

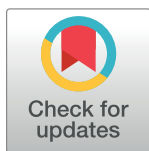
RESEARCH ARTICLE

Coastal carbon sentinels: A decade of forest change along the eastern shore of the US signals complex climate change dynamics

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Abstract

Increased frequency and intensity of storms, sea level rise, and warming temperatures are affecting forests along the eastern coast of the United States. However, we lack a clear understanding of how the structure of coastal forests is being altered by climate change drivers. Here, we used data from the Forest Inventory and Analyses program of the US Forest Service to examine structure and biomass change in forests along the mid-Atlantic, South-eastern, and Gulf coasts of the US. We selected plots that have been resampled at low (5 m) and mid (30–50 m) elevations in coastal areas of states from Texas to New Jersey, allowing us to determine change in live trees, standing dead wood, and downed dead wood biomass (and carbon) stocks across a decade at the county level. Forest area increased by 1.9% and 0.3% in low and mid elevation counties, respectively. Live tree biomass density increased by 13% and 16% in low mid elevation counties, respectively. Standing dead biomass decreased by 9.2% and 2.8% in low and mid elevation counties, respectively. Downed dead wood increased by 22% in low elevation counties and decreased 50% in mid elevation counties. Annualized growth and harvest were both higher (16% and 58% respectively) in mid elevation than low elevation counties, while annualized mortality was 25% higher in low elevation counties. Annualized growth in low elevation counties was negatively correlated to sea level rise rates, and positively correlated to number of storms, illustrating tradeoffs associated with different climate change drivers. Overall, our results illustrate the vulnerability of US coastal low and mid elevation forests to climate change and sea level rise, with indications that the complexity and rate of change in associated ecosystem functions (growth, mortality, and carbon storage) within the greater social environment (agricultural abandonment) may increase.

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[10.5061/dryad.c2fqz61g3](https://doi.org/10.5061/dryad.c2fqz61g3) The dataset is now public.

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Introduction

Coastal forests are important ecotones, located between upland forests and lower elevation marshes, that are vulnerable to, and under threat from, climate change and sea level rise [1, 2]. Coastal forests provide important ecosystem services, such as carbon sequestration, flood protection, habitat for migratory birds, and water purification in coastal settings, which will be degraded and lost as coastal forests decline [3]. Recent work has described the simultaneous transgression of salt-tolerant species (e.g. *Juncus* spp. and *Spartina* spp.) into and the death of characteristic forested wetlands and upland forests species (e.g. *Taxodium distichum* and *Pinus* spp.), creating ghost forests [4–6]. These ghost forests are visual reminders of the “invisible” climate change stressors that coastal ecosystems are experiencing, such as saltwater intrusion, increased flooding, changes in the magnitude and frequency of storms [7, 8]. While vegetative restructuring is likely happening in many parts of the world, most research to date has focused on the Gulf of Mexico and Atlantic coast of the US [9–11]. Insights from previous works are critical, but we still lack a clear understanding of how the structure of forested wetlands is changing across a broad geographic range.

While there has been work on the spatial extent of forested wetland loss [12, 13], there is still limited understanding of how this ecosystem change alters the structure of forests and carbon (C) stocks within forests. Forests store C in live biomass, standing dead biomass (snags), coarse woody debris (logs), litter, soils, and below ground vegetative structures (roots; [14]). Disturbances, both chronic, such as sea level rise, and episodic, such as storms or droughts, can impact tree recruitment, mortality, and the decomposition of dead biomass in forests [15]. Climate change can accelerate the mortality of trees [16], the longevity of standing dead C [17], and the decomposition of coarse woody debris [18], all of which could decrease the terrestrial C sink in coastal forests [2]. As sea level rise leads to the transition of forests to marshes, carbon stores move from stable and/or accreting biomass stocks in live trees to more labile and declining dead wood C stores [19, 20]. A better understanding of the current stores of C in different pools of coastal forests via examination of biomass dynamics, and how such stores might be influenced by climate change drivers, may help address the conservation of these ecological C dense systems.

