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Carbon dynamics in old-growth forests of the Central Hardwoods Region, USA

Jacob S. Fraser [a,2,*], Lauren S. Pile Knapp [a,2], Brad Graham [b], Michael A. Jenkins [c], John Kabrick [a], Michael Saunders [c], Martin Spetich [d], Steve Shifley [a,1]

[a] Northern Research Station, USDA Forest Service, Columbia, MO 65211, United States
[b] Terrestrial Habitat Science Unit, Missouri Department of Conservation, West Plains, MO 65775, United States
[c] Department of Forestry and Natural Resources and Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907, United States
[d] USDA Forest Service, Southern Research Station, Hot Springs, AR 71902, United States

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ABSTRACT

Managing old-growth forests and promoting old-growth complexity in aging forests for carbon emissions mitigation has become an important component of diversified land management strategies. In the midwestern US, the Central Hardwoods Region (CHR) is the largest continuous deciduous forested area and includes a diverse range of species compositions, forest structures, and topoedaphic environments. Understanding carbon storage potential in old-growth forests across the CHR is important for evaluating climate-adaptive management strategies to increase carbon sequestration in the region's aging forests. We assessed forest carbon in two time periods (the early 1990s and the 2010s) in ten old-growth forests across a 770 km east-west productivity gradient from Indiana to Missouri. Further, we related anomalies in carbon pools between the two sampling periods to documented or observable disturbances. As expected, old-growth forests on more productive sites in the eastern portion of the study range stored more aboveground carbon (120–177 Mg C ha^{-1}) than less productive sites to the west (93–117 Mg C ha^{-1}). Over the twenty-year period, old-growth forests accumulated 9.2 ± 1.5 (mean ± SE) Mg C ha^{-1} or a 7 % increase in total aboveground carbon. Further, downed dead wood carbon increased 5 % (0.4 ± 0.7 Mg C ha^{-1}), standing dead increased 7 % (0.3 ± 0.7 Mg C ha^{-1}), live roots increased 4 % (1.0 ± 0.3), and dead roots increased by 68 % (0.3 ± 0.1 Mg C ha^{-1}). However, stochastic disturbances can positively or negatively impact total carbon and carbon pools. Documenting carbon trends and disturbance effects in old-growth forests provides guidance to enhance the representation of structurally complex, late successional forests using active forest management. Old-growth forests are currently rare in the CHR landscape, but the abundance of aging forests in the region provides immense potential to store carbon, particularly when combined with strategies that optimize early- and late-successional habitats for carbon sequestration along with other ecological goods and services.

1. Introduction

Forest ecosystems are an important component to help mitigate the effects of anthropogenic climate change due to their uptake of significant quantities of atmospheric CO_2 (IPCC 2007, 2014). Because forest systems globally store large quantities of carbon and are a potential source or further carbon sequestration, they serve as a "natural solution" to climate change (Zhu et al. 2019). Further, recent US policy has advocated for restoration of the structure and composition of old-growth forest stands to take advantage of their contributions to carbon storage, biodiversity, and fire resilience with these goals extending beyond old-growth to carbon-rich aging forests (U.S. Department of Agriculture Office of the Secretary 2022).

A long-standing assumption is that old-growth forests are carbon neutral, whereby carbon captured by photosynthesis and carbon released by respiration are equal. However, Luyssaert et al. (2008)

* Corresponding author.
E-mail address: Jacob.Fraser@usda.gov (J.S. Fraser).
[1] Retired.
[2] Equal contribution.

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suggested that forests over 200 years old continue to sequester 2.4 ± 0.8 Mg C ha^{-1} yr^{-1} which was later disputed by Gundersen et al. (2021) as an overestimate (reanalysis estimated 1.6 ± 0.6 Mg C ha^{-1} yr^{-1} for forests exceeding 200 years in age and 1.3 ± 0.4 Mg C ha^{-1} yr^{-1} for unmanaged forests). Although young forests may yield greater rates of carbon accumulation on an annual basis, disturbances that facilitate their successional development often increase carbon loss beyond the net primary production of their regrowth (Harmon et al. 1990, Kowalski et al. 2004, Pregitzer and Euskirchen 2004). For this reason, the conservation of old-growth forests and the management of late-successional forests is one strategy aimed at reducing net carbon dioxide emissions and moderate the influence of future climate change (Keeton 2018) as well as to maintain diverse, healthy forest landscapes.

The Central Hardwood Region (CHR) of the US is the largest contiguous assemblage of deciduous tree species in the world with an extent that covers approximately 609,000 km^2 including the lower Midwestern forests of Missouri and Arkansas and extending east to New York and Georgia. Although oak species (*Quercus* spp.) occur throughout the region and constitute a greater proportion of growing stock than any other genus, the Central Hardwood Region is not defined by any single species or genus (Hicks 1998). Old-growth forests in this region meet many of the functional and structural characteristics associated with old-growth forests of other regions; likewise, these forests are rarely in steady-state conditions (Runkle 1996, Barton 2018). Due to historical land-use, alterations to environmental conditions including climate change and nutrient deposition, and impacts from introduced pests, plants, and disease, CHR old-growth forests are constantly responding to human-induced changes to their pre-European disturbance regimes (Runkle 1996).

Currently, much of the landscape in the CHR is dominated by second-growth forests that are mature and both structurally and compositionally homogeneous, with half of the forests exceeding 70 years of age (Shifley et al. 2014). In 2012, oak-dominated forests represented 47 percent of the forest area in the eastern United States (Oswalt et al. 2012). During that 2012 inventory, 67.8 percent of those forests were 40 to 99 years old. Now millions of hectares of these forests are aging beyond 100 years. Further, capacity to actively manage forests is less than the rate of successional development, resulting in much of the forested landscape developing towards unmanaged, late-seral structures and compositions (Curtis and Gough 2018, Spetich et al. 2022). Very few undisturbed old-growth forests in the CHR remain, but evaluating the influence of site productivity and disturbance as it relates to carbon dynamics in these forests is important as the region's second growth forests continue to age, and with it, the potential to manage these aging forests for late-successional, old-growth complexity.

Forest productivity is an important metric in determining a site's potential for carbon storage. In addition to topoedaphic variations in productivity at the local level, a gradient of productivity occurs across the CHR from west (less productive) to east (more productive) that is influenced by regional and subcontinental differences in geology, soils, and climate (Hicks 1998, Spetich et al. 1999, Wilfahrt et al. 2016). This variability in climate and soils, coupled with natural and anthropogenic disturbances, influences the structure and composition of CHR forests across landscapes and time (Wilfahrt et al. 2016). For example, forests in the western portion of this region are characterized by more open, drought-tolerant communities (e.g., *Quercus* and *Carya)*. In contrast, more productive forests to the east are taller, more diverse, closed-canopy, communities with greater shade tolerance and leaf nitrogen (e.g., forests with *Acer* and *Tilia*) (Wilfahrt et al. 2016).

Natural disturbance (e.g., wind events, insect outbreaks) and historic land use can have long-lasting effects on the future forest carbon cycle (Thom et al. 2018). Future climate scenarios predict warmer temperatures which are expected to alter the magnitude, severity and frequency of insect and pathogen outbreaks, and extreme weather events, ultimately influencing relationships among climate change, disturbance, and the carbon cycle (Brandt et al., 2014, Dale et al. 2016). Further, recent studies suggest that moderate levels of disturbance may increase physical and biological complexity of forest ecosystems, thus moderating declines or sustaining productivity with forest age (Gough et al. 2016, Curtis and Gough 2018). In the CHR, wind disturbance is one of the most prevalent disturbance agents, and in contrast to the regional productivity gradient, increases in frequency from east (less frequent) to west (more frequent) (Peterson et al. 2016). Integrating dynamic disturbance processes and their influence on carbon stocks for late successional and old-growth forests is important for climate change mitigation strategies and ecosystem management, especially as large proportions of forested landscapes advance in age.

The objectives of this study are to 1) describe structural changes over two decades for ten remeasured old-growth forests located along a 770 km productivity gradient in the CHR; 2) determine change in carbon storage capacity related to forest productivity; and 3) evaluate the influence of disturbance on carbon dynamics for CHR old-growth forests.

2. Methods

2.1. Site descriptions

Our study includes ten old-growth forests located in the midwestern US CHR with locations in Indiana, Illinois, and Missouri (Fig. 1; Table 1). This network of old-growth forests was originally established in the early 1990s (Spetich 1995). These sites were originally selected because they were representative of the structural and compositional characteristics associated with old-growth forests of the Region. This includes little anthropogenic disturbance in the past 80–100 years, vertical and horizontal heterogeneity, with an uneven-aged structure composed of large canopy dominants of mid- to late-seral stages that are >150 years old, conservative ground flora, and the presence of snags and coarse woody debris (CWD) (Parker 1989). Sites were also a minimum of 8 ha to accommodate 30 (0.1 ha) gridded plots (described below).

2.2. Data collection

At each site, a systematic grid of 30 sampling points was established, with spacing ranging from 40 to 180 m depending on the total area of the site. Sampling points were buffered at least 50 m from the forest edge. A 0.1-ha fixed area, circular plot with nested subplots was permanently established at each sampling point (Fig. 2). Plots were established and initially measured in 1992–1993 (referenced as '1990', hereafter) and remeasured in 2012–2013 (referenced as '2010', hereafter) (Table 1).

To characterize standing carbon pools, within each of the 0.1-ha plots, all woody stems, >10-cm diameter at breast height (1.3 m; DBH, referred to as the 'overstory' hereafter) were recorded by species, status (live or dead), DBH, crown class (dominant, co-dominant, intermediate, or overtopped), and live crown ratio. Tree height was recorded for all snags. A 0.01-ha nested subplot, located at plot center, was established to record all stems 2 to 10 cm DBH (referred to as the 'midstory' hereafter), living or dead, by species, status, and DBH. Within the 0.01-ha subplot, four nested 2.5 m^2 quadrats were established in cardinal directions, 3-m from subplot center, to assess the abundance (tallied) of woody reproduction (<2 cm DBH, referred to as the 'understory' hereafter) by species.

