^2 values up to 0.70 for leaf litter and up to 0.80 for SOL). Fire history significantly influenced these relationships with stronger relations in fire-managed stands of mixed pine hardwood forests, highlighting the need for considering both forest type and fire regime in forest floor biomass and C estimations. Our findings provide a foundation for more accurate forest floor monitoring, enhancing C storage and fuel load estimates and fire behavior predictions in southeastern U.S. forests. This improved understanding will contribute to more effective forest management practices and climate change mitigation strategies.

Introduction

The significance of forest floor layers – comprising leaf litter (Oi) and underlying soil organic layers (Oe + Oa; SOL) has gained increasing attention in recent years (Babl-Plauche et al., 2022; Pellegrini et al., 2022). These layers play crucial physical, chemical, and microbiological roles in forest ecosystems, contributing to C sequestration and often forming a significant portion of fuel loads (Clark et al., 2020; Wang et al., 2021). For example, decomposition of the forest floor contributes to the formation of a large, stable C reservoir in soil organic C (SOC) and transfer of dissolved organic C (DOC) into deeper mineral soil layers (Currie et al., 2002). Combined, leaf litter, SOL, and surface (100 cm depth) mineral soils collectively account for ~ 58% of the total C in U.S. forests, with SOL and litter specifically contributing ~8% to this pool (Heath et al., 2011). Leaf litter and SOL also represent a large proportion of pre-fire fuel load, driving fire behavior in many forest ecosystems (Coates et al., 2020; Reid et al., 2012; Smith and Hagan, 2020). Thus, understanding forest floor characteristics is critical for monitoring and predicting C pools and fire behavior.

Many upland hardwood, mixedwood, and pine forests of the southeastern U.S. depend on fire to maintain ecosystem function and are commonly managed using prescribed fire (Cabrera et al., 2023; Hanberry et al., 2020; Kreye et al., 2023; Willis et al., 2024). Variations in forest types and fire history lead to challenges in adequate characterization and accurate estimation of forest floor attributes (e.g., depth, bulk density and % C) (Woodall et al., 2012). For example, natural variability in forest floor microclimate and litter quality and quantity across forests types impacts decomposition rates, and thus, forest floor development (Ladegaard-Pedersen et al., 2005; Schulp et al., 2008). Prescribed fire used to restore and maintain fire-dependent forests in the region (Kobziar et al., 2015; Ryan et al., 2013), contributes to the uneven distribution of forest floor layers across the landscape through varying intensity, severity and frequency (Carter and Darwin Foster, 2004; Clark et al., 2024; Murphy et al., 2006). Difficulties in characterizing unevenly distributed forest floor attributes are further compounded by subjectivity in differentiating the SOL from leaf litter and mineral soil, as there is gradual vertical transition of color, texture, and material composition, and this transition may become obscured with frequent fire, as char-mixed soil organic matter gradually mixes with the mineral soil (Federer, 1982; Yanai et al., 2003). Collectively, these factors—diverse forest types, fire history, natural variability in forest floor development, prescribed fire management, and challenges in layer differentiation—contribute to the complexity of accurately characterizing and estimating forest floor attributes in southeastern U.S. forests.

Such uncertainties in estimation limit our ability to effectively monitor the leaf litter and SOL for improved C storage and fuel load estimations and effective fire behavior modeling (Parresol et al., 2012a; Perry et al., 2009). Inaccurate estimation of forest floor biomass and C stock can lead to failure in understanding the actual role of forest floors in C dynamics, which may impact our ability to monitor leaf litter and SOL layers for C sequestration (Hoover and Smith, 2021; Nunes et al., 2020; Ontl et al., 2020; Pellegrini et al., 2022). Inaccuracies in estimating leaf litter and SOL fuel loads can lead to unexpected outcomes during forest fires, failure in achieving prescribed fire objectives and reduced accuracy of fire effects models (Andreu et al., 2012; Keane, 2012; Parresol et al., 2012b). This can lead to the release of substantial amount of forest C into the atmosphere that had accumulated over a long period, as well as unintentional fire damage to trees and tree mortality, mineral soil exposure, nutrient loss and air pollution (Dey and Schweitzer, 2018; Jaffe et al., 2020; Robbins et al., 2022). These challenges underscore the necessity of precise monitoring, which relies on accurate estimation of forest floor attributes.

To achieve effective monitoring, it is essential to refine the methods used for estimating the mass and % C of leaf litter and SOL, given their critical role in global C sequestration and fire behavior prediction (Ottmar and Andreu, 2007). Current methods, which rely on discrete measurements of depth and published standardized bulk density estimates face several challenges, including 1) high variability in depth, bulk density, % C, 2) lack of bulk density and % C data for many forest types, and 3) difficulty of applying existing data (mostly based on western forest types and individual tree species) to forest types of southeastern U.S. (Woodall and Monleon, 2008; Woodall and Williams, 2005). Direct measurement of mass and C is often impractical due to time and effort constraints, hindering the ability to answer complex ecological questions and fire behavior modeling. Developing models that account for variability in litter and SOL attributes can aid researchers in estimating mass and C stock more efficiently.

Despite the need for revision and importance of using local or regional values when available, relatively few studies have focused on forest floor layers. Ottomar (2007) provided depth and bulk density data for some southeastern U.S. forest types but did not connect these to C pool estimation. Chojnacky (2009) emphasized the need for separate field and laboratory studies of leaf litter and SOL (i.e., duff) to accurately estimate forest floor biomass and Woodall et al. (2011) highlighted concerns about the variability of estimation constants, such as bulk density, and recommended developing site- and forest-type-specific % C and bulk density values, along with consistent field protocols.

To address these gaps, this study aims to 1) develop models that relate a relatively easy to measure forest floor characteristic (depth) to more complicated ones (bulk density, % C, biomass, C pools) and 2) provide standardized bulk density and % C values for different forest types and fire histories that can be used when only mean depth values are available, or relationships with depth are very weak or non-existent. Using models developed from this study, researchers will be able to quantify biomass and C stock of forest floor layers for future studies, ultimately aiding to effectively monitor forest floor, improve C sequestration, and increase efficiency of fire behavior models.

Methods

Study Sites

To characterize leaf litter and SOL attributes, we sampled 14 sites across the southeastern U.S. selected based on tree species composition and fire disturbance history (Figure 8; Table 2). Some sites were sampled for more than one forest type. The study sites were spread out across five southeastern U.S. states: Mississippi, Alabama, Tennessee, Florida, Georgia, and Kentucky to capture the variation in forest species composition and disturbance histories and topography. We collected samples at Spirit Hills Farm, Weeks Bay National Estuarine Research Reserve, Perdido River Reserve, Oakmulgee, Flagg Mountain, Cahaba River National Wildlife Refuge, Bankhead National Forest, Mountain Longleaf National Wildlife Refuge, Tall Timbers, Jones Center at Ichauway, Mary Olive Thomas Demonstration Forest, Bridgestone Firestone Centennial Wilderness Wildlife Management Area, Catoosa Wildlife Management Area, and Bernheim Arboretum and Research Forest (Detailed site information: Table 2).

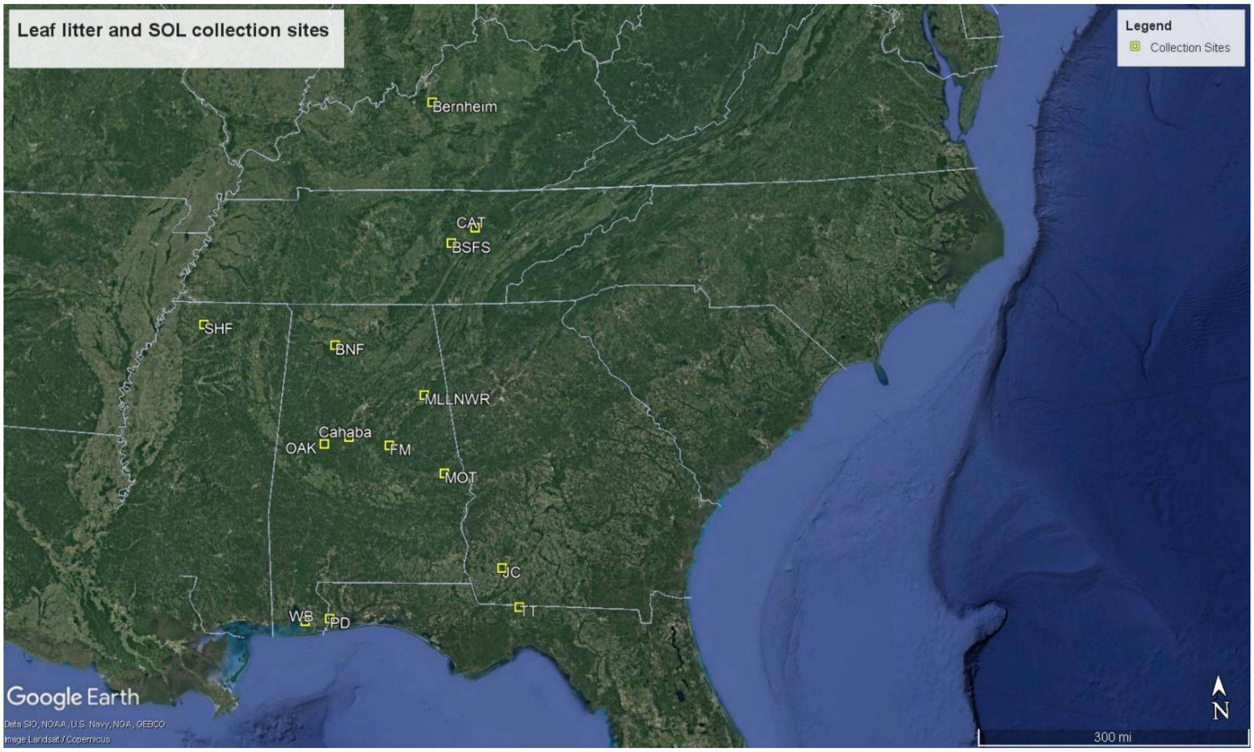

Figure 8: Locations of 14 sites across the southeastern U.S. used for leaf litter and soil organic layer (SOL) collection. Note: SHF - Spirit Hills Farm, WB - Weeks Bay National Estuarine Research Reserve, PD - Perdido River Reserve, Oak - Oakmulgee, FM - Flagg Mountain, Cahaba - Cahaba River National Wildlife Refuge, BNF - Bankhead National Forest, MLLNWR - Mountain Longleaf National Wildlife Refuge, TT - Tall Timbers, JC - Jones Center at Ichauway, MOT - Mary Olive Thomas Demonstration Forest, BSFS - Bridgestone Firestone Centennial Wilderness Wildlife Management Area, CAT - Catoosa Wildlife Management Area, and Bernheim - Bernheim Arboretum and Research Forest.