Much of the most recent literature on this phenomenon has leveraged remote sensing data to assess the spatial extent of this change. The change in spatial extent of forested wetlands across the east coast of the US has been well documented [12], with accelerating rates of forest retreat documented in coastal states from New Jersey to Texas [4, 13]. In the most extensive analyses to date, using classified satellite imagery, White et al. (2022) reported a net loss of 13,682 km² of forested wetlands along the Atlantic and Gulf coasts of the US, in the time period 1996–2016. Using the Landsat record for the Alligator River Wildlife Refuge in North Carolina, Ury et al. found 193 km² of forest turned into ghost forests, scrub-shrub, or marshes [21]. Using lidar in a similar area, Smart et al. [22] found similar areal extent of forest loss (167 km²) near estuarine shore and calculated 0.13 Tg C reduction in tree biomass. A common finding of these studies is that low elevation areas are more vulnerable to sea level rise, saltwater intrusion, and flooding stressors. While these studies provide insight on changes to the areal extent of coastal forested wetlands, we still lack a clear understanding of how forest structure and associated biomass dynamics might be changing ahead of potential forest decline and conversion into other land uses (i.e., salt marshes). Large scale survey data, such as from the U. S. Department of Agriculture (USDA) Forest Service’s nationwide Forest Inventory and Analysis program (FIA, Burrill et al. 2021) have not been used to examine structural changes to coastal forests. The FIA data provide a more regional understanding that extends beyond the single-site approach that has dominated past field examinations.

There has been active debate over whether marsh expansion will compensate for the seaward loss of wetlands [23]. A recent study found that landward migration of marshes will not compensate, leading to loss of freshwater forested wetlands, uplands, and croplands [12]. The mechanisms driving changes in wetland extent will vary due to geomorphology, hydrology, and biological settings [10], making it challenging to forecast the ecosystem consequences. Even before there is ecosystem change from forests to marshes, there could be changes in the structure of coastal forests; such as in the relationships between forest biomass stocks (i.e. live, standing dead, and downed dead) that could serve as early warning signals of further forest decline and/or structural/functional change.

Given that the impacts of sea level rise on coastal systems are linked to elevation [24, 25], we examined forest dynamics within two elevational zones as a proxy for exposure to sea level rise and climate change stressors. We hypothesized that low elevation forests are more vulnerable, and thus forest dynamics should reflect more frequent disturbances. We used data from the FIA program to answer the following questions:

1. What was the change in area, biomass, and carbon for live, standing dead, and downed dead wood in low (<5m) and mid elevation (~40m) coastal forests in counties across the North American Coastal Plain of the US over the last 10 years?
2. How do climate change drivers (changes in temperature, precipitation, rate of sea level rise, and number of storms) alter biomass stocks, growth, and mortality of low and mid elevation forests?

We hypothesized that: (1) low elevation counties experienced more areal forest loss and biomass loss, and (2) had lower stocks of live and dead biomass than mid elevation counties; and (3) drivers related to sea level rise (rate of sea level rise) and climate change (number of storms, change in precipitation and temperature) explain variability in dynamics (growth, mortality and change in stocks) of low elevation forests, but not mid elevation forests.

Methods

We used data from the National Forest Inventory and Analysis (FIA) program which, administered by the USDA Forest Service, provides a comprehensive statistical inventory and associated database of forests across the United States [26]. The program applies standardized techniques to measure forest characteristics across a national plot sampling network of approximately one plot per 2,428 ha, with plot locations determined using a hexagonal sampling framework designed to be as spatially balanced as possible [27]. The plot location within each 2,428 ha hexagon was visited by field crews if remotely sensed data indicated it was in forest land use (having $\geq 10\%$ tree canopy cover, or evidence of such cover) that was at least 0.4 ha in area and 37 m wide [28]. We focused on data for the mid-Atlantic and Southeast coast of the US, from Texas to New Jersey. We selected information from forested plots located in low (~5m) and mid elevation (30–50 m) areas with slopes less than 15%, and had either hydric conditions, or were near a water feature, which are indicative of forested wetlands. We included the code used to query the FIA database in the data repository. We used the FIA methodologies to estimate forest resources attributes from plot level to the county level [27, 28]. We looked at changes in live trees (biomass and C), standing dead wood (SD, biomass and C), and downed dead wood (biomass and C, DD). The systematic FIA sample design further allowed for statistical population-level estimates of various forest attributes, such as the area of a low-elevation forest in a county, using an “expansion factor” assigned to each plot condition [27, 28]. Using a design-based approach to population inference, expansion factors can be summed across plots in a population to provide an estimate of the total area within that

population. Similarly, the FIA sample design allows individual trees inventoried on plots to be scaled via an expansion factor to estimate the total C of trees within an area. In this case, we calculated the area and biomass (from standing live, standing dead, and downed dead) of low-elevation and mid-elevation forests in low-elevation and mid-elevation counties, respectively, and within each state.