To characterize the forest floor carbon pools, all CWD (≥10 cm diameter at smallest end) within the 0.1-ha plot were measured for length and midpoint diameters. Branches were considered segments. Decay class was assigned following the methods of Maser et al. (1979). Fine woody debris (FWD) < 10 cm diameter was sampled using planar intersect methods along three randomly oriented 15 m transects radiating from plot center in a Y-shaped arrangement. Within the 0.1-ha plot, at four sampling points located at 6 to 18 m from plot center in each cardinal direction, forest floor depth and condition (notable features including water courses, exposed bedrock, or windthrow pits and

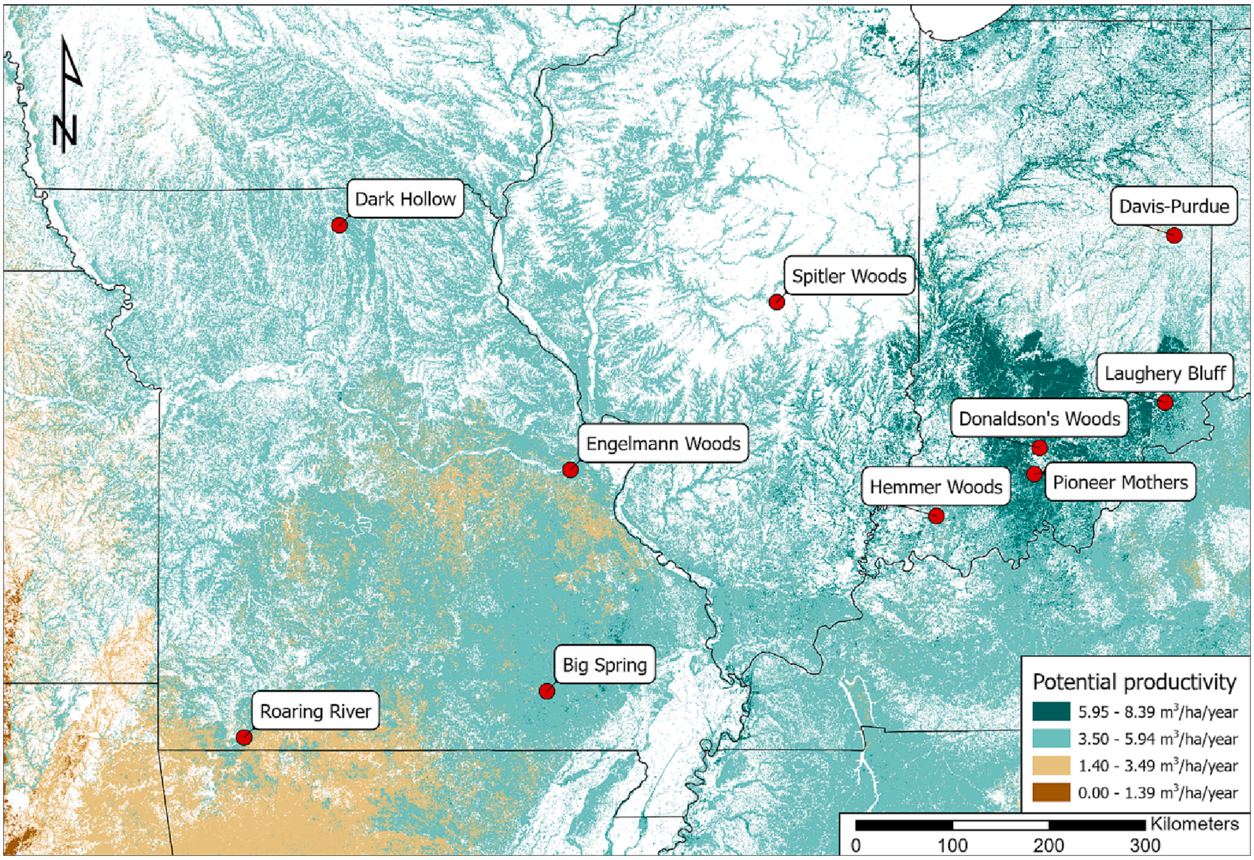

Fig. 1. Location of 10 old-growth sites sampled. Potential productivity estimated from imputed USDA Forest Service inventory and analysis plots. Productivity on plots is estimated using a combination of repeated tree measurements or relationship to calculated site index. Source: https://diusfs.img.arcgis.com/arcgis/rest/services/CONUS_site_productivity_2018_masked_20210603210303/ImageServer.

mounds) were assessed using a 35.4 cm^2 sampling frame. The depth of the forest floor was measured using 20-cm steel nails inserted so that the head of the nail was flush with the litter surface prior to removal. Litter was removed down to mineral soil and the depth of the forest floor was then measured by the length of the nail exposed. Samples were placed in a cooler and returned to the lab for processing and aggregation to the plot level.

To characterize soil carbon in 2012 and 2013, two approaches were taken depending on soil conditions assessed at the time of plot measurement. For both approaches, the samples were randomly collected 6 to 18 m from plot center in each cardinal direction. For soils with lower proportions of coarse fragments (>2 mm by volume), a 5.1 cm diameter AMS split-tube soil core sampler was used to collect four soil samples within each plot. For soils where coarse fragment levels prevented the use of the split-tube soil core sampler, a soil sample was collected from a 5 to 10 cm^2 by 20 cm deep excavation that was backfilled with sand to determine the exact volume. Soil samples were placed in poly bags, labeled, and stored in iced coolers until returned to the lab and subsequently frozen prior to processing. Mineral soil carbon was not measured during the 1992–1993 inventory.

2.3. Laboratory analyses

Forest floor samples were processed and analyzed to determine physical and chemical properties. Samples were sorted and living vegetation and all woody debris>2 cm were discarded. For samples collected in 1990, litter was oven-dried at 80 °C for 72 h (Spetich 1995). Due to advances in estimation methods, forest floor samples collected in 2010 were oven dried at 55 °C until constant mass was achieved to reduce the risk of volatilizing chemical properties at higher temperatures. Additionally, in 2010, 30 random forest floor samples were subset and dried at 80 °C to test for differences in carbon volatilization against those dried at 55 °C. Oven-dried samples were sorted through a 2 mm mesh sieve with the material passing through the sieve floated in a 5-gallon bucket of water to sort organic material from soil. The organic material (OM) was removed, oven dried at 55 °C until constant mass was reached and weighed. To determine carbon and nitrogen concentration, the samples were homogenized using a two-part process by first grinding in a Wiley mill then transferred to a mechanical shaker and processed until particles were small enough to pass a 40-mesh sieve and measured by dry combustion using a Costech ECS 4010 elemental analyzer.

Mineral soil samples collected using the AMS core sampler were cut into two sections: from the surface of mineral soil to a depth of 20.0 cm and 20.0–30.5 cm and processed separately. Soil samples were air-dried and then ground using a U.S. Stoneware unitized jar mill, alumina fortified mill jar, and zirconia grinding media to break down clumped soil particles and detach soil particles adhered to stone and gravel. Samples were sieved through a 10 mm stainless steel screen to separate coarse fragments and organic material. Stones were weighed and volume estimated using an assumed particle density of 2.65 g cm^{-3}. The remaining portion of the sample (<10.0 mm) were passed through a 2 mm sieve to separate the fine earth fraction (FE) and was weighed. Carbon and nitrogen concentration for soil organic material and fine earth fraction portions were measured by dry combustion in a Costech ECS 4010 elemental analyzer. Gravel retained on the 2 mm sieve was separated from the other unpassed material (2.0–10.0 mm) and weighed. The volume of the 2–10 mm gravel was estimated by dividing weight by an assumed particle density of 2.65 g cm^{-3}.

Table 1
Site descriptions for the study old-growth forests in the Central Hardwoods Region including location, area, inventory years, ecological description and soil unit, potential productivity, site age, and known recent disturbance history.

Site Name	County	State	Total site area (ha)	Inventory Years	Ecological Subsection[1]	Soil Unit[2]	Subsoil Texture class[2]	Potential Productivity (m^3/ha/yr)[3]	Site Age[4]	Documented Disturbance History[5]
Big Spring	Carter	MO	140	1992, 2012	Current River Hills	Alred-Rueter complex, extremely cobbly loam or very gravelly silt loam, 15–35 % slopes, very stony	loamy-skeletal over clayey; loamy skeletal	4.2	63–141; >200[7]	1992 inventory noted black oak mortality.
Dark Hollow	Sullivan	MO	95	1993, 2012	Chariton River Hills	Winnegan loam, 20–35 % slopes	fine	4.0	130	1993 inventory noted recent tree gaps from ice or storm damage. Some plots assumed to be second growth. In 1994, a significant ice storm impacted the site (Rebertus et al. 1997).
Davis-Purdue	Randolph	IN	21	1992, 2011	Bluffton Till Plains	Pewamo silty clay loam, 0–1 % slopes	fine	5.5	132–300	2011 inventory noted potential blowdown event occurring between the two measurement periods.
Donaldson Woods	Lawrence	IN	27	1992, 2011	Mitchell Karst Plains	Cider-Frederick silt loams, karst, 6–20 % slopes, eroded complex	fine-silty; fine	5.5	173–185	High mortality in overstory and midstory trees was recorded in 1984 when compared to earlier measurement periods, with 79 % of the total basal area in dead oaks and hickories (Schmelz et al., 1974).
Engelmann Woods	Franklin	MO	59	1992, 2012	Outer Ozark Border	Menfro-Gatewood complex, silt loam or gravelly silt loam, 20–50 % slopes	very-fine; fine-silty	3.5	95–204	1992 inventory mentioned numerous canopy gaps.
Hemmer Woods	Gibson	IN	30	1993, 2011	Outer Western Coalfields	Hosmer silt loam, 2–5 % slopes, eroded	fine-silty	4.5	141–208	Overstory mortality rates for Hemmer Woods are reported as higher than comparative other old-growth sites in Indiana, including Donaldson's Woods and Davis-Purdue Research Forest (McCune et al. 1988). 2011 inventory noted northern red oak mortality.
Laughery Bluff	Ripley	IN	15	1993, 2011	Muscatatuck Flats and Valleys	Cincinnati silt loam, 2–6 % slopes, eroded	fine-silty	6.0	132–292	Two weeks prior to 1992 inventory, the site was impacted by a windstorm. Large, American beech were predominately impacted by the event.
Pioneer Mothers	Orange	IN	36	1992, 2011	Crawford Escarpment	Adyeville-Wellston silt loams, 18–50 % slopes	fine-silty	5.5	152–296	
Roaring River	Barry	MO	49	1992, 2012	White River Hills	Rueter-Hailey complex, very gravelly or extremely gravelly silt loams, 35–60 % slopes, rocky	loamy-skeletal	3.8	200–250[8]	
Spitler Woods	Macon	IL	59	1993, 2011	Southern Grand Prairie	Senachwine silt loam, 18 to 35 percent slopes	fine-loamy	not available[6]	166–260	