All sites, except oak savanna, were sampled for two fire history categories 1) stands with frequent fire via prescribed burning or a wildfire event in the last 10 years (i.e., fire-managed) and 2) adjacent stands that had not received fire for at least the last 10 years (i.e., fire-excluded). Oak savannas, which are maintained with periodic fire, were sampled for only fire managed stands. Most fire-managed stands were treated with low-intensity, surface fire using prescribed burn. Some sites, such as WB and PD, also experienced wind and fire disturbances, as discussed in Chapter 1. At each site, we collected ~ 20 samples each of leaf litter and SOL from both fire-excluded and fire-managed stands, totaling 591 SOL and 514 leaf litter samples each. One fire-managed site, Flagg Mountain, had an accidental wildfire after a long fire-free period of ~ 60 years, and was also fire-managed during prescribed fire a year later.

Sample collection:

Leaf litter and SOL were collected in the field following the Forest Inventory and Analysis (FIA) protocol for soil sampling (2005b). Sampling points were randomly chosen at sites, with each sampling point located 100-150 meters apart from each other. At each sampling location, a 25-cm x 25-cm quadrat was intentionally placed to ensure the leaf litter and SOL was present within the quadrat. The quadrat perimeter was carefully delineated using clippers and a hand saw to ensure that only materials inside the quadrat were included. We recorded leaf litter depth (cm) at the four corners of the quadrat. After measurement, leaf litter (undecomposed leaves) within the quadrat was collected and stored in a labeled paper bag. After collecting leaf litter, SOL was collected without disturbing the quadrat. A known rectangular area (usually ~15-cm x-15 cm) was delineated using a hand saw and soil knife. We collected SOL (darker in color, lighter in weight, fluffy, and composed of decomposed plant materials) by scraping it to the mineral soil layer (lighter in color, grainy or sandy texture). Each sample's perimeter was carefully delineated using clippers and a hand saw to avoid including material outside the designated area. When possible, the SOL thickness of extracted sample was measured, otherwise SOL depths were measured on the ground, to the nearest 1-3 mm using a caliper. We measured SOL depth at the four corners of SOL sample area. The SOL sample was then carefully collected in labeled, Ziploc plastic bags and sealed immediately to prevent moisture loss.

Table 2: Leaf litter and soil organic layer (SOL) sampling site locations, fire history, and # of leaf litter and SOL samples (n) each collected in fire-excluded and fire-managed areas across the southeastern U.S. representing major forest types.

Forest Type and Site Name	**Location**	**Lat/Long**	**Fire History**		**# of samples**	
			Fire-excluded (years)	Burn-interval (years)	Fire-excluded (n =286)	Fire-managed (n =316)
Coastal Longleaf Pine						
Perdido River Reserve	Escambia, FL	30.4691 N, 87.4073 W		2		5
Jones Center at Ichauway	Newton, GA	31.2646 N, 84.4777 W	20+	2-4	20	19
Mountain Longleaf						
Flagg Mountain	Coosa, AL	32.9783 N, 86.3545 W	60+	2*	19	20
Mountain Longleaf NWR	Calhoun, AL	33.7085 N, 85.7619 W	37	3-7	19	14
Slash Pine						
Weeks Bay NERR	Fairhope, AL	30.4193 N, 87.8305 W	5	3-5	15	20
Hardwood						
Mountain Longleaf NWR	Calhoun, AL	33.7085 N, 85.7619 W	15+	2-5	20	15
Bernheim Arboretum	Clermont, KY	37.9022 N, 85.6218 W	10+	3-7	20	20
Spirit Hills Farm	Wyatte, MS	34.6710 N, 89.7010 W	10+	2-5	10	10
Mary Olive Thomas Demonstration Forest (MOT)	Auburn, AL	32.5784 N, 85.4237 W	15+	1-3	20	18
Catoosa WMA	Catoosa, TN	36.0766 N, 84.8461W	10+		15	
Loblolly Pine						
MOT	Auburn, AL	32.5784 N, 85.4237 W	15+	1-3	20	20
Oak-Savanna						
Catoosa WMA	Catoosa, TN	36.0766 N, 84.8461W		2-4		7
Bridgestone Firestone CWWMA	White, TN	35.8617 N, 85.2666 W		1-3		26
Mixed Pine Hardwood						
Bankhead National Forest	Bankhead, AL	34.2284 N, 87.3509W	15+	2-4	20	19
Spirit Hills Farm	Wyatte, MS	34.6710 N, 89.7010 W	10+	2-5	10	13
Cahaba River NWR	Bibb, AL	33.0983 N, 87.0607 W	20+	2-5	20	19

Forest Type and Site Name	Location	Lat/Long	Fire History		# of samples	
			Fire-excluded (years)	Burn-interval (years)	Fire-excluded (n =286)	Fire-managed (n =316)
Tall Timbers	Leon, FL	30.6563 N, 84.2089 W	30+	2-5	30	40
MOT	Auburn, AL	32.5784 N, 85.4237 W	15+	1-4	22	19
Oakmulgee	Talladega, AL	32.9770 N, 87.4855 W		2-5		12
Bridgestone Firestone CWWMA	White, TN	35.8617 N, 85.2666 W	15+		6	

Note: leaf litter samples were not collected at some sites, *= site received two fires in two years after long absence of fire.

Laboratory analyses and calculations

Upon return to the laboratory, leaf litter and SOL samples were examined for materials not considered part of the organic layer (e.g., live vegetation, fine and coarse woody debris > 6 mm in diameter, bark, animal feces, and seeds), and these items were discarded. Samples were processed immediately when possible or stored at 2 – 4 °C upon arrival from the field and processed within one week of collection. To process samples, we first removed and measured the volume of rocks and weight of any coarse materials (roots and rocks, > 2 mm in diameter) so that we could account for these materials during bulk density calculations. We then homogenized each sample by gently mixing the remaining material by hand. We took a small subsample, placed in a labeled aluminum tin of known weight, and air-dried at 60 °C for ~ 48 hours to achieve constant weight. We determined the oven-dried sample weights and moisture contents using the current FIA soil analysis protocols (Amacher et al. 2003). Oven dried weight of leaf litter was divided by sample volume to get bulk density. For the SOL samples, we recorded the wet weight of a subsample and its dry weight after oven-drying. We then calculated the moisture content of this subsample. This moisture content was applied to the weight of the whole sample (minus coarse roots and rocks) to determine the dry weight of the SOL. We measured the volume of the entire SOL sample and subtracted the volume of rocks. Finally, we calculated the bulk density by dividing the dry weight of the SOL by its volume (excluding rocks). Dried leaf litter samples (~5 grams) and dried SOL samples were ground into a fine powder using SPEX SamplePrep 8000D Mixer/Mill ball grinder (SPEX SamplePrep LLC, Metuchen, NJ). Each sample was assigned a unique ID and sent to the USFS laboratory for % C analysis using Flash EA1112 Nitrogen/Carbon analyzer (CE Elantech, Milan, Italy). To calculate leaf litter and SOL C pools, equation: C pool (tons ha^{-1}) = depth(cm) x bulk density (g cm^{-3}) x % C x 100 was used.

Data analysis

We studied leaf litter and soil organic layer (SOL) attributes separately, focusing on depth (cm), bulk density (g cm^{-3}), % C, and C pool (converted to tons ha^{-1}). Prior to analysis, we tested homogeneity and normality using Levene's and Shapiro-Wilk Tests, respectively, on depth, %C, bulk density and C pool. When there were violations of assumptions, we transformed the variable using a logarithmic transformation, but we report back-transformed means and standard errors for ease of interpretation. For both leaf litter and SOL, we developed linear regression models to explore relationships between depth and other attributes (bulk density, % C, and C pool). These models were created for each forest type, and in cases where significant interactions with fire history were found, separate models were developed for fire-managed and fire-excluded stands. We assessed the significance of these relationships using p-values, with a threshold of $\alpha = 0.05$, and evaluated model fit using R-squared values. For standardized % C and bulk density values, we also compared depth, % C, bulk density and C pool attributes across forest types and fire history. We conducted one-way ANOVA tests for fire-managed and fire-excluded data separately to assess differences among forest types, followed by Tukey's HSD tests when significant differences were found. To examine the impact of fire history within each forest type, we performed t-tests comparing fire-managed and fire-excluded stands for each attribute. We calculated and reported mean values for each attribute, stratified by forest type and fire history. All statistical analyses were performed using R software (version 2024.04.2), with significance set at $\alpha = 0.05$. We excluded 15 of 529 (2.8%) leaf litter samples and 11 of 602 (1.8%) SOL samples when they were highly inconsistent with the rest of the dataset and fell outside ±2.5 standard deviations from the mean.