Field crews collected a wide variety of data using standardized protocols from each FIA plot, which covered 0.067 hectares within four 7.31-m radius subplots arranged at the vertices and center of a triangle [28]. This included the diameter, height and species for every live and dead tree with a diameter at breast height (DBH) ≥ 12.7 cm. All trees with DBH ≥ 2.54 cm but < 12.7 cm were measured in a single 2.07-m-radius microplot within each of the plot's four subplots. Using the component ratio method, the FIA program estimates the above-ground dry biomass of each tree with DBH ≥ 2.54 cm in pounds [29]. Biomass and C densities were calculated by scaling plot-level data to per hectare estimates for the counties [28]. We estimated change in the stocks of different pools by subtracting time 2 from time 1 [30]. We also looked at changes in different size classes and decay classes (for dead wood). We used data from the two latest survey evaluation periods, spanning a decade of change (Table 1). We estimated forest biomass standing stocks and change among key structural components using data from 1700 plots in low elevation counties and 3200 plots in mid elevation counties. We estimated population level values for 126 low elevation counties and 179 mid elevation counties (Fig 1). We excluded counties for which there were less than three plots in any survey year.

To examine potential climate change drivers of forest dynamics we used publicly available datasets. We obtained sea level rise rates for 43 of the National Oceanic and Atmospheric Administration (NOAA) tide gauges from the Permanent Service for Mean Sea Level (PSMSL, S1A Table in S1 Text). We used the website to estimate rates of sea level rise from 2010–2020 to match the FIA dataset, given reports of accelerating rates of sea level rise in the Southeastern US [31]. We calculated mean annual temperature and mean annual precipitation from the GridMet dataset (4 km² spatial resolution), accessed through the Climate Engine portal (<https://app.climateengine.org/climateEngine>) for the period 2010–2020, to roughly match the FIA measurements. We also estimated change in temperature and precipitation by estimating the sen slope [32] of each factor over the same time period using the Climate Engine portal. We used the NOAA National Hurricane Center Atlantic Hurricane Catalog (HURDAT2), accessed through Google Earth Engine, to count the number of tropical cyclones that passed

Table 1. Years of the surveys for the two time periods used in this study.

State name	Time 1	Time 2
Alabama	2005–2010	2015–2021
Delaware	2005–2010	2015–2019
Florida	2005–2010	2015–2019
Georgia	2005–2010	2015–2020
Louisiana	2005–2010	2015–2018
Maryland	2005–2010	2015–2019
Mississippi	2005–2010	2015–2020
New Jersey	2005–2010	2015–2019
North Carolina	2005–2010	2015–2021
Pennsylvania	2005–2010	2015–2019
South Carolina	2005–2010	2015–2020
Texas	2005–2010	2015–2018
Virginia	2005–2010	2015–2020