[1]Cleland et al. (2007).
[2]Soil unit and soil texture information complied across plots at each location using SSURGO.
[3]Potential productivity derived from SSURGO site index.
[4]Site age based on tree cores.
[5]Disturbance history taken from field notes during 1992–1993 inventories and literature search.
[6]Forest productivity data not provided.
[7]Nigh et al. (1992), Shifley et al. (1995).
[8]Stahle et al. (1985)

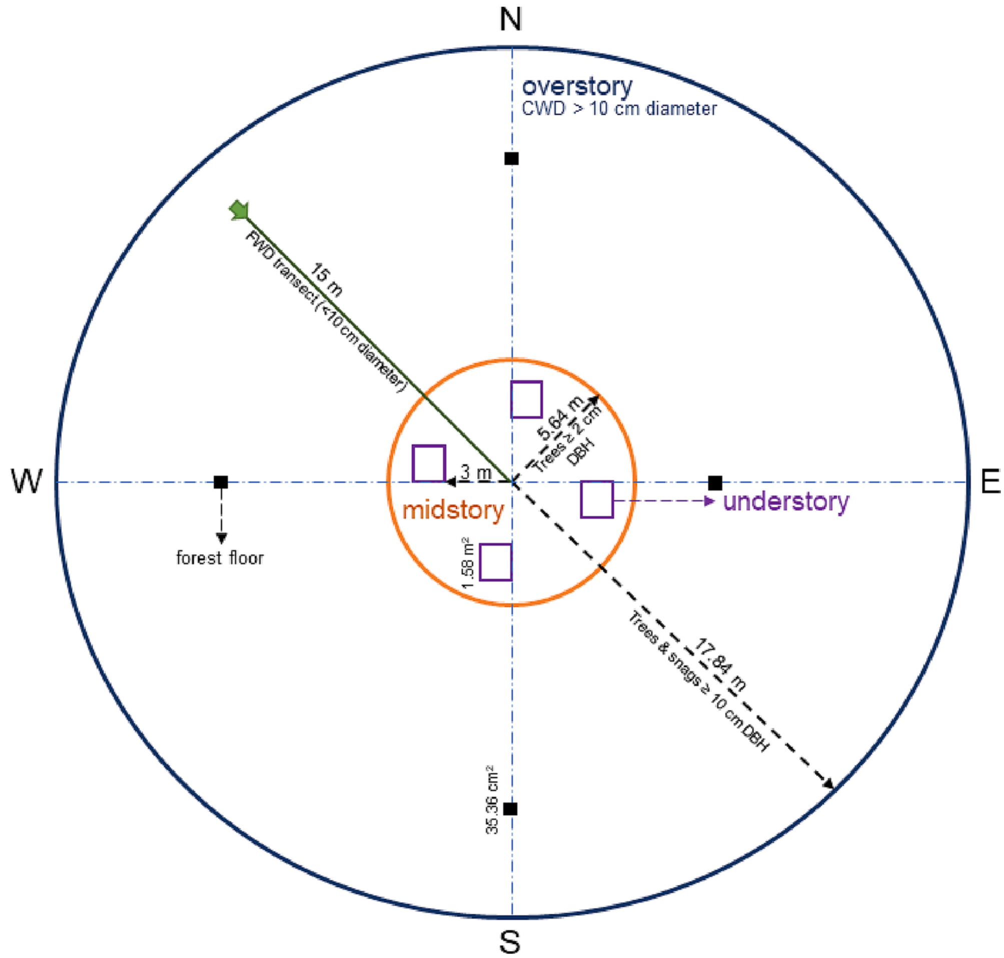

Fig. 2. Sample plot schematic for estimating structure, composition, and carbon pools at ten old-growth sites in Missouri, Illinois, and Indiana.

2.4. Carbon estimations and statistical analyses

To estimate individual live tree biomass and carbon, we used field measurements and species-specific allometric equations (Jenkins et al. 2003, Jenkins et al. 2004, Chojnacky et al. 2013). Biomass was converted to carbon by tree component (i.e., stem, bark, branch, and leaves) and derived from species-specific carbon concentration values (Lamlom and Savidge 2003, Martin et al. 2015). The sum of carbon within individual components was used for total aboveground live tree carbon.

To estimate aboveground snag biomass and carbon, we calculated biomass for intact, recently dead trees (decay category 3) using allometric equations with a deduction for missing crown foliage (Thomas et al. 1979, Harmon et al. 2008). We estimated the volume of decadent snags (decay category 4–7) and recently dead snags with broken tops using height measurements along with top and basal diameter estimates (Hoover 2008). Volume was then converted to biomass estimates using species-specific densities when identifiable or using a generic density when species was unidentifiable (Harmon et al. 2008). We then converted the derived biomass estimates to carbon using general carbon concentration values for decaying wood (Harmon et al. 2013).

To estimate forest floor carbon pools, we derived the volume of CWD by decay category with Huber's equation for volume of a cylinder (Harmon and Sexton 1996). Published density and density reduction factors were then used to convert volume estimates to mass (Harmon et al. 2008). To account for a lack of complete species-specific estimates, we calculated composite density values that were weighted by each overstory species' basal area for volume-to-mass conversions. We calculated the volume of FWD by fuel size class (1, 10, 100, 1000 hr) using the line intersect sampling formula (Harmon and Sexton 1996). We calculated mass from the volume estimates by multiplying by weighted composite density values and used those mass estimates to derive carbon (Harmon et al. 2013). We aggregated subsamples of forest floor depth to the plot-level. We estimated forest floor volume samples by multiplying the mean plot depth by the total sample area. The carbon content of the forest floor was calculated by multiplying the oven-dry sample mass by carbon concentration measurements and dividing by the sample area (Hoover 2008).

To estimate soil and incorporated organic matter (to 20 cm depth) carbon, we converted the components to their oven-dry weight equivalent prior to estimating carbon. Total volume and oven-dry weight was calculated by summing component measurements (<2 mm fine earth, 2–10 mm and > 10 mm coarse fragments, 2–10 mm and > 10 mm roots and other organic material). Volume of the FE and OM fractions were calculated by subtracting remaining component volume measurements from the total volume. Fine earth and OM carbon stock for individual samples was estimated using the following equation and then used to calculate a plot-level mean:

$$S_{FEorOM} = \left(\frac{C_{fe}}{100}\right) \times D \times \rho_b \times 100 \times \left[1 - \left(\frac{V_{cf}}{100} + \frac{V_{om}}{100} + \frac{V_{cr}}{100}\right)\right]$$

where:
S_{FE} or S_{OM} = FE or OM carbon stock (Mg ha^{-1});
C_{fe} = FE or OM carbon concentration (% of total sample weight);
D = Sample depth (cm);
ρ_b = FE or OM bulk density (g cm^{-3});
V_{cf} = > 2 mm coarse fragments fraction (% of total sample volume);

V_{om} = > 2 mm OM fraction (% of total sample volume); and.
V_{cr} = > 10 mm coarse root fraction (% of total sample volume).

Biomass of live and dead coarse and fine roots was estimated using tree DBH measurements along with allometric equations (Jenkins et al. 2003, Chojnacky et al. 2013), and then converted to carbon using species-specific carbon concentration values (Lamlom and Savidge 2003, Martin et al. 2015). All carbon estimates for woody biomass were made using the assumption that C comprised 50 % of dry biomass weight.

We calculated plot-level basal area (m^2 ha^{-1}), density (trees per hectare, TPH), and quadratic mean diameter (QMD, cm) for trees in the overstory (≥10 cm DBH) and midstory (>2 cm & < 10 cm DBH). From these plot-level totals, we calculated the site-level mean and standard error for each metric. We estimated dominant species at the site-level for the overstory and midstory classes by calculating importance value for each species using the equation: IV = (total density for species / total density) + (total BA for species / total BA). The three species with the largest IV in the overstory and midstory were reported as dominant species in each size group. We calculated the Shannon-Wiener (S-W) diversity index at the plot-level using total basal area by species as well as species richness using the package *vegan* (Oksanen et al. 2022) within the R programming environment (R Core Team 2022).