Results

Among the forest types studied, relationships between leaf litter depth and % C were non-significant for most forests (Figure 9). Weak positive linear relationships were found at hardwood forest (R2 = 0.04, p = 0.046; Figure 9B) and mountain longleaf pine forest ($R^2 = 0.05$, p =0.049;, Figure 9E), while fire management history did not affect depth % C relationship at all (all $p > 0.05$; Figure 9A, 9C-9D, 9F-9G).

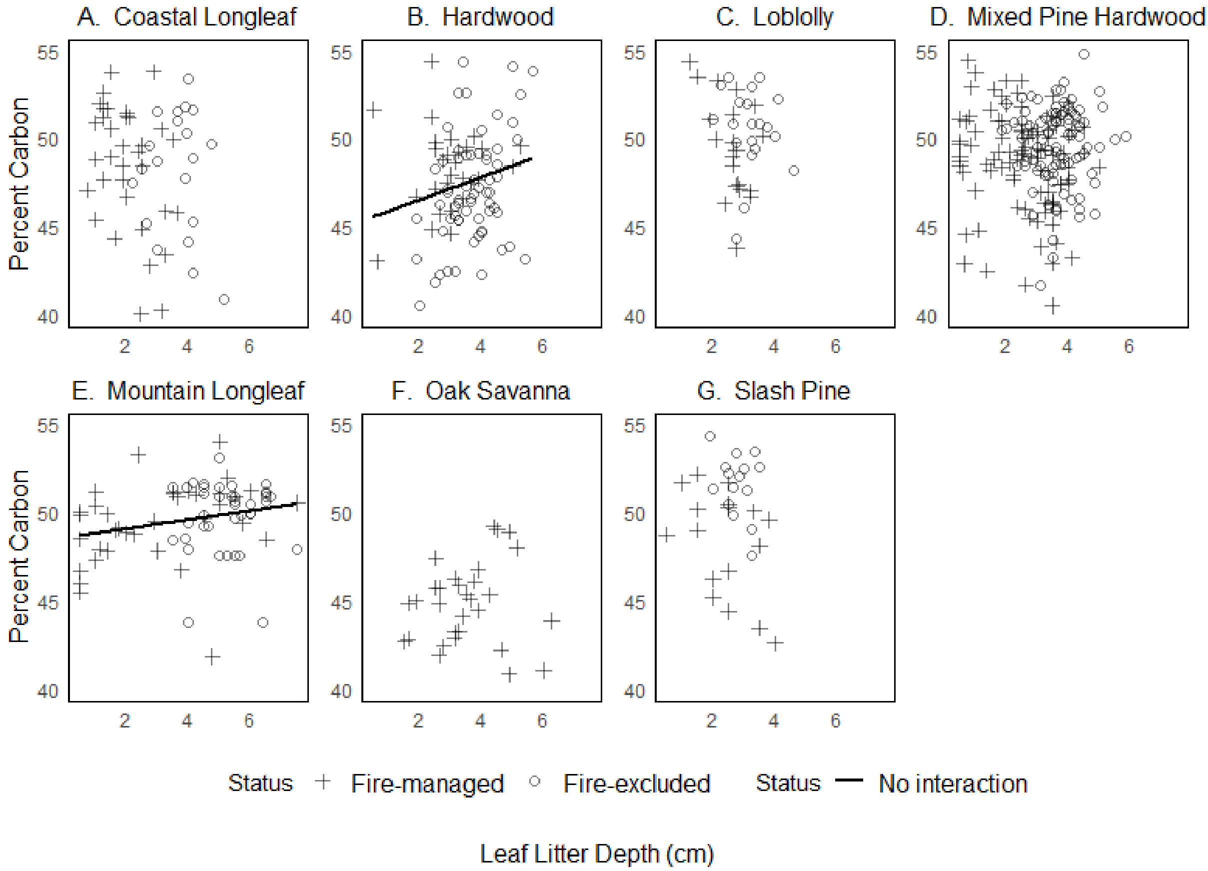

Figure 9: Figure 9: Relationship between leaf litter depth (cm) and % carbon in different forest types of the southeastern U.S.

Leaf litter bulk density decreased with increase in depth for four forests out of seven, while history of fire management did not affect this relationship for all forests (Figure 10). Coastal longleaf pine ($R^2 = 0.09$, p =0.026; Figure 10A), hardwood ($R^2 = 0.28$, p = < 0.001; Figure 10B), mixed pine hardwood ($R^2 = 0.03$, p =0.03; Figure 10D), and mountain longleaf pine forests ($R^2 = 0.23$, $p < 0.001$; Figure 10E) displayed weaker but still significant negative relationships. Loblolly, slash pine, and oak savanna forests did not show significant relationships between litter depth and bulk density (all $p > 0.05$, Figure 10C, 10G, and 10F).

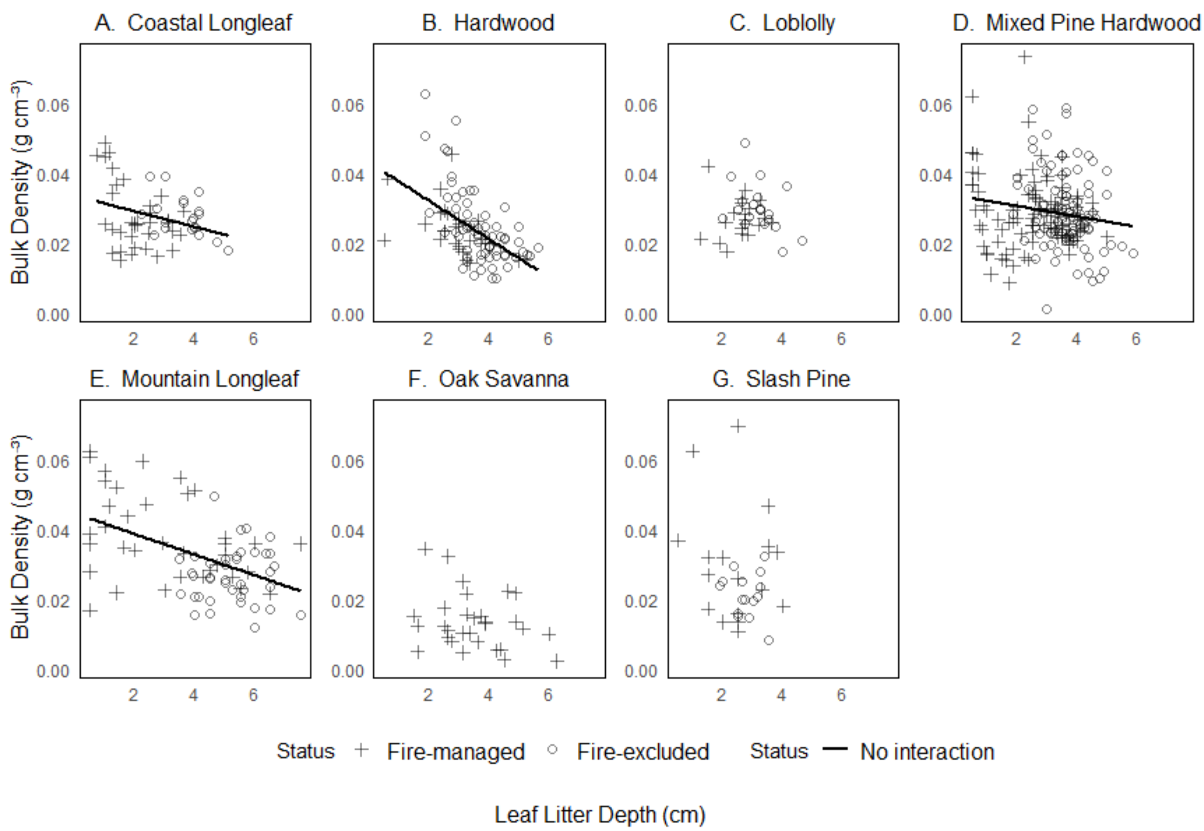

Figure 10: Relationship between leaf litter depth (cm) and bulk density (g cm^{-3}) in different forest types of the southeastern U.S.

Carbon pool for leaf litter layer exhibited positive linear trend for all forests except oak savanna (Figure 11). Coastal longleaf pine ($R^2 = 0.64$, $p < 0.001$), hardwood ($R^2 = 0.10$, $p < 0.001$), loblolly ($R^2 = 0.43$, $p < 0.001$), mountain longleaf ($R^2 = 0.57$, $p < 0.001$), and slash pine ($R^2 = 0.24$, $p < 0.05$), all exhibited positive linear relationships (Figure 11A-11C, 11E, 11G). In mixed pine hardwood forests, fire-managed stands exhibited the stronger positive relationship ($R^2 = 0.65$, $p < 0.001$) compared to fire-excluded stands ($R^2 = 0.07$, $p < 0.006$; Figure 11D). No relationship was found for oak savanna forests (Figure 11F). Detailed model coefficients are listed in Table 3.