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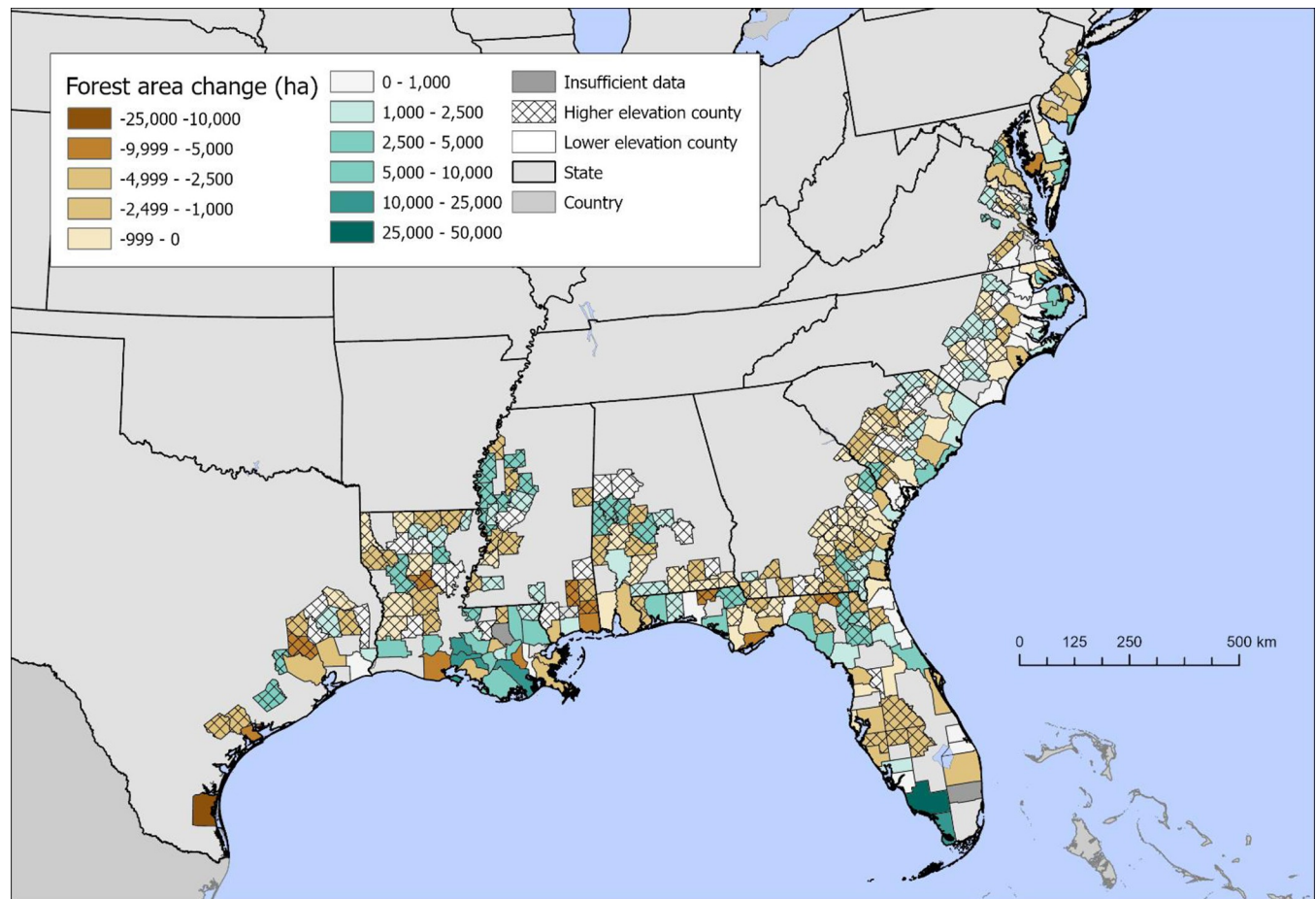


Fig 1. Map of change between sampling intervals in forest area for low and mid elevation (crossed) counties derived from the FIA. Vector shapefiles were retrieved from the U.S. Census Bureau (<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>) and ESRI (<http://www.ArcGIS.com>). The map was created using ESRI Arc GIS Pro 3.2.0.

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through a 100 km radius buffer of the NOAA tide gauges for the same period. On average, low elevation counties were located 22.4 ± 2.6 km, while mid elevation counties were 108 ± 5.9 km from the NOAA tide gauges.

To compare standing stocks and change in stocks between low and mid elevation counties we used non-parametric Kruskal-Wallis test given the lack of normality of the data [33]. We compared change in stocks both as direct change ($T2-T1$) and proportional change [$(T2-T1)/T1$]. We used Pearson correlations to examine relationships between estimated annualized growth and mortality to climate change drivers (mean annual temperature, annual precipitation, change in temperature, change in precipitation, sea level rise rate, and number of storms). All analyses were conducted in R statistical software using the Basic Statistics and Data Analyses (Arnholt and Evans 2017), and moments (Komsta and Novomestky 2015). We used p higher than 0.1 as our threshold of significance. We included the R code in the data archive.

Results

We used plot level data to identify the dominant species in terms of abundance and biomass in low and mid elevation plots (Table 2). Eight of the ten most common species by abundance were the same between both low and mid elevation plots (Table 2). In low elevation plots four

Table 2. List of 20 most common species (by abundance) in low and mid elevation FIA plots.

Low elevation				Mid elevation			
Common name	Scientific name	% RA	WI	Common name	Scientific name	% RA	WI
Red maple	<i>Acer rubrum</i>	15.55	FAC	