We estimated mean annual increment (MAI) of carbon productivity at the plot-level by summing the change in aboveground carbon for trees present during both measurement periods plus total carbon of ingrowth during the most recent measurement and multiplied by the plot expansion factor. This total was then divided by the years between measurements. Potential site productivity was estimated from Web Soil Survey (SSURGO) data by taking the area-weighted mean site index estimate from all soil series mapped to each site and standardizing the value to a site index model for black oak (Soil Survey Staff). We then transformed the black oak site index estimate to potential annual productivity using maximum volume yield estimates from corresponding site index tables for upland oak forests (Schnur 1937). We applied linear mixed models using the R package *nlme* (Pinheiro et al. 2022) to test for the effect of changes in basal area, density, QMD, S-W diversity, and species richness in the overstory on MAI, including site as the random effect. Significance was determined at an alpha of 0.05. We calculated the fixed and random effects variance explained (R^2) using the methods from Nakagawa and Schielzeth (2013).

Plot-level mortality was calculated using individual tree identification numbers assigned during the first inventory and status codes measured during each visit. Tree records were filtered to identify individual stems that were recorded with a living status code during the first inventory and had a status code of dead, removed, or missing during the subsequent remeasurement. We calculated the plot-level basal area and density of mortality using the diameter and expansion factor recorded in the first inventory for the subset of records.

We calculated the mean and standard error for the sum of total carbon in the overstory, midstory, down woody debris, forest floor, standing dead, live root, and dead root pools, as well as the mean and standard error for the net change across measurement periods and the net percent change at the site level. Soil carbon and FWD carbon is only reported for the 2010 measurement due to those pools not being measured in the 1990 inventory. Carbon estimates for seedlings and herbaceous plants were not included in this study.

3. Results

The old-growth forests varied in overstory and midstory composition, as well as in metrics of species diversity (Table 2). The dominant overstory species at six of the ten sites was white oak (*Quercus alba*; Table 2). The sites with the estimated lowest and highest productivity, Engelmann Woods and Davis-Purdue, had overstories composed of sugar maple (*Acer saccharum*) and oaks. The dominant midstory species composition of most sites was primarily shade-tolerant midstory species including pawpaw (*Asimina triloba*), flowering dogwood (*Cornus florida*), eastern hophornbeam (*Ostrya virginiana*), and serviceberry (*Amelanchier arborea*). Sugar maple was the species that most often occurred simultaneously in the dominant overstory and midstory classes. The mean S-W diversity index of species in the overstory ranged from 1.13 at Dark Hollow to 1.75 at Davis-Purdue. Laughery Bluff had the lowest mean species richness in the overstory (5.6) and Davis-Purdue had the highest (11.1). In the midstory, the mean S-W diversity ranged from 0.53 at Laughery Bluff to 0.98 at Roaring River. Mean richness in the midstory class ranged from 2.34 at Laughery Bluff to 4.00 at Roaring River.

Table 2
Mean values for Shannon-Wiener (S-W) diversity index, species richness, and dominant species by importance value in 1990 for overstory (>10 cm DBH) and midstory (2–10 cm DBH) trees in ten old-growth sites located in Missouri, Illinois, and Indiana. Sites in this table and following tables are arranged from lowest to highest potential productivity as presented in Table 1.

Site	S-W diversity		Species richness		Dominant species	
	Overstory	Midstory	Overstory	Midstory	Overstory[1]	Midstory[2]
Engelmann Woods	1.4	0.6	7	2.7	sugar maple, northern red oak, chinkapin oak	pawpaw, sugar maple, eastern hophornbeam
Roaring River	1.4	1	8.5	4	white oak, black oak, mockernut hickory	flowering dogwood, common serviceberry, mockernut hickory
Dark Hollow	1.1	0.9	7.4	3.7	white oak, northern red oak, shagbark hickory	eastern hophornbeam, common serviceberry, American basswood
Big Spring	1.6	1	9.5	3.7	white oak, black oak, scarlet oak	flowering dogwood, blackgum, white oak
Spitler Woods	1.5	0.6	8.7	2.7	white oak, sugar maple, American basswood	sugar maple, Ohio buckeye, American basswood
Hemmer Woods	1.4	0.8	8.3	3.3	white oak, black oak, northern red oak	flowering dogwood, pawpaw, slippery elm
Pioneer Mothers	1.4	0.7	6.1	3	sugar maple, American beech, yellow-poplar	sugar maple, slippery elm, pawpaw
Davis-Purdue	1.7	0.7	11.1	3.3	sugar maple, white oak, northern red oak	sugar maple, slippery elm, American hornbeam, musclewood
Donaldson Woods	1.4	0.7	7.1	2.8	white oak, yellow-poplar, American beech	flowering dogwood, pawpaw, slippery elm
Laughery Bluff	1.2	0.5	5.6	2.3	sugar maple, yellow-poplar, American beech	sugar maple, flowering dogwood, pawpaw

[1] white oak (*Quercus alba*); black oak (*Q. velutina*); scarlet oak (*Q. coccinea*); northern red oak (*Q. rubra*); chinquapin oak (*Q. muehlenbergii*); shagbark hickory (*Carya ovata*); Mockernut hickory (*C. tomentosa*); sugar maple (*Acer saccharum*); American beech (*Fagus grandifolia*); yellow-poplar (*Liriodendron tulipifera*); American basswood (*Tilia americana*).

[2] flowering dogwood (*Cornus florida*); blackgum (*Nyssa sylvatica*); eastern hophornbeam (*Ostrya virginiana*); common serviceberry (*Amelanchier arborea*); American hornbeam (*Carpinus caroliniana*); slippery elm (*Ulmus rubra*); pawpaw (*Asminia triloba*); Ohio buckeye (*Aesculus glabra*).

Objective 1: Structural changes in old-growth forests over two decades.

For live overstory trees in 1990, mean basal area was generally lower for sites in the west and higher for eastern sites. Donaldson Woods had the highest mean basal area (31.3 m^2/ha), and Laughery Bluff had the lowest (19.4 m^2/ha; Table 3). Big Spring had the highest mean density (467 TPH), and Laughery Bluff had the lowest (218 TPH). The lowest QMD was 24.7 cm at Big Spring and the highest was 41.3 cm at Donaldson Woods.

When remeasured in 2010, Engelmann Woods had the largest relative decrease (−5 %) in overstory BA, while Laughery Bluff had the largest relative increase (+17 %; Table 3). Nine sites experienced a decrease in living overstory tree density, with Donaldson Woods decreasing by 20 %. Laughery Bluff was unique in that it was the only site with a decrease in overstory QMD (−8 %), an increase in overstory density (+44 %), and the largest relative increase in overstory BA (+17 %). All other sites had an increase in overstory QMD, with Dark Hollow experiencing the greatest (+13 %).

In 1990, Roaring River had the highest basal area for midstory trees at 2.9 m^2 ha^{-1} and Pioneer Mothers had the lowest with 1.1 m^2 h^{-1} (Table 3). Dark Hollow had the highest mean midstory density with 1313 TPH and Laughery Bluff had the lowest at 755 TPH. Midstory QMD ranged from 4.0 cm at Donaldson Woods to 5.5 cm at Roaring River.

In the 2010 remeasurement, seven sites experienced a decrease in midstory BA with Big Spring experiencing the largest decline (−49 %; Table 3). Conversely, Dark Hollow, Donaldson Woods, and Davis-Purdue all had increases in midstory BA at +2 %, +17 %, and +23 %, respectively. Seven sites had decreases in midstory density ranging from −7 % at Davis-Purdue to −59 % at Big Spring. Engelmann Woods had a 3 % increase, Laughery Bluff had a 10 % increase, and Donaldson Woods had a 16 % increase. Midstory QMD increased at seven sites ranging from +2 % at Hemmer Woods to +16 % at Davis-Purdue. Midstory QMD decreased at Donaldson Woods (−2 %), Laughery Bluff (−9 %), and Engelmann Woods (−13 %).

Mean annual increment (MAI) was calculated to provide an estimate of productivity. Sites with the highest MAI included Spitler Woods, Donaldson Woods, and Laughery Bluff (Fig. 3), while Engelmann Woods and Dark Hollow were the lowest. Mean annual increment was positively related to changes in BA ($p < 0.001$) and QMD ($p < 0.001$), and negatively related to changes in TPH ($p < 0.05$) (**Table S1**; **Figures S1 and S2**). For the BA net change model the fixed and random R^2 levels were equal, however, in the TPH and QMD net change models much of the variance explained was from the random effect of the site variable. We found no other statistically meaningful relationships between MAI and metrics of diversity or richness (**Figures S3-S6**).

Objective 2. Carbon storage capacity of old-growth forests and how it relates to site productivity.

Averaged across our old-growth sites, total aboveground carbon was estimated at 125 ± 2.4 Mg ha^{-1} in 1990 with a relative increase of 7 % (134.2 ± 2.6 Mg ha^{-1}) in 2010 (Table 4). However, sites varied in their total aboveground carbon and their relative change between measurement periods. Sites with the largest initial aboveground carbon estimates included the three Indiana sites, Donaldson Woods, Davis-Purdue, and Pioneer Mothers. The lowest initial carbon estimates were recorded in the Missouri sites, namely Big Spring, Dark Hollow, Engelmann Woods, and Roaring River. Sites located in the west with lower initial carbon estimates, such as Big Spring and Dark Hollow, had similarly high net gains in carbon as sites with higher initial carbon, such as Spitler Woods. Further, some sites lost carbon (Laughery Bluff), had no change (Hemmer Woods), or had comparatively minimal increases in aboveground carbon (Roaring River) during the twenty-year period.

Old-growth forests had trends in increasing living and dead overstory carbon, as well as CWD, with decreases in living midstory and forest floor carbon. Specifically, on average during the twenty-year period, carbon in the living overstory increased 5 % (+5.6 Mg ha^{-1}; Table 5), in the standing dead increased 7 % (+0.3 Mg ha^{-1}; Table 6), in the CWD increased 4.9 % (+0.4 Mg ha^{-1}; Table 6), in the living roots increased 4 % (1.0 Mg ha^{-1}; Table 7), and in the dead roots increased 68 % (+0.3 Mg ha^{-1}; Table 7). Conversely, carbon in the living midstory decreased 16 % (−0.5 Mg ha^{-1}; Table 5) and in the forest floor decreased 25 % (−1.5 Mg ha^{-1}; Table 8).