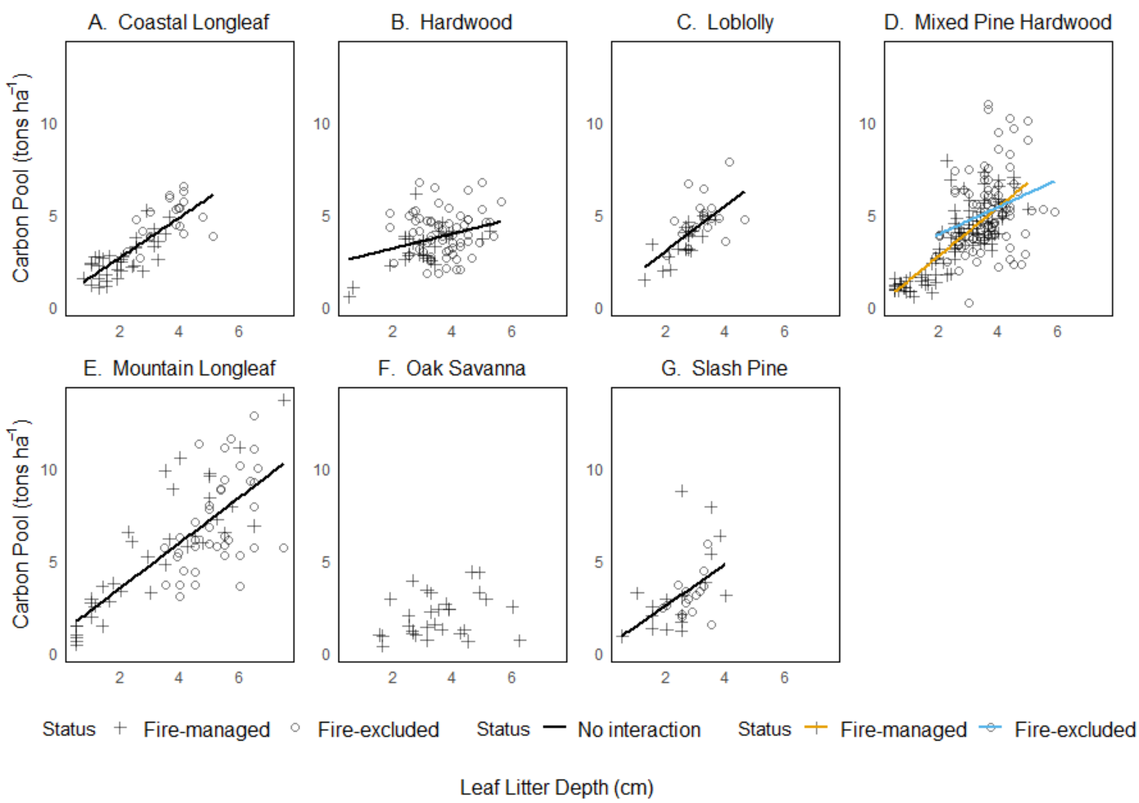

Figure 11: Relationship between leaf litter depth (cm) and carbon pool (tons ha^{-1}) in different forest types of southeastern U.S. Note: Regression lines represent fire-managed (yellow) and fire-excluded (sky blue) stands when fire status significantly influences the relationship. If fire status is not significant, a single black colored regression line models the data for both fire histories.

Percent C for SOL exhibited a positive linear relationship with depth across all except hardwood and oak savanna forests, where effect of fire history was significant only on slash pine and loblolly forests (Figure 12). Coastal longleaf ($R^2 = 0.18$, $p = 0.005$ 0.01; Figure 12A), mixed pine hardwood ($R^2 = 0.03$, $p = 0.01$; Figure 12D), mountain longleaf ($R^2 = 0.34$, $p < 0.001$; Figure 12E) forests all demonstrated positive relationships, while fire management history affected this relationship at slash pine and loblolly pine forests with fire-managed slash pine stand exhibiting the strongest positive relationship ($R^2 = 0.58$, $p < 0.001$; Figure 12G).

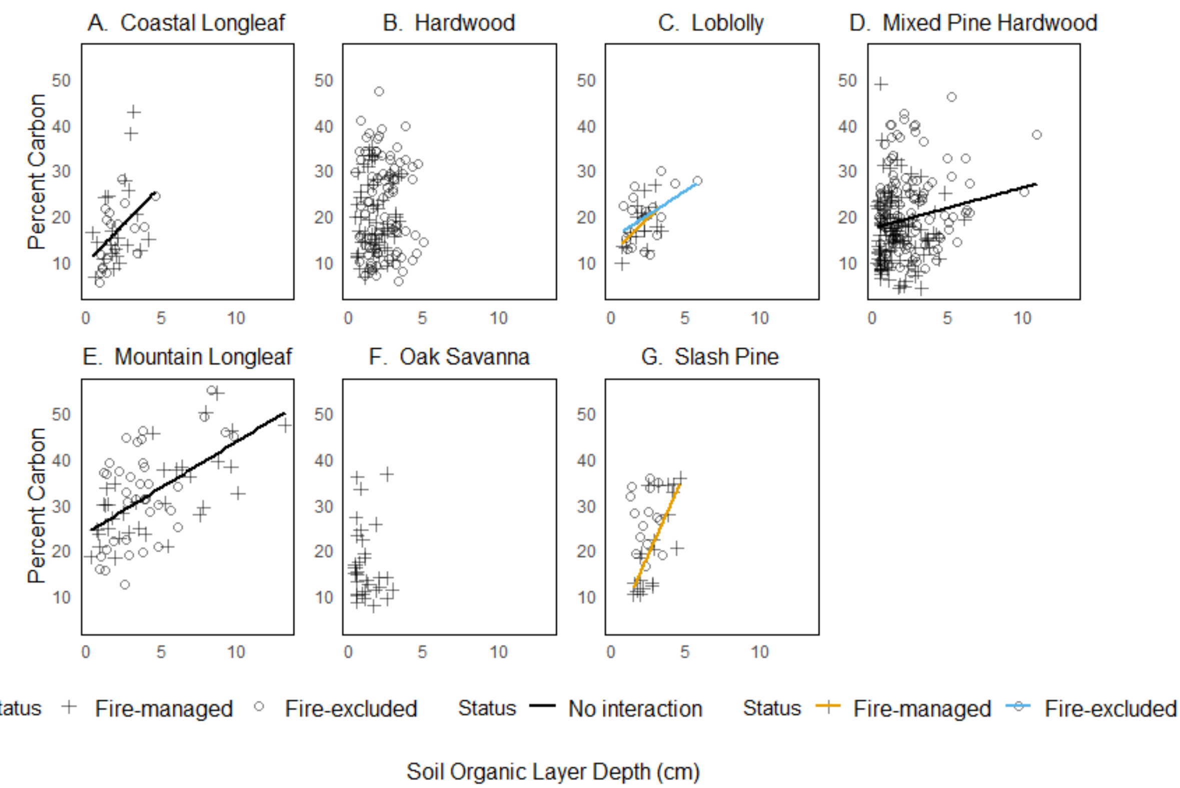

Figure 12: Relationship between soil organic layer depth (cm) and % carbon in different forest types of southeastern U.S. Note: Regression lines represent fire-managed (yellow) and fire-excluded (sky blue) stands when fire status significantly influences the relationship. If fire status is not significant, a single black colored regression line models the data for both fire histories.

Soil organic layer bulk density decreased with increase in SOL depth for all but two forests which were coastal longleaf pine forests and oak savanna (Figure 13). Hardwood ($R^2 = 0.08$, p = 0.003; Figure 13B), , mixed pine hardwood ($R^2 = 0.06$, $p < 0.001$; Figure 13D), mountain longleaf ($R^2 = 0.30$, $p < 0.001$; Figure 13E), fire-managed loblolly ($R^2 = 0.39$, p = 0.002; Figure 13C) fire-managed slash pine ($R^2 = 0.52$, $p < 0.001$; Figure 13G) forests all exhibited the negative relationship. Other forest stands did not show significant relationships between SOL depth and bulk density (all $p > 0.05$; Figure 13A, 13F).

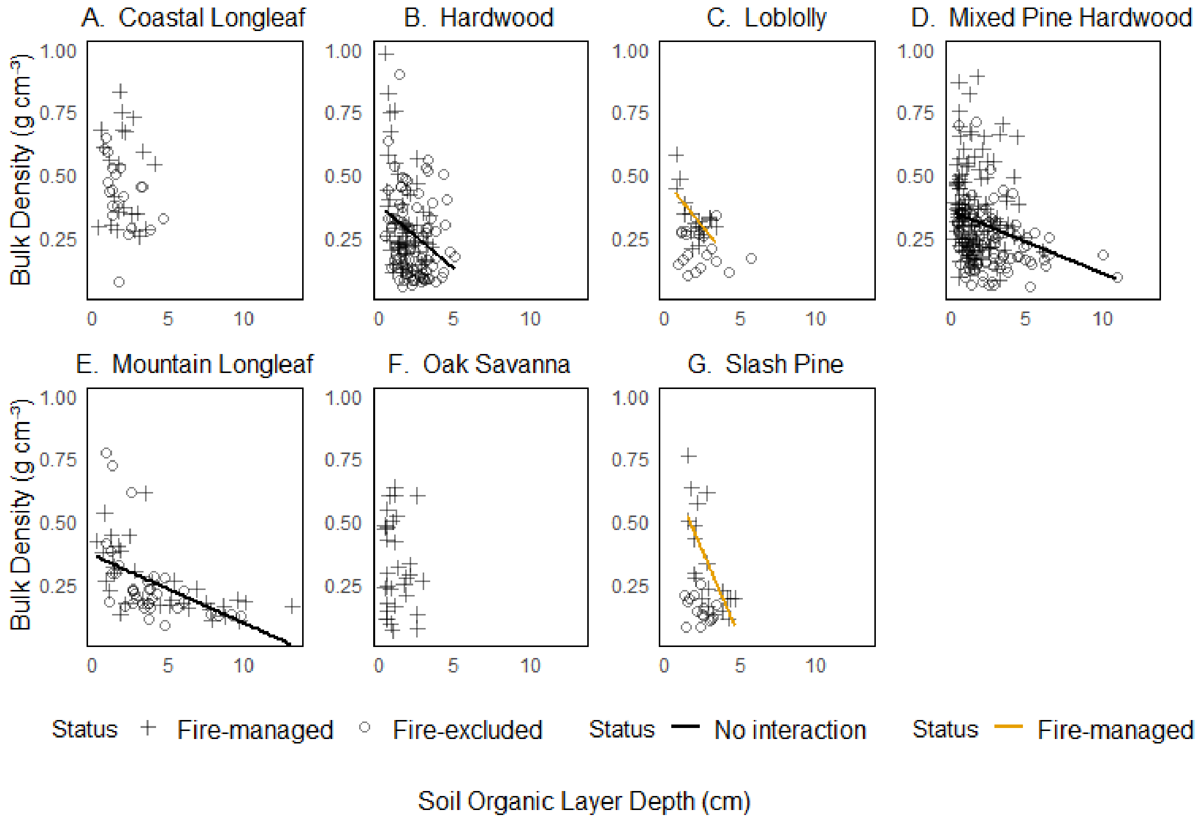

Figure 13: Relationship between soil organic layer depth (cm) and bulk density (g cm-3) in different forest types of southeastern U.S. Note: Regression lines represent fire-managed (yellow) and fire-excluded (sky blue) stands when fire status significantly influences the relationship. If fire status is not significant, a single black colored regression line models the data for both fire histories.

Soil organic layer C pool increased with depth at all forest types exhibiting positive linear trend with fire management history affecting the trend only at mixed pine hardwood forest (Figure 14). Coastal longleaf ($R^2 = 0.69$, $p < 0.001$; Figure 14A), hardwood ($R^2 = 0.47$, $p < 0.001$; Figure 14B), loblolly ($R^2 = 0.64$, $p < 0.001$; Figure 14C), mountain longleaf ($R^2 = 0.79$, $p < 0.001$; Figure 14E), oak savanna ($R^2 = 0.44$, $p < 0.001$; Figure 14F) and slash pine forest ($R^2 = 0.53$, $p < 0.001$;

Figure 14G) all exhibited significant relationship. The effect of fire history was significant on only mixed pine hardwood forest with relationship more pronounced on fire-excluded mixed pine hardwood stand ($R^2 = 0.82$, $p < 0.001$; Figure 14D) compared to fire-managed ($R^2 = 0.64$, $p < 0.001$; Figure 14D. Detailed model coefficients are listed in Table 3.

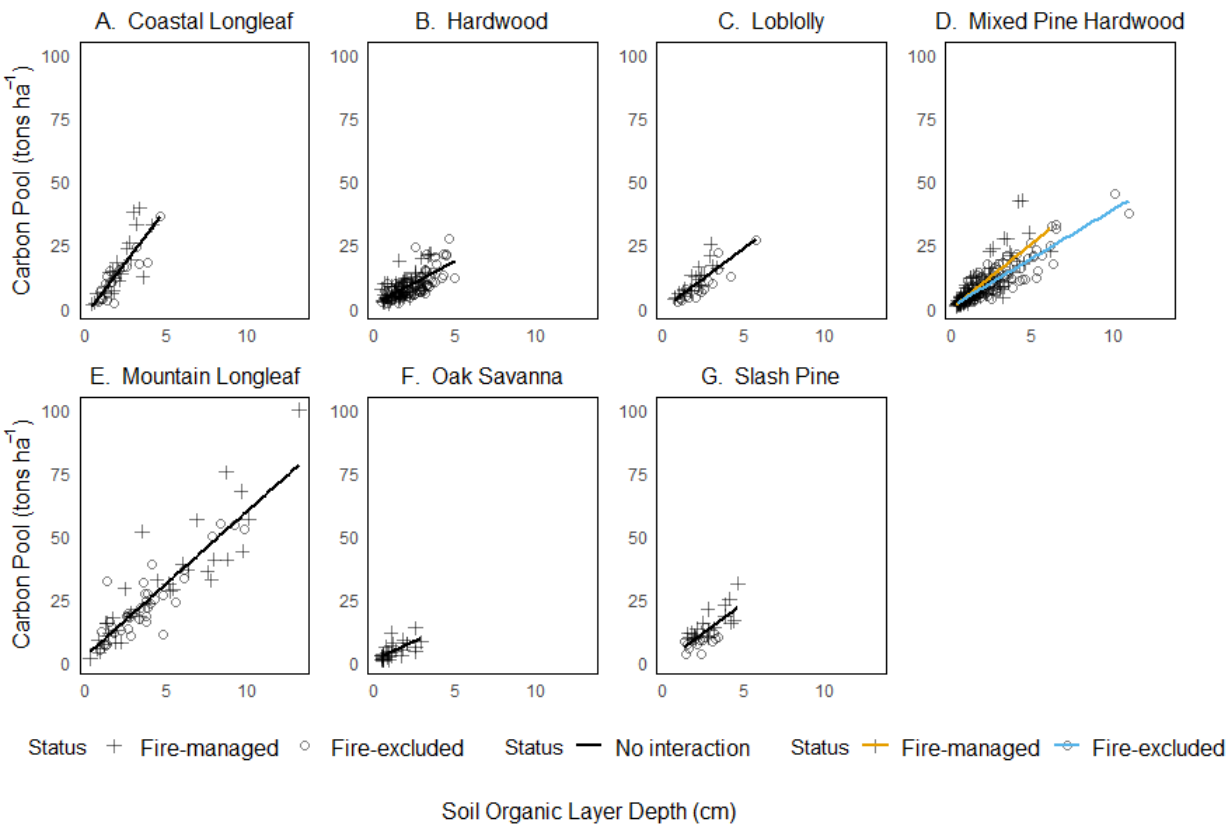

Figure 14: Relationship between soil organic layer depth (cm) and carbon pool (tons ha^{-1}) in different forest types. Note: Regression lines represent fire-managed (yellow) and fire-excluded (sky blue) stands when fire status significantly influences the relationship. If fire status is not significant, a single black colored regression line models the data for both fire histories.

Table 3: Model coefficients for the relationships between depth and bulk density, percent carbon (%C), and carbon pool (C Pool) for leaf litter and soil organic layer (SOL) across different forest types. CLP: Coastal Longleaf Pine, HW: Hardwood, LOB: Loblolly Pine, MPH: Mixed Pine Hardwood, MLP: Mountain Longleaf Pine, OS: Oak Savanna, SP: Slash Pine. R² represents the coefficient of determination, and p represents the p-value for the slope. P-values <0.001 are reported as <0.001

	Bulk Density				% C				C Pool			
Forest Type	*y-Intercept*	*Slope*	R^2	*p*	*y-Intercept*	*Slope*	R^2	*p*	*y-Intercept*	*Slope*	R^2	*p*
Leaf litter												
CLP	0.03	0.00	0.09	0.03	50.26	-0.73	0.05	0.09	0.55	1.08	0.65	<0.001
HW	0.04	0.00	0.28	<0.001	45.22	0.64	0.04	0.04	1.80	0.56	0.19	<0.001
LOB	0.03	0.00	0.01	0.62	52.12	-0.73	0.04	0.24	0.64	1.21	0.43	<0.001
MPH (fire-managed)	0.03	0.00	0.02	0.02	49.97	-0.50	0.04	0.05	0.17	1.31	0.65	<0.001
MPH (fire-excluded)	0.04	0.00	0.07	0.01	49.53	0.02	0.00	0.94	2.47	0.73	0.07	0.006
MLP	0.04	0.00	0.23	<0.001	48.56	0.25	0.05	0.05	1.11	1.22	0.57	<0.001
OS	0.07	-0.01	0.70	<0.001	44.15	0.19	0.01	0.58	5.39	-0.51	0.30	0.004
SP	0.02	0.00	0.07	0.15	51.52	-0.66	0.03	0.33	0.37	1.11	0.24	0.00
SOL												
CLP	0.53	-0.04	0.05	0.14	9.88	3.37	0.18	0.00	-2.22	8.35	0.69	<0.001
HW	0.37	-0.05	0.08	0.003	20.92	-0.45	0.00	0.56	2.12	3.22	0.49	<0.001
LOB	0.34	-0.03	0.12	0.03	13.47	2.48	0.26	0.00	-0.08	4.76	0.64	<0.001
MPH (fire-managed)	0.39	-0.01	0.00	0.28	16.00	0.13	0.00	0.81	0.02	5.14	0.64	<0.001
MPH (fire-excluded)	0.27	-0.01	0.05	0.02	20.64	0.58	0.01	0.21	0.94	3.86	0.82	<0.001
MLP	0.36	-0.03	0.30	<0.001	23.83	1.99	0.34	<0.001	3.34	5.67	0.79	<0.001
OS	0.34	-0.02	0.01	0.52	17.87	-1.00	0.12	0.01	1.42	2.88	0.44	<0.001
SP	0.45	-0.07	0.15	0.02	12.98	4.14	0.18	0.01	0.13	4.70	0.53	<0.001

Forest floor attributes by forest type and fire history

All leaf litter attributes (% C, bulk density, and C pool) varied by fire history and forest types. Litter bulk density showed minimal variation among all forest types and fire management history, with only mountain longleaf pine forest (0.038 g/cm³) being significantly different from other forest types. Leaf litter % C content was relatively constant around 50% with only oak savanna showing the lowest (45%). Mountain longleaf had the highest C pool (7.01 tons ha^{-1}), significantly greater than all other types, while oak savanna had the lowest (2.00 tons ha^{-1}).

Similarly, variation in attributes were also observed in SOL, as bulk density was highest for fire managed coastal longleaf (0.48 g/cm³) and was the lowest for fire excluded slash pine (0.15 g/cm³). Fire excluded mountain longleaf had the highest % C (32%) and fire excluded coastal longleaf had the lowest % C (15%). In contrast, fire managed mountain longleaf exhibited the highest C pool (29.96 tons ha^{-1}), significantly greater than all other types ($p < 0.001$).