The living overstory carbon in 1990 ranged from 76.7 Mg ha^{-1} at Big Spring to 142.8 Mg ha^{-1} at Donaldson Woods (Table 5). The largest net gain occurred at Spitler Woods (+21.8 Mg ha^{-1}, +19 %) and the largest

Table 3
Changes in mean basal area (m^2/ha), stem density (trees/ha), and quadratic mean diameter (cm) for all overstory and midstory trees in ten Central Hardwood Region old-growth sites located in Missouri, Illinois, and Indiana that were measured in 1990 and 2010.

Overstory (>10 cm DBH)									
Site	Basal area (m^2/ha)			Density (trees/ha)			Quadratic mean diameter (cm)		
	1990	2010	% Δ	1990	2010	% Δ	1990	2010	% Δ
Engelmann Woods	22.3	21.2	−5	398	328	−18	27.6	29	5
Roaring River	21.9	22	1	442	409	−7	25.3	26.5	5
Dark Hollow	22.8	25.1	10	331	287	−13	29.8	33.5	13
Big Spring	21.6	22.2	3	467	402	−14	24.7	26.7	8
Spitler Woods	28.7	32.6	14	406	375	−8	30.3	33.4	10
Hemmer Woods	22.7	21.9	−4	259	224	−14	33.4	35.3	6
Pioneer Mothers	27.2	27.5	1	260	226	−13	37.1	39.5	6
Davis-Purdue	30.3	29	−4	314	293	−6	35.3	35.4	0
Donaldson Woods	31.1	31.3	1	239	192	−20	41.3	45.8	11
Laughery Bluff	19.4	22.7	17	218	314	44	32.8	30	−8
Midstory (2–10 cm DBH)									
Site	Basal area (m^2/ha)			Density (trees/ha)			Quadratic mean diameter (cm)		
	1990	2010	% Δ	1990	2010	% Δ	1990	2010	% Δ
Engelmann Woods	1.8	1.5	−13	940	971	3	5.1	4.4	−13
Roaring River	2.9	1.6	−43	1,223	673	−45	5.5	6	10
Dark Hollow	2	2.1	2	1,313	1010	−23	4.5	5.1	14
Big Spring	2.5	1.2	−49	1159	472	−59	5.4	5.7	6
Spitler Woods	1.7	1.2	−26	830	500	−40	5.2	5.7	8
Hemmer Woods	2.3	2	−12	1,220	1,000	−18	5	5.1	2
Pioneer Mothers	1.1	1.1	−2	910	652	−28	4.4	4.8	7
Davis-Purdue	1.8	2.2	23	1047	977	−7	4.6	5.4	16
Donaldson Woods	1.2	1.4	17	993	1157	16	4	3.9	−2
Laughery Bluff	1.5	1.4	−9	755	833	10	5.3	4.8	−9

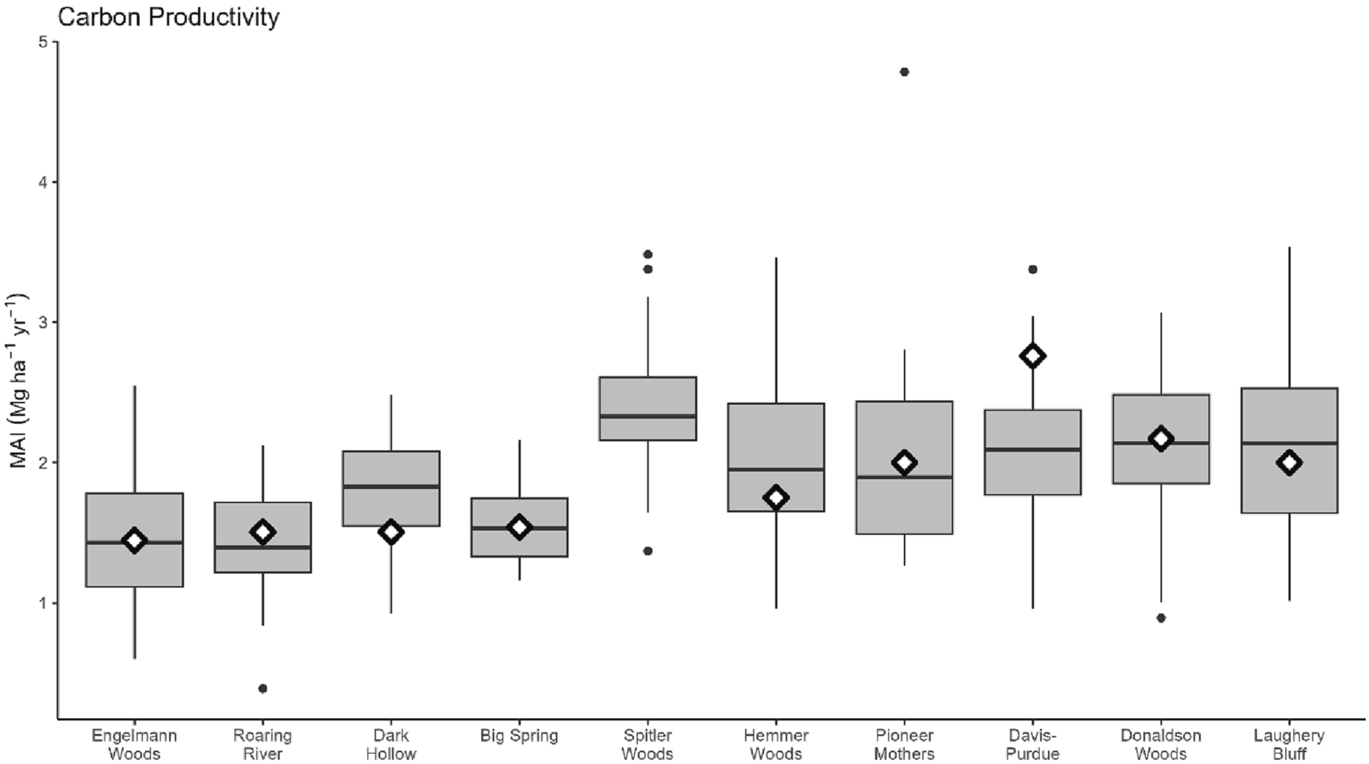

Fig. 3. Mean annual increment of aboveground carbon across Central Hardwood Region old growth sites. The boxplot solid line corresponds to median value, upper and lower hinges correspond to 25th and 75th percentiles and whiskers extend to highest and lowest value or one and a half times the distance of the interquartile range. Diamond symbol indicates the weighted mean annual potential aboveground carbon productivity calculated with SSURGO data for soil map units at each site where productivity estimates were available.

Table 4
Total aboveground carbon estimates for Central Hardwood Region old-growth forests. Site-level mean and standard error carbon mass for both measurement periods (1990 and 2010) with net change (Δ), relative net change (%Δ), and mean net annual carbon change.

Site	Total aboveground carbon (Mg ha^{-1})				
	1990	2010	Δ	% Δ	Mg C ha^{-1} yr^{-1}
Engelmann Woods	98.8 (6.3)	105.8 (6.5)	7.1 (4.1)	7	0.4 (0.2)
Roaring River	99.1 (4.1)	101.9 (4.3)	2.8 (2.8)	3	0.1 (0.1)
Dark Hollow	97.2 (2.9)	116.8 (3.5)	19.6 (2.9)	20	1.0 (0.2)
Big Spring	93.0 (2.5)	105.6 (3.1)	12.6 (2.2)	14	0.6 (0.1)
Spitler Woods	135.0 (6.9)	158.9 (7.1)	23.9 (2.9)	18	1.3 (0.2)
Hemmer Woods	131.3 (6.4)	131.8 (6.6)	0.5 (4.9)	0	0.0 (0.3)
Pioneer Mothers	146.5 (5.0)	154.7 (5.7)	8.2 (4.6)	6	0.4 (0.2)
Davis-Purdue	161.0 (9.0)	175.0 (10.5)	14.0 (6.9)	9	0.7 (0.4)
Donaldson Woods	168.0 (6.3)	176.6 (7.6)	8.6 (5.4)	5	0.5 (0.3)
Laughery Bluff	120.0 (7.8)	114.5 (7.6)	−5.5 (5.0)	−5	−0.3 (0.3)
All sites	125.0 (2.4)	134.2 (2.6)	9.2 (1.5)	7	0.5 (0.1)

net loss occurred at Davis-Purdue (−4.7 Mg ha^{-1}, −3 %). Carbon estimates for the live midstory pool in 1990 ranged from 1.7 Mg ha^{-1} at Donaldson Woods to 4.5 Mg ha^{-1} at Roaring River (Table 5). The largest net gain in live midstory carbon occurred at Davis-Purdue (+1.0 Mg ha^{-1}, +33 %) and the largest net loss occurred at Roaring River (−1.9 Mg ha^{-1}, −43 %).

Standing dead carbon ranged from 1.7 Mg ha^{-1} at Dark Hollow to 7.0 Mg ha^{-1} at Donaldson Woods in 1990 (Table 6). Donaldson Woods, Laughery Bluff, Pioneer Mothers, and Roaring River had net losses of dead standing carbon. All other sites had net gains in standing dead carbon, with Davis-Purdue increasing by 215 % (+8.5 Mg ha^{-1}). The CWD pool had estimates ranging from 3.5 Mg ha^{-1} at Dark Hollow to 24.2 Mg ha^{-1} at Laughery Bluff (Table 6). The largest net gain in CWD was Donaldson Woods (+5.2 Mg ha^{-1}, +56 %) and the largest net loss was Laughery Bluff (−15.0 Mg ha^{-1}, −62 %). In 1990, forest floor carbon ranged from 2.1 Mg ha^{-1} at Spitler Woods to 10.0 Mg ha^{-1} at Hemmer Woods (Table 8). Net changes to forest floor carbon were relatively stable within the four western sites located in Missouri, while the largest increase occurred at Spitler Woods (+0.5 Mg ha^{-1}, +26 %) and the largest decrease occurred at Laughery Bluff −4.4 Mg ha^{-1}, −54 %). Six sites had a net gain in live root carbon, with the largest occurring at Spitler Woods (+4.3 Mg ha^{-1}, +17 %; Table 7). Engelmann Woods, Davis-Purdue, Hemmer Woods, and Roaring River all had net losses to live root carbon of 3 % or less. Nine sites had net increases in dead root carbon ranging from + 5 % at Spitler Woods to +663 % (+0.2 Mg ha^{-1}) at Laughery Bluff. Donaldson Woods was the only site with a net loss of dead root carbon (−0.6 Mg ha^{-1}, −68 %). Fine woody debris (FWD, < 10 cm) was was generally higher in eastern forests with the maximum occurring at Laughery Bluff (8.54 ± 0.86 Mg ha^{-1}) and the minimum measured at Dark Hollow (4.43 ± 0.74 Mg ha^{-1}) (**Table S2**).

Across geographies, the sites in Missouri had lower measured MAI compared to the sites in Illinois and Indiana. This observation followed a similar trend in potential MAI estimated for the mapped SSURGO soil series at each site. Further, MAI corresponded positively with the change in total aboveground carbon over the twenty-year period.

The mean of total soil carbon measured in 2010 across all sites was 47.9 Mg ha^{-1}. Mean site-level soil carbon ranged from 26.5 Mg ha^{-1} at

Table 5
Live overstory (DBH > 10 cm) and live midstory (2–10 cm DBH) site-level mean and standard error carbon estimates for both measurement periods (1990 and 2010) with net change (Δ) and relative net change (% Δ) in living overstory and live midstory.

	Live overstory carbon (Mg ha^{-1})				Live midstory carbon (Mg ha^{-1})			
Site	1990	2010	Δ	% Δ	1990	2010	Δ	% Δ
Engelmann Woods	83.8 (6.0)	82.6 (6.0)	−1.1 (4.6)	−1	2.9 (0.4)	2.2 (0.3)	−0.7 (0.4)	−25
Roaring River	81.2 (4.0)	82.7 (4.1)	1.5 (2.8)	2	4.5 (0.4)	2.5 (0.2)	−1.9 (0.4)	−43
Dark Hollow	84.9 (3.0)	98.9 (3.9)	14.0 (3.2)	16	3.0 (0.3)	3.3 (0.3)	0.3 (0.2)	10
Big Spring	76.7 (2.2)	81.4 (2.7)	4.7 (2.5)	6	3.6 (0.4)	1.9 (0.2)	−1.7 (0.3)	−48
Spitler Woods	115.4 (6.9)	137.2 (7.2)	21.8 (3.1)	19	2.9 (0.3)	2.1 (0.3)	−0.8 (0.3)	−29
Hemmer Woods	102.5 (6.7)	101.0 (6.2)	−1.5 (5.6)	−1	3.2 (0.4)	2.5 (0.4)	−0.7 (0.4)	−22
Pioneer Mothers	121.6 (5.3)	126.0 (7.1)	4.4 (5.7)	4	1.8 (0.2)	1.8 (0.3)	−0.0 (0.3)	−3
Davis-Purdue	137.9 (8.2)	133.3 (11.4)	−4.7 (7.4)	−3	3.0 (0.3)	4.1 (0.4)	1.0 (0.4)	33
Donaldson Woods	142.8 (6.9)	147.7 (8.5)	4.9 (6.5)	3	1.7 (0.2)	2.0 (0.3)	0.3 (0.3)	19
Laughery Bluff	78.2 (7.0)	89.8 (7.6)	11.6 (4.7)	15	2.8 (0.4)	2.3 (0.4)	−0.5 (0.5)	−16
All sites	102.5 (2.3)	108.1 (2.6)	5.6 (1.6)	5	2.9 (0.1)	2.5 (0.1)	−0.5 (0.1)	−16

Table 6
Coarse woody debris and standing dead wood site-level mean and standard error carbon estimates for both measurement periods (1990 and 2010) with net change (Δ) and relative net change (% Δ).

	Coarse woody debris carbon (Mg ha^{-1})				Standing dead carbon (Mg ha^{-1})			
Site	1990	2010	Δ	% Δ	1990	2010	Δ	% Δ
Engelmann Woods	6.6 (1.1)	7.7 (1.3)	1.1 (1.3)	17	2.1 (0.6)	4.5 (1.6)	2.4 (1.6)	110
Roaring River	5.0 (0.9)	4.7 (0.5)	−0.3 (0.8)	−6	4.1 (0.7)	4.1 (0.7)	−0.0 (1.0)	0
Dark Hollow	3.5 (0.4)	5.2 (0.8)	1.7 (0.9)	48	1.7 (0.4)	1.7 (0.3)	0.0 (0.4)	3
Big Spring	4.3 (0.6)	8.3 (1.2)	4.0 (1.1)	93	2.9 (0.7)	4.0 (0.8)	1.1 (1.1)	37
Spitler Woods	10.5 (1.4)	7.8 (0.9)	−2.7 (1.5)	−26	4.1 (0.7)	4.8 (1.0)	0.7 (1.1)	17
Hemmer Woods	10.7 (1.8)	11.5 (1.5)	0.8 (2.3)	7	5.0 (1.1)	5.4 (1.9)	0.5 (2.3)	10
Pioneer Mothers	9.0 (1.5)	13.9 (1.9)	4.9 (2.1)	54	5.5 (1.3)	4.1 (1.1)	−1.3 (1.5)	−24
Davis-Purdue	8.1 (1.1)	12.8 (1.6)	4.8 (1.4)	59	3.9 (2.3)	12.4 (3.3)	8.5 (4.3)	215
Donaldson Woods	9.3 (1.3)	14.5 (1.9)	5.2 (2.3)	56	7.0 (2.1)	2.9 (1.3)	−4.1 (2.6)	−59
Laughery Bluff	24.2 (4.0)	9.2 (1.0)	−15.0 (3.8)	−62	6.7 (1.5)	2.0 (0.4)	−4.7 (1.7)	−70
All sites	9.1 (0.6)	9.6 (0.5)	0.4 (0.7)	5	4.3 (0.4)	4.6 (0.5)	0.3 (0.7)	7

Table 7
Belowground live root carbon and dead root carbon site-level mean and standard error carbon estimates for both measurement periods (1990 and 2010) with net change (Δ) and relative net change (% Δ).

	Live root carbon (Mg ha^{-1})				Dead root carbon (Mg ha^{-1})			
Site	1990	2010	Δ	% Δ	1990	2010	Δ	% Δ
Engelmann Woods	18.7 (1.2)	18.2 (1.2)	−0.5 (0.9)	−3	0.3 (0.1)	0.7 (0.3)	0.4 (0.3)	141
Roaring River	18.5 (0.9)	18.4 (0.9)	−0.2 (0.6)	−1	0.4 (0.1)	0.9 (0.3)	0.5 (0.3)	128
Dark Hollow	19.0 (0.6)	21.9 (0.8)	2.9 (0.7)	15	0.1 (0.0)	0.2 (0.1)	0.1 (0.1)	128
Big Spring	17.5 (0.5)	18.0 (0.6)	0.5 (0.5)	3	0.4 (0.1)	0.7 (0.2)	0.3 (0.2)	57
Spitler Woods	25.2 (1.4)	29.4 (1.5)	4.3 (0.6)	17	0.7 (0.2)	0.7 (0.2)	0.0 (0.2)	5
Hemmer Woods	22.3 (1.4)	21.7 (1.3)	−0.5 (1.1)	−2	0.3 (0.1)	0.7 (0.4)	0.4 (0.4)	114
Pioneer Mothers	26.1 (1.1)	26.9 (1.4)	0.8 (1.2)	3	0.3 (0.2)	0.5 (0.2)	0.3 (0.3)	94
Davis-Purdue	29.5 (1.6)	28.8 (2.3)	−0.7 (1.5)	−2	0.5 (0.5)	1.7 (0.7)	1.2 (0.8)	219
Donaldson Woods	30.2 (1.4)	31.2 (1.7)	1.0 (1.3)	3	0.9 (0.4)	0.3 (0.3)	−0.6 (0.5)	−68
Laughery Bluff	17.2 (1.5)	19.6 (1.5)	2.4 (1.0)	14	0.0 (0.0)	0.2 (0.1)	0.2 (0.1)	663
All sites	22.4 (0.5)	23.4 (0.5)	1.0 (0.3)	4	0.4 (0.1)	0.7 (0.1)	0.3 (0.1)	68

Roaring River to 83.6 Mg ha^{-1} at Davis-Purdue (Fig. 4, **Table S3**). Dark Hollow, Engelmann Woods, Hemmer Woods, Pioneer Mothers, and Spitler Woods all had mean soil carbon between 44 and 49 Mg ha^{-1}. Donaldson Woods and Laughery Bluff both had soil carbon measured at 53.9 Mg ha^{-1}. Soil carbon was lowest in soils with coarse fragments (i.e., gravel or cobbles) and greatest in sites associated with a soil having a high clay content and few or no coarse fragments (Table 1).

Objective 3. Evaluate the influence of disturbance on carbon dynamics for old-growth forests.