Overall, mixed pine hardwood forest showed significant differences between fire-managed and fire-excluded conditions for most attributes for both leaf litter and SOL ($p < 0.05$). Slash pine exhibited significant differences in bulk density, % C, and C pool, while Loblolly only differed in bulk density. Mountain longleaf and coastal longleaf showed no significant differences between fire-managed and fire-excluded conditions for any attribute. Standard % C, bulk density and C pool for all forest types and fire management history are listed in the table below (Table 4 and Table 5).

Table 4: Percent carbon (C), bulk density and C pool of leaf litter for 514 samples (n) collected in 7 forest types of southeastern U.S. Notes: CLP = coastal longleaf pine, HW = hardwood, MPH = mixed pine hardwood, MLP = mountain longleaf pine, OS = oak savanna, SP = slash pine, n = no of samples, BD = bulk density, C = carbon, se = standard error, min = minimum, max = maximum, bold mean values = different when compared to fire-managed stands of same forest type; different superscript letter indicate significant differences among forest types for a given forest floor attributes.

Status	Fire-excluded						Fire-managed						
Forest Type	CLP	HW	LOB	MPH	MLP	SP	CLP	HW	LOB	MPH	MLP	OS	SP
n	20	64	20	96	39	15	34	28	20	95	36	30	17
% C													
min	40.87	40.48	44.29	41.69	43.79	47.54	40.04	43.06	43.74	40.53	41.83	40.83	42.58
mean	48.15 ^{ab}	47.09 ^{a}	50.51 ^{bc}	49.62 ^{bc}	49.81 $^{\mathbf{bc}}$	51.60 ^{c}	48.45 ^{a}	48.29 ^{a}	49.52 ^{a}	48.72 ^{a}	49.42 ^{b}	44.83 ^{c}	48.26 ^{ab}
(se)	(1.10)	(0.96)	(1.45)	(0.23)	(1.25)	(0.95)	(0.98)	(0.88)	(1.33)	(0.79)	(1.90)	(0.41)	(0.73)
max	53.38	54.35	53.43	54.35	53.14	54.30	53.79	54.37	54.35	54.41	54.00	49.20	52.17
BD (g cm^{-3})													
min	0.02	0.01	0.02	0.00	0.01	0.01	0.02	0.01	0.02	0.01	0.02	0.00	0.01
mean	0.03 ^{ab}	0.02 ^{a}	0.03 ^{ab}	**0.03** $^{\mathbf{b}}$	0.03 ^{ab}	**0.02** $^{\mathbf{ab}}$	0.03	0.02	0.03	0.03	0.04	0.01	0.03
(se)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)
max	0.04	0.06	0.05	0.06	0.05	0.03	0.05	0.05	0.04	0.07	0.06	0.03	0.07
C Pool (tons ha^{-1})													
min	2.67	1.79	2.78	0.21	3.08	1.53	1.03	0.54	1.46	0.57	0.43	0.36	0.90
mean	**4.75** $^{\mathbf{a}}$	**3.97** $^{\mathbf{a}}$	**4.79** $^{\mathbf{ab}}$	**5.17** $^{\mathbf{b}}$	**7.01** $^{\mathbf{c}}$	3.05 ^{d}	2.56	3.24	3.50	3.47	5.30	2.00	3.37
(se)	(0.24)	(0.18)	(0.26)	(0.21)	(0.41)	(0.28)	(0.17)	(0.20)	(0.22)	(0.19)	(0.57	(0.21)	(0.57)
max	6.52	6.76	7.82	10.95	12.81	5.86	5.22	6.12	4.91	7.90	13.68	4.37	8.77

Table 5: Percent carbon (C), bulk density and C pool of soil organic layer for 591 samples (n) collected in 7 forest types of southeastern U.S. Notes: CLP = coastal longleaf pine, HW = hardwood, MPH = mixed pine hardwood, MLP = mountain longleaf pine, OS = oak savanna, SP = slash pine, n = no of samples, BD = bulk density, C = carbon, se = standard error, min = minimum, max = maximum, bold mean values = different when compared to fire-managed stands of same forest type; different superscript letter indicate significant differences among forest types for a given forest floor attributes.

Status	Fire-excluded						Fire-managed						
Forest Type	CLP	HW	LOB	MPH	MLP	SP	CLP	HW	LOB	MPH	MLP	OS	SP
n	20	85	18	108	37	15	22	60	20	120	34	32	20
% C													
min	5.41	5.63	11.25	7.56	12.34	16.29	6.43	6.48	9.41	4.04	18.27	7.69	10.20
mean	15.21^{a}	22.30^{ab}	19.73^{ab}	**22.05^{b}**	32.27^{c}	**26.90^{bc}**	17.63^{a}	19.58^{a}	17.91^{a}	16.22^{a}	31.71^{b}	16.76^{a}	21.34^{a}
(se)	(1.98)	(1.01)	(0.97)	(0.66)	(1.59)	(2.18)	(1.43)	(1.18)	(1.36)	(0.92)	(1.74)	(1.73)	(1.62)
max	27.78	47.12	29.61	45.96	55.01	35.73	42.69	35.04	26.58	48.83	54.39	36.62	35.82
BD (g cm^{-3})													
min	0.07	0.05	0.10	0.05	0.08	0.07	0.25	0.11	0.20	0.08	0.10	0.06	0.11
mean	0.42^{a}	0.24^{b}	**0.20^{bc}**	**0.23^{b}**	0.25^{b}	**0.15^{c}**	0.48^{b}	0.31^{a}	0.33^{a}	0.36^{a}	0.26^{a}	0.32^{a}	0.33^{ab}
(se)	(0.04)	(0.02)	(0.02)	(0.02)	(0.02)	(0.04)	(0.03)	(0.02)	(0.02)	(0.01)	(0.03)	(0.01)	(0.01)
max	0.65	0.90	0.33	0.71	0.77	0.25	0.83	0.98	0.58	0.89	0.61	0.63	0.76
C Pool (tons ha^{-1})													
min	1.75	2.01	2.50	1.46	5.43	3.52	1.64	1.72	3.73	0.91	1.79	1.00	9.48
mean	11.72^{a}	8.85^{a}	8.73^{a}	**10.42^{a}**	23.48^{b}	**8.55^{a}**	16.31^{b}	8.39^{a}	11.33^{ab}	8.15^{a}	29.96^{c}	4.61^{a}	15.18^{b}
(se)	(2.41)	(0.62)	(1.25)	(0.70)	(3.85)	(1.34)	(1.93)	(0.56)	(1.58)	(0.83)	(2.19)	(1.30)	(0.71)
max	36.45	27.48	26.69	44.92	54.86	14.11	39.38	21.35	25.32	42.46	99.75	13.91	31.31

Discussion

Our findings indicate that biomass and C estimation models for forest floor layers in southeastern U.S. forests can be modeled best using depth alone. Specifically, we found that % C and bulk density of leaf litter and SOL vary by depth, consequently C pool also varied by depth with fire history influencing this relationship on some forests. This finding suggests that depth-based biomass and C estimation models can be developed, which rely on identification of forest type, fire history and simple depth measurements. These models could provide an alternative way for current biomass and C estimation methods which use standardized values, primarily based on Western U.S. forests ecosystems. This study suggests that using linear models with depth as the predictor variable can be used for leaf litter and SOL C pool estimation for many forest types, but that standardized values of bulk density and % C may be useful when linear correlations are weak. This study attempts to provide accurate estimation of forest floor mass and C in these forest ecosystems, which will allow future studies to focus on answering more complex ecological questions.

Leaf litter % C, bulk density and C pool models based on depth

There were contrasting relationships of leaf litter depth with % C and bulk density with very minimal effect of fire history. Leaf litter % C did not show significant correlations with depth for most forest types, with the exception of hardwood and mountain longleaf forests. This suggests that the C content of leaf litter does not depend on depth of the litter layer in general, and the finding is similar to previous studies (Chojnacky et al., 2009; Woodall et al., 2012). In contrast, leaf litter bulk density exhibited a significant negative relationship with depth for all but loblolly, oak savanna, and slash pine, which is partly due to leaf litter morphology affecting leaf litter bulk density (Belcher, 2016; Kauf et al., 2018). The variation in strength of relation is most likely due to the variation among forest types in compaction of leaf litter due to leaf litter shapes and sizes, decomposition rates and environmental conditions (Burton et al., 2020; Kauf et al., 2018). While measuring leaf litter depth is easier when there is a distinct accumulated layer, measuring shallower leaf litter depths can be challenging as initiation of decomposition and mineralization process results in higher contamination with SOL and mineral soil (Prescott, 2005; Zhang et al., 2021).

Positive linear relationships between leaf litter C pool and depth with varying strengths. reflects the natural variability in forest floor depth such as non-uniform leaf litter accumulation (Overby et al., 2002; Schulp et al., 2008). As fire history only affected this relationship in mixed pine hardwood forests, this finding indicates disturbances, including fire, can make variability of forest floor properties greater (Coates et al., 2020; Ladegaard-Pedersen et al., 2005). The relationship was slightly weaker on fire-excluded stands than in fire-managed stand in mixed pine hardwood, which is most likely consequence of higher bulk density of leaf litter at shallower depth. The smaller C pool at oak savanna compared to other forests is likely due to several factors such as frequent fire and fewer overstory trees in the ecosystem leading to reduced leaf litter input. Additionally, open canopy at oak savanna allows more sunlight to reach the forest floor, potentially accelerating litter decomposition and mineralization rates (O'Halloran et al., 2013). Considering the effect of fire history on C pool estimation, using forest type specific linear models or standard % C and bulk density values based on fire history could be useful, although leaf litter C pool models explain only up to 56 % of variation. These findings align with previous studies emphasizing the need for region-specific forest floor assessments (Woodall et al. 2011).

Soil organic layer % C, bulk density and C pool models based on depth

Soil organic layer depth strongly correlated with % C and bulk density in contrasting way. While the % C increased with increase in depth apart from hardwood forest, possibly due to the accumulation of decomposed organic material, as degree of decomposition of SOL increases with depth (Raaflaub and Valeo, 2009). This leads to thicker, distinct SOL layers, and easier visual identification and collection of SOL samples. On other hand, shallower SOL are more likely to mix with mineral soil. This mixing makes depth measurement of SOL layer harder based on visual estimation. As a result, collection of mineral soil contaminated SOL samples takes place at shallower depth. The effect of fire history was evident on only slash pine forest, which may be due to small sample size. All sites with pine components exhibited higher % C at deeper depths due to slower decomposition rate of pine leaf litter due to their different chemical composition such as high lignin content (Gholz et al., 2000; Polyakova and Billor, 2007). Same arguments, which were attributed to SOL C pool and depth relationship, can be made for the SOL bulk density and depth relationship. The lower % C in shallower SOL depth means our shallower SOL samples contained a higher proportion of mineral soil, which are denser than SOL (Hossain et al., 2015). This higher mixing in shallower SOL depth may be due to natural movements, animals, or land use practices. The effect of fire history was evident on SOL bulk density on loblolly and slash pine forest only, where fire-excluded stands did not show significant correlations. This suggests the effect of fire history on SOL bulk density might not be same in all pine forests (Kreye et al., 2014b; Šamonil et al., 2008).

As a result, SOL C pool strongly correlated with its depth in all forest types while the effect of fire history on such relationship was evident only on mixed pine hardwood forests. This positive linear relationship is mostly the consequence of higher % C at deeper SOL depths. The significant interactions between SOL depth and forest type in predicting C pools across the entire study area emphasize the importance of forest-type-specific approaches in C estimation (Woodall et al. 2011). These findings align with previous study that emphasize the importance of easily measurable forest floor characteristics for biomass and C estimation (Ottomar 2007) and that suggest mass and C estimation can be modeled best using depth alone (Chojnacky et al., 2009; Stephens and Finney, 2002).

Implications for Forest Management and C sequestration

Our results have significant implications for biomass and C estimation for southeastern U.S. forests. The marked differences in forest floor attributes across forest types suggest that one-size-fits-all approaches to forest floor management and C estimation are likely to be inaccurate. Forest managers should consider these forest type-specific characteristics when developing management plans, particularly for fire-dependent ecosystems. For instance, the deeper forest floor in mountain longleaf pine forests, especially in fire-excluded stands, suggests a greater potential for C storage, but also a higher fuel load that may require careful fire management. Conversely, the shallower forest floor in fire-managed coastal longleaf pine forests might indicate a more frequent fire regime, which necessitates caution on use of prescribed fire, to prevent excessive loss of C from forest floor. The consistent reduction in litter depth and C pools in fire-managed areas suggests that frequent fires will minimize fire hazards. However, the variable effects on SOL characteristics indicate that managers should carefully consider the long-term impacts of repeated burning on soil organic matter and nutrient cycling.

The contrasting trends in bulk density and % C between litter and SOL layers emphasize the importance of considering both components when assessing the overall impact of fire on forest floor attributes and C storage. While prescribed burning may reduce surface fuel loads and C in the litter layer, it may also lead to changes in SOL structure and composition that could affect long-term soil fertility and C sequestration potential. The strong relationships between forest floor depth and C pools suggest that relatively simple depth measurements could provide reasonably accurate estimates of C storage, potentially streamlining forest inventory processes. However, the variations in these relationships across forest types and fire history underscore the need for forest type specific models or standardized bulk density, and % C for better biomass and C estimation. Forest-type-specific models and, where relevant, incorporate fire history into their estimation methods and provide a nuanced approach that can improve the accuracy of C storage and fuel load estimates, which will ultimately help in studies focusing on forest C pool dynamics of southeastern U.S. and enhance our understanding of C.

Conclusions

Our study emphasizes the need for forest-type-specific approaches in forest floor biomass and C estimation. The depth of leaf litter and SOL emerged as reliable predictors of C pools, with SOL depth showing particularly strong relationships across all forest types. Fire history consistently impacted forest floor attributes, reducing depths and altering bulk densities, which has implications for both C storage and fire management strategies. For forest managers, our results highlight the need to balance C sequestration goals with fire management practices, especially in fire-dependent ecosystems. Although depth-based C models could streamline forest inventory processes, the variability across forest types and fire history necessitates a nuanced, type-specific approach to forest floor management and C estimation.

References

Andreu, A.G., Shea, D., Parresol, B.R., Ottmar, R.D., 2012. Evaluating fuel complexes for fire hazard mitigation planning in the southeastern United States. For. Ecol. Manag., Assessing wildland fuels and hazard mitigation treatments in the southeastern United States 273, 4–16. https://doi.org/10.1016/j.foreco.2011.06.040

Babl-Plauche, E.K., Alexander, H.D., Siegert, C.M., Willis, J.L., Berry, A.I., 2022. Mesophication of upland oak forests: Implications of species-specific differences in leaf litter decomposition rates and fuelbed composition. For. Ecol. Manag. 512, 120141. https://doi.org/10.1016/j.foreco.2022.120141

Belcher, C.M., 2016. The influence of leaf morphology on litter flammability and its utility for interpreting palaeofire [WWW Document]. https://doi.org/10.1098/rstb.2015.0163

Burton, J.E., Cawson, J.G., Filkov, A.I., Penman, T.D., 2020. Leaf traits predict global patterns in the structure and flammability of forest litter beds.

Cabrera, S., Alexander, H.D., Willis, J.L., Anderson, C.J., 2023. Midstory removal of encroaching species has minimal impacts on fuels and fire behavior regardless of burn season in a degraded pine-oak mixture. For. Ecol. Manag. 544, 121157. https://doi.org/10.1016/j.foreco.2023.121157

Carter, M.C., Darwin Foster, C., 2004. Prescribed burning and productivity in southern pine forests: a review. For. Ecol. Manag. 191, 93–109. https://doi.org/10.1016/j.foreco.2003.11.006

Chojnacky, D., Amacher, M., Gavazzi, M., 2009. Separating Duff and Litter for Improved Mass and Carbon Estimates. South. J. Appl. For. 33, 29–34. https://doi.org/10.1093/sjaf/33.1.29

Clark, K.L., Heilman, W.E., Skowronski, N.S., Gallagher, M.R., Mueller, E., Hadden, R.M., Simeoni, A., 2020. Fire Behavior, Fuel Consumption, and Turbulence and Energy Exchange during Prescribed Fires in Pitch Pine Forests. Atmosphere 11, 242. https://doi.org/10.3390/atmos11030242

Clark, K.L., Skowronski, N.S., Gallagher, M.R., 2024. Carbon dynamics of prescribed fire in pine- and oak-dominated forests on the mid-Atlantic coastal plain, USA. For. Ecol. Manag. 553, 121589. https://doi.org/10.1016/j.foreco.2023.121589

Coates, T.A., Johnson, A., Aust, W.M., Hagan, D.L., Chow, A.T., Trettin, C., 2020. Forest composition, fuel loading, and soil chemistry resulting from 50 years of forest management and natural disturbance in two southeastern Coastal Plain watersheds, USA. For. Ecol. Manag. 473, 118337. https://doi.org/10.1016/j.foreco.2020.118337

Currie, W.S., Yanai, R.D., Piatek, K.B., Prescott, C.E., Goodale, C.L., 2002. Processes Affecting Carbon Storage in the Forest Floor and in Downed Woody Debris, in: The Potential of U.S. Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press.

Dey, D.C., Schweitzer, C.J., 2018. A Review on the Dynamics of Prescribed Fire, Tree Mortality, and Injury in Managing Oak Natural Communities to Minimize Economic Loss in North America. Forests 9, 461. https://doi.org/10.3390/f9080461

Federer, C.A., 1982. Subjectivity in the Separation of Organic Horizons of the Forest Floor. Soil Sci. Soc. Am. J. 46, 1090–1093. https://doi.org/10.2136/sssaj1982.03615995004600050041x

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Glob. Change Biol. 6, 751–765. https://doi.org/10.1046/j.1365-2486.2000.00349.x

Hanberry, B.B., Bragg, D.C., Alexander, H.D., 2020. Open forest ecosystems: An excluded state. For. Ecol. Manag. 472, 118256. https://doi.org/10.1016/j.foreco.2020.118256

Heath, L.S., Smith, J.E., Skog, K.E., Nowak, D.J., Woodall, C.W., 2011. Managed Forest Carbon Estimates for the US Greenhouse Gas Inventory, 1990—2008. J. For. 109, 167–173. https://doi.org/10.1093/jof/109.3.167

Hoover, C.M., Smith, J.E., 2021. Current aboveground live tree carbon stocks and annual net change in forests of conterminous United States. Carbon Balance Manag. 16, 17. https://doi.org/10.1186/s13021-021-00179-2

Hossain, M.F., Chen, W., Zhang, Y., 2015. Bulk density of mineral and organic soils in the Canada’s arctic and sub-arctic. Inf. Process. Agric. 2, 183–190. https://doi.org/10.1016/j.inpa.2015.09.001

Jaffe, D.A., O’Neill, S.M., Larkin, N.K., Holder, A.L., Peterson, D.L., Halofsky, J.E., Rappold, A.G., 2020. Wildfire and prescribed burning impacts on air quality in the United States. J. Air Waste Manag. Assoc. 70, 583–615. https://doi.org/10.1080/10962247.2020.1749731