Six of our 10 old-growth forests had documented disturbance or high levels of mortality (Table 1). These ranged in observations of substantial tree mortality (Big Spring, Engelmann Woods, and Donaldson Woods) to discrete weather-related events from ice and wind (Dark Hollow, Davis-Purdue, and Laughery Bluff). The basal area of mortality (trees that died between time periods) across sites ranged from 5.6 m^2/ha at Dark Hollow to 10.5 m^2/ha at Davis-Purdue (Table 9). However, proportionally, Davis-Purdue had the lowest loss of living BA (22 %) between the two time periods, whereas Hemmer Woods had the greatest loss in BA (38 %). The density of mortality ranged from 511 TPA at Davis-Purdue to 1051 TPA at Hemmer Woods. The largest proportional reduction in tree density occurred at Hemmer Woods (72 %) and the lowest at Engelmann Woods (41 %). Mortality had a significant effect on carbon pools, reducing living tree carbon while increasing standing dead and coarse woody debris carbon pools (**Table S4**).

4. Discussion

Based on our study, old-growth forests in the CHR stored an average of 125 Mg ha^{-1} of total aboveground carbon and had a 7 % mean increase over a twenty-year period (Table 4). In addition, the forests store

Table 8
Forest floor mean and standard error carbon estimates for both measurement periods (1990 and 2010) with net change (Δ) and relative net change (% Δ).

	Forest floor carbon (Mg ha^{-1})			
Site	1990	2010	Δ	% Δ
Engelmann Woods	3.3 (0.3)	3.4 (0.2)	0.0 (0.3)	1
Roaring River	4.5 (0.2)	4.1 (0.3)	−0.2 (0.4)	−5
Dark Hollow	4.1 (0.3)	4.2 (0.3)	0.1 (0.3)	3
Big Spring	5.5 (0.3)	5.8 (0.3)	0.2 (0.3)	4
Spitler Woods	2.1 (0.2)	2.6 (0.2)	0.5 (0.2)	26
Hemmer Woods	10.0 (0.7)	8.2 (0.9)	−1.8 (1.1)	−18
Pioneer Mothers	8.6 (0.6)	4.0 (0.2)	−4.6 (0.6)	−53
Davis-Purdue	8.0 (0.5)	6.0 (0.4)	−2.0 (0.5)	−25
Donaldson Woods	7.3 (0.4)	3.8 (0.2)	−3.5 (0.4)	−48
Laughery Bluff	8.2 (0.5)	3.8 (0.5)	−4.4 (0.6)	−54
All sites	6.2 (0.2)	4.6 (0.2)	−1.5 (0.2)	−25

27 to 84 Mg C ha^{-1} in the upper 20 cm of the mineral soil. Although these old-growth forests co-occur within the broader CHR association, they vary widely in their structure, composition, soil type, and productivity. Results from our work suggest that 1) site productivity influences both the baseline amount of carbon storage as well as its potential accretion rate and 2) disturbance is an influential process as both an agent of carbon gain and loss in old-growth forest carbon dynamics.

The structure and composition of midwestern CHR old-growth forests reflect both local environmental influences of site productivity and a broader regional trend of lower productivity on an east-to-west gradient. The more productive sites, located in Indiana and Illinois, were associated with silty soils and contained mesophytic species such as sugar maple, American beech, slippery elm (*Ulmus rubra*), and pawpaw. In contrast, our least productive sites, located in Missouri, were located on steeper slopes and coarser, stonier soils where oaks and hickories (*Carya* spp.) predominate. Observed BAs, QMDs and MAIs generally declined along the east–west productivity gradient. Although more mesophytic species were present in the productive forests, seven of our 10 old-growth forests included white oak as an overstory dominant. However, other than Big Spring, a site characterized by stony soils, no species of oak was common in any midstory. This pattern is consistent with other inventories of mature, remnant forest stands in the region (Aldrich et al. 2005, Cowell et al. 2010). Species richness was greatest at one of the most productive forests (Davis-Purdue), but consistent trends in productivity and species richness were not discernable. However, studies suggest that at larger spatial scales, environmental conditions may override the effect of species richness on productivity that is found at local scales (Loreau et al. 2001, Potter and Woodall 2014). Further, successional diversity (i.e., stands containing a mix of early and late successional species) or evolutionary diversity may be better predictors of productivity and carbon storage than simple measures of richness (Caspersen and Pacala 2001, Potter and Woodall 2014).

4.1. Site Productivity and Old-growth Carbon Storage

There is much agreement that old-growth forests store more carbon than younger forests (Hoover et al. 2012, Gunn et al. 2014, Keeton 2018). Further, as expected, old-growth forests on more productive sites had greater carbon storage capacities. Except for Laughery Bluff, all sites gained aboveground carbon over the twenty-year period and the MAI of carbon generally corresponded to a site's productivity. Aboveground carbon at our least productive sites (Big Spring, Dark Hollow, Engelmann Woods, and Roaring River), ranged from 93 ± 3 to 117 ± 3 Mg ha^{-1}. Compared to the two sites with the greatest carbon storage (Davis Purdue and Donaldson Woods) with total aboveground carbon ranging 161 ± 9 to 177 ± 8 Mg C ha^{-1}. These estimates for productive old-growth forests in the CHR are comparable to old-growth forest estimates in the Mid-Atlantic Region (154 ± 47 Mg C ha^{-1}) (McGarvey et al. 2015). In unmanaged pine and oak plantations in the Missouri Ozarks, total aboveground carbon leveled off at 100 Mg C ha^{-1} at 50 years for pines and 80 years for oaks (Anderson et al. accepted), which is comparable to other unmanaged oak, oak-pine forests in the Ozarks (Li et al.

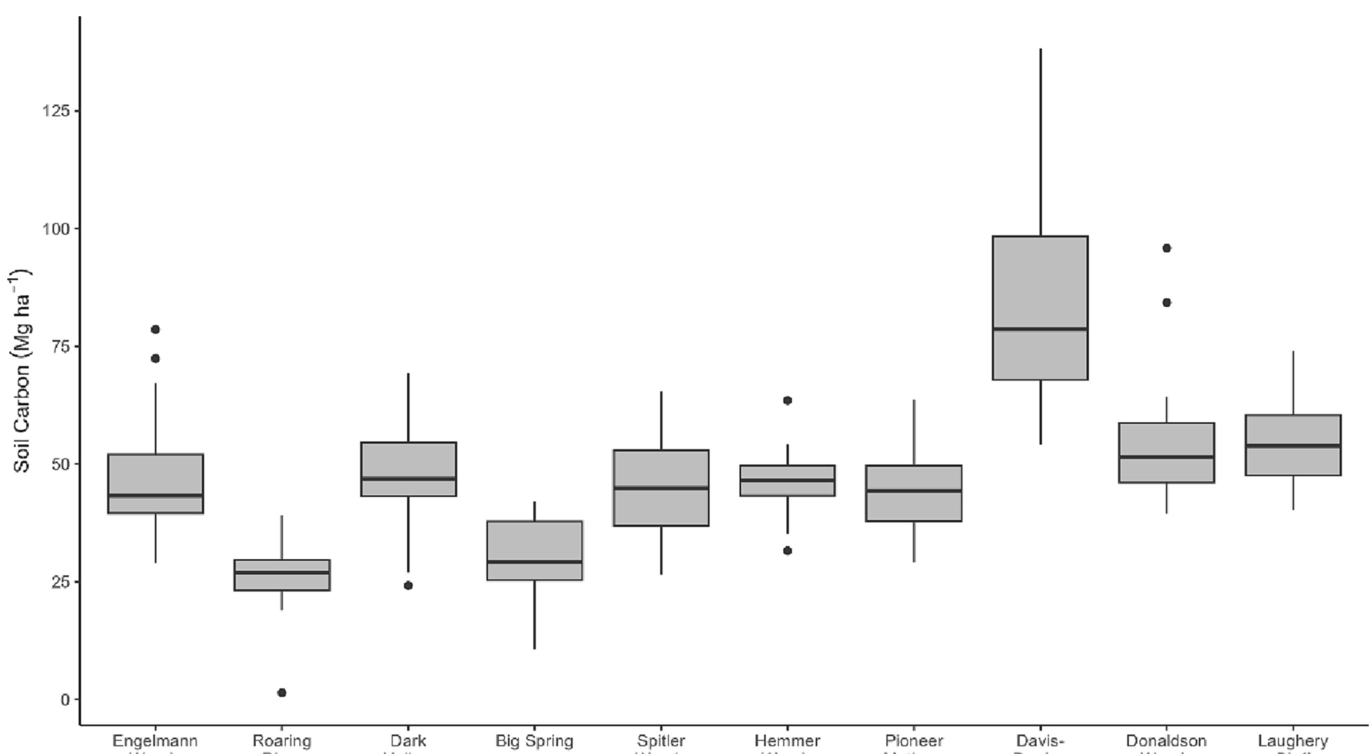

Fig. 4. Total soil carbon across all Central Hardwood Region old growth sites estimated as the sum of fine earth carbon (<2.0 mm) and organic material carbon (≥2.0 mm) collected from a depth up to 20 cm in the years 2012 and 2013.

Table 9
Mean measurements with standard error and relative basal area (m^2/ha) and density (trees/ha) of all trees that were recorded as alive during 1992–1993 measurement and dead or missing in the 2010 measurement.

Site	Mortality			
	BA (m2 ha^{-1})	Relative BA Mortality (%)	Density (trees ha^{-1})	Relative Density Mortality (%)
Engelmann Woods	8.4 (0.9)	35	715.3 (108.6)	50
Roaring River	8.1 (0.6)	33	853.0 (61.4)	51
Dark Hollow	5.6 (0.6)	22	723.3 (75.3)	43
Big Spring	8.0 (0.4)	33	850.3 (88.1)	50
Spitler Woods	5.9 (0.6)	20	518.3 (43.9)	41
Hemmer Woods	9.9 (1.1)	38	1,050.7 (95.1)	72
Pioneer Mothers	7.6 (0.9)	27	619.3 (91.1)	47
Davis-Purdue	10.5 (1.2)	34	511.3 (54.3)	37
Donaldson Woods	7.6 (1.0)	24	763.7 (115.3)	58
Laughery Bluff	6.7 (1.0)	32	462.7 (66.0)	45
All sites	7.8 (0.3)	30	706.8 (27.7)	49

2007). Total aboveground carbon in unmanaged, mixed conifer-hardwood stands in Maine averaged 146 ± 20 Mg C ha^{-1} which was significantly greater than stands that included silvicultural treatment (i.e., selection, shelterwood, or clearcut; (Puhlick et al. 2016b). Further, Hoover et al. (2012), reported that hardwood and softwood old-growth forests in New England had above-ground carbon estimates of 116–125 Mg C ha^{-1}. Hoover (2011) and Hoover et al. (2012) also reported that temperate forest soils across the northern US stored about 32 to 78 Mg C ha^{-1} in the upper 20 cm of mineral soil, although the authors acknowledged that estimates may be a high because coarse fragments were not accounted for in their calculations. Nonetheless, our soil carbon estimates are comparable to those reported by Hoover (2011) and the range that we observed in our study appears to be related to differences in the quantity of coarse fragments and clay in the soil. It has been widely reported that soils with fewer coarse fragments or greater clay content potentially store more carbon because they provide a greater mineral surface area in the fine-earth fraction for adsorbing and stabilizing organic matter (D'Amore and Kane 2016). Studies conducted in stands in the Acadian Forest region found that soils with a higher coarse fragment percentage had lower C concentration and that mineral soils with finer texture tended to have lower C concentration (Puhlick et al. 2016a, Puhlick et al. 2019). Our findings suggest that texture is an important determinant of soil carbon storage capacity in the CHR.

4.2. *Influence of stochastic disturbance on Old-growth forest carbon*

Natural disturbances, through their intensity and extent, can influence carbon dynamics in old-growth forests and can contribute to maintaining them as carbon sinks (Keeton 2018). As evidenced by the dominance of disturbance-dependent species, such as yellow-poplar, oaks, and hickories, old-growth forests in the CHR experience natural disturbance events and, historically, were heavily influenced by humans through fire, grazing, tending and selective harvesting (Shifley et al. 1995). Past and future disturbance, forest type, and productivity can influence variation in the allocation of biomass to different carbon pools as well as the rate of biomass accumulation (Hicke et al. 2012, Eisen 2015). Further, pulse disturbances can alter aboveground carbon pools by moving living overstory carbon to the down deadwood pool, which can be a sizable carbon sink in old-growth forests (Harmon 2001, Keeton 2018). Over long time periods, old-growth carbon pools can fluctuate so dynamically from disturbance that short-term trends might over-emphasize sink and source processes (Woods and Kern 2022).

Dark Hollow experienced a significant ice storm in 1994 (Rebertus et al. 1997), a year following the original inventory. Even two decades later, this event had residual effects on the allocation of carbon. There was a 20 % increase in total aboveground carbon, primarily driven by increases in overstory carbon. Davis-Purdue was noted as having a blowdown event occurring between measurement periods. This resulted in reductions basal area and density with increases in QMD. Davis-Purdue accumulated carbon between measurement periods, even with the reduction in live carbon which was transferred to substantial increases in down dead and standing dead pools. At Laughery Bluff, a major wind event impacted the forest two weeks prior to the first measurement period. Large dominant and co-dominant trees were blown down throughout Laughery Bluff forming relatively large canopy gaps. Over the following 20-year period, total aboveground carbon decreased, while overstory carbon increased with gaps created by disturbance likely facilitating midstory release and recruitment of reproduction. Initial measurements of down dead carbon were the highest among all forests examined, likely from the wind event, but down dead carbon declined over the twenty-year period by 62 %. Laughery Bluff was the only old-growth forest that did not accumulate carbon between measurement periods which was likely driven by the decomposition of woody debris.

Big Spring had notable black oak mortality in the 1990 survey and is a site that edaphically supports oaks, including white oak and scarlet oak. Big Spring is also the only old-growth forest in our study that includes a component of shortleaf pine (*Pinus echinata*; 13.6 % of the relative BA) and is considered a representative pine-oak old-growth woodland (Murphy and Nowacki 1997). Big Spring had continued reductions in BA and density over the twenty-year period while trees that did survive were likely larger in size, reflecting the increases in QMD and overstory carbon. Big Spring also had the largest increase in down dead carbon of all the old-growth forests. The black oak mortality witnessed at Big Spring may be attributable to similar red oak group mortality patterns in the Ozarks and more broadly, the eastern US (Jenkins and Pallardy 1995). Both black oaks and scarlet oaks are considered relatively short-lived and can have mortality rates 10 times higher than white oaks (Kabrick et al. 2004) but their high rates of mortality are not directly correlated with site conditions (Kabrick et al. 2008). Hemmer Woods, which had dominant overstory species composed of white oak, black oak, and northern red oak, has been documented as having higher baseline mortality rates than other old-growth forests in Indiana (McCune et al. 1988). Field observations also indicated that surface mining activity in the adjacent area was increasing in pressure over the 20-year period (approximately 1.6 km from the site in 1990 to active mining occurring at the edge of the forest in 2010; Lowney et al. (2016)). Hemmer Woods was further impacted by a major storm in 2012 (after the 2010 remeasurement), losing a substantial amount of its overstory trees (Indiana Department of Natural Resources).

5. Managing late successional forests for old-growth characteristics

As old-growth forests provide a diverse array of ecosystem services and store more carbon than production forests (Luyssaert et al. 2008, Knohl et al. 2009, Keeton et al. 2011, McGarvey et al. 2015, Keeton 2018), managing for them will be in important component of a diverse forest carbon portfolio. Unfortunately, the overriding paradigm of minimizing disturbances in old-growth forests may no longer be an adequate strategy to maintain complex ecosystems that function similarly to those of the past (Keeton et al. 2018). Contrary to this, it is proposed that intermediate-severity disturbance plays an important role in the formation of complex vertical structure and spatial heterogeneity for oak dominated old-growth stands (Hart and Cox 2017). Field notes for at least three of the sites included references to intermediate-severity wind or ice events occurring immediately prior to the first measurement or in between measurement periods. These disturbances can create pulses in particular carbon pools that persist for long periods of time. In addition, on oak-hickory dominated sites, prescribed fire may be necessary to reduce competition and to secure desired oak advanced reproduction (Spetich et al. 2022). Further, similar to all other forest types in the eastern US, the conservation and management of old-growth forests is at risk from a myriad of agents including climate change, species invasions, urbanization and fragmentation, among others (Shifley et al. 2014, Gunn and Orwig 2018, Keeton et al. 2018), which is only exacerbated by the rarity and small size of old-growth forests on the landscape.

There is increased interest in using silviculture to increase structural complexity and diversity in aging second-growth forests for enhancing carbon storage (Ford and Keeton 2017, Keeton et al. 2018), including storage in the form of durable wood products. Further, the acceleration of currently rare, late-successional structural complexity has benefits that extend beyond carbon mitigation including habitat for sensitive species [e.g., lichens and fungi; (Selva 2003, McMullin and Wiersma 2019)] and ecosystem functionality. However, as both late and early successional habitats provide important habitat and high biodiversity, optimizing treatments and habitat continuity across the landscape will be critical. Silviculture to promote old-growth characteristics must be adaptive to include a range of acceptable structural attributes (Bauhus et al. 2009), so that management targets do not unintentionally reduce complexity by being overly prescriptive. Applying mature and late-successional, old-growth classification schemes to sites may help in evaluating if management is meeting structural complexity goals through time (Lorimer and Halpin 2014). As evidenced in this study, old-growth is dynamic in its structure and composition both within and between sites and through time, as a result, this range of variation will be required of its management.

6. Conclusions

Old-growth forests in the CHR store about 125 to 134 Mg ha^{-1} of carbon above ground with an additional 27 to 84 Mg ha^{-1} of carbon stored in their mineral soils. Annual changes in above-ground carbon range from −0.3 to 1.3 Mg ha^{-1}. Total carbon storage, including contributions from the forest floor, mineral soil, roots, fine and coarse woody debris, and standing live and dead trees, varied across the CHR, generally following a west-to-east productivity gradient. On the less productive western sites, total carbon storage ranged from 93 to 117 Mg C ha^{-1} and on the more productive eastern sites, total carbon ranged from 120 to 177 Mg C ha^{-1}. However, disturbances including blowdown from wind events, ice storms, and mortality associated with disease complexes also were important factors affecting carbon storage in the CHR. Although old-growth forests are rare in the CHR, documenting carbon trends in them provides empirical estimates of the amount of carbon that potentially can be stored in these forests as they age. Examining their structure and composition provides insight needed for developing silvicultural methods for managing second growth forests to store more carbon, often in conjunction with other management objectives. There are millions of hectares of mature forests in the eastern US that are aging and have the potential to be managed to hasten development of old-growth attributes including carbon storage/sequestration through optimal adaptive strategies.

CRediT authorship contribution statement

Jacob Fraser: Conceptualization, Writing – original draft, Visualization, Formal analysis, Methodology. **Lauren S. Pile Knapp:** Conceptualization, Visualization, Formal analysis, Methodology, Writing – original draft. **Brad Graham:** Methodology, Investigation, Data curation, Writing – original draft. **Michael A. Jenkins:** Methodology, Writing – review & editing. **John Kabrick:** Methodology, Writing – review & editing. **Michael Saunders:** Methodology, Writing – review & editing. **Martin Spetich:** Investigation, Methodology, Writing – review & editing. **Steve Shifley:** Conceptualization, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120958.

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