Kauf, Z., Damsohn, W., Fangmeier, A., 2018. Do relationships between leaf traits and fire behaviour of leaf litter beds persist in time? PLOS ONE 13, e0209780. https://doi.org/10.1371/journal.pone.0209780

Keane, R.E., 2012. Describing wildland surface fuel loading for fire management: a review of approaches, methods and systems. Int. J. Wildland Fire 22, 51–62. https://doi.org/10.1071/WF11139

Kobziar, L.N., Godwin, D., Taylor, L., Watts, A.C., 2015. Perspectives on Trends, Effectiveness, and Impediments to Prescribed Burning in the Southern U.S. Forests 6, 561–580. https://doi.org/10.3390/f6030561

Kreye, J.K., Kane, J.M., Varner, J.M., 2023. Multivariate roles of litter traits on moisture and flammability of temperate northeastern North American tree species. Fire Ecol. 19, 21. https://doi.org/10.1186/s42408-023-00176-5

Kreye, J.K., Varner, J.M., Dugaw, C.J., 2014. Spatial and temporal variability of forest floor duff characteristics in long-unburned Pinus palustris forests. Can. J. For. Res. 44, 1477–1486. https://doi.org/10.1139/cjfr-2014-0223

Ladegaard-Pedersen, P., Elberling, B., Vesterdal, L., 2005. Soil carbon stocks, mineralization rates, and CO2 effluxes under 10 tree species on contrasting soil types. Can. J. For. Res. 35, 1277–1284. https://doi.org/10.1139/x05-045

Masuda, C., Kanno, H., Masaka, K., Morikawa, Y., Suzuki, M., Tada, C., Hayashi, S., Seiwa, K., 2022. Hardwood mixtures facilitate leaf litter decomposition and soil nitrogen mineralization in conifer plantations. For. Ecol. Manag. 507, 120006. https://doi.org/10.1016/j.foreco.2021.120006

Murphy, J.D., Johnson, D.W., Miller, W.W., Walker, R.F., Blank, R.R., 2006. PRESCRIBED FIRE EFFECTS ON FOREST FLOOR AND SOIL NUTRIENTS IN A SIERRA NEVADA FOREST. Soil Sci. 171, 181. https://doi.org/10.1097/01.ss.0000193886.35336.d8

Nunes, L.J.R., Meireles, C.I.R., Pinto Gomes, C.J., Almeida Ribeiro, N.M.C., 2020. Forest Contribution to Climate Change Mitigation: Management Oriented to Carbon Capture and Storage. Climate 8, 21. https://doi.org/10.3390/cli8020021

O'Halloran, L.R., Borer, E.T., Seabloom, E.W., MacDougall, A.S., Cleland, E.E., McCulley, R.L., Hobbie, S., Harpole, W.S., DeCrappeo, N.M., Chu, C., Bakker, J.D., Davies, K.F., Du, G., Firn, J., Hagenah, N., Hofmockel, K.S., Knops, J.M.H., Li, W., Melbourne, B.A., Morgan, J.W., Orrock, J.L., Prober, S.M., Stevens, C.J., 2013. Regional Contingencies in the Relationship between Aboveground Biomass and Litter in the World's Grasslands. PLOS ONE 8, e54988. https://doi.org/10.1371/journal.pone.0054988

Ontl, T.A., Janowiak, M.K., Swanston, C.W., Daley, J., Handler, S., Cornett, M., Hagenbuch, S., Handrick, C., Mccarthy, L., Patch, N., 2020. Forest Management for Carbon Sequestration and Climate Adaptation. J. For. 118, 86–101. https://doi.org/10.1093/jofore/fvz062

Ottmar, R., Andreu, A., 2007. Litter and Duff Bulk Densities in the Southern United States. Jt. Fire Sci. Program Proj. 04-2-1-49.

Overby, S.T., Hart, S.C., Neary, D.G., 2002. Impacts of Natural Disturbance on Soil Carbon Dynamics in Forest Ecosystems, in: The Potential of U.S. Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press.

Parresol, B.R., Blake, J.I., Thompson, A.J., 2012a. Effects of overstory composition and prescribed fire on fuel loading across a heterogeneous managed landscape in the southeastern USA. For. Ecol. Manag., Assessing wildland fuels and hazard mitigation treatments in the southeastern United States 273, 29–42. https://doi.org/10.1016/j.foreco.2011.08.003

Parresol, B.R., Scott, J.H., Andreu, A., Prichard, S., Kurth, L., 2012b. Developing custom fire behavior fuel models from ecologically complex fuel structures for upper Atlantic Coastal

Plain forests. For. Ecol. Manag., Assessing wildland fuels and hazard mitigation treatments in the southeastern United States 273, 50–57. https://doi.org/10.1016/j.foreco.2012.01.024

Pellegrini, A.F.A., Harden, J., Georgiou, K., Hemes, K.S., Malhotra, A., Nolan, C.J., Jackson, R.B., 2022. Fire effects on the persistence of soil organic matter and long-term carbon storage. Nat. Geosci. 15, 5–13. https://doi.org/10.1038/s41561-021-00867-1

Perry, C.H., Woodall, C.W., Amacher, M.C., O'Neill, K.P., 2009. An Inventory of Carbon Storage in Forest Soil and Down Woody Material of the United States, in: Carbon Sequestration and Its Role in the Global Carbon Cycle. American Geophysical Union (AGU), pp. 101–116. https://doi.org/10.1029/2006GM000341

Polyakova, O., Billor, N., 2007. Impact of deciduous tree species on litterfall quality, decomposition rates and nutrient circulation in pine stands. For. Ecol. Manag. 253, 11–18. https://doi.org/10.1016/j.foreco.2007.06.049

Prescott, C.E., 2005. Decomposition and Mineralization of Nutrients from Litter and Humus, in: BassiriRad, H. (Ed.), Nutrient Acquisition by Plants: An Ecological Perspective. Springer, Berlin, Heidelberg, pp. 15–41. https://doi.org/10.1007/3-540-27675-0_2

Raaflaub, L., Valeo, C., 2009. Hydrological properties of duff. Water Resour. Res. 45. https://doi.org/10.1029/2008WR007396

Reid, A.M., Robertson, K.M., Hmielowski, T.L., 2012. Predicting litter and live herb fuel consumption during prescribed fires in native and old-field upland pine communities of the southeastern United States. Can. J. For. Res. 42, 1611–1622. https://doi.org/10.1139/x2012-096

Robbins, Z.J., Loudermilk, E.L., Reilly, M.J., O'Brien, J.J., Jones, K., Gerstle, C.T., Scheller, R.M., 2022. Delayed fire mortality has long-term ecological effects across the Southern Appalachian landscape. Ecosphere 13, e4153. https://doi.org/10.1002/ecs2.4153

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11, e15–e24. https://doi.org/10.1890/120329

Šamonil, P., Král, K., Douda, J., Šebková, B., 2008. Variability in forest floor at different spatial scales in a natural forest in the Carpathians: effect of windthrows and mesorelief. Can. J. For. Res. 38, 2596–2606. https://doi.org/10.1139/X08-100

Schulp, C.J.E., Nabuurs, G.-J., Verburg, P.H., de Waal, R.W., 2008. Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. For. Ecol. Manag., Impacts of forest ecosystem management on greenhouse gas budgets 256, 482–490. https://doi.org/10.1016/j.foreco.2008.05.007

Smith, C.N., Hagan, D.L., 2020. Assessing the Relationship between Litter + Duff Consumption and Post-Fire Soil Temperature Regimes. Fire 3, 64. https://doi.org/10.3390/fire3040064

Stephens, S.L., Finney, M.A., 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For. Ecol. Manag. 162, 261–271. https://doi.org/10.1016/S0378-1127(01)00521-7

Wang, Y.-P., Zhang, H., Ciais, P., Goll, D., Huang, Y., Wood, J.D., Ollinger, S.V., Tang, X., Prescher, A.-K., 2021. Microbial Activity and Root Carbon Inputs Are More Important than Soil Carbon Diffusion in Simulating Soil Carbon Profiles. J. Geophys. Res. Biogeosciences 126, e2020JG006205. https://doi.org/10.1029/2020JG006205

Willis, J.L., Milton, T.F., Alexander, H.D., 2024. Cone and fruit impacts on understory flammability depend on traits and forest floor coverage. Fire Ecol. 20, 52. https://doi.org/10.1186/s42408-024-00281-z

Woodall, C., Monleon, V., 2008. Sampling Protocol, Estimation, and Analysis Procedures for the Down Woody Materials Indicator of the FIA Program.

Woodall, C., Williams, M.S., 2005. Sampling Protocol, Estimation, and Analysis Procedures for the Down Woody Materials Indicator of the FIA Program. USDA Forest Service, North Central Research Station.

Woodall, C.W., Perry, C.H., Westfall, J.A., 2012. An empirical assessment of forest floor carbon stock components across the United States. For. Ecol. Manag. 269, 1–9. https://doi.org/10.1016/j.foreco.2011.12.041

Yanai, R.D., Stehman, S.V., Arthur, M.A., Prescott, C.E., Friedland, A.J., Siccama, T.G., Binkley, D., 2003. Detecting Change in Forest Floor Carbon. Soil Sci. Soc. Am. J. 67, 1583–1593. https://doi.org/10.2136/sssaj2003.1583

Zhang, M., Dong, L.-G., Fei, S.-X., Zhang, J.-W., Jiang, X.-M., Wang, Y., Yu, X., 2021. Responses of Soil Organic Carbon Mineralization and Microbial Communities to Leaf Litter Addition under Different Soil Layers. Forests 12, 170. https://doi.org/10.3390/f12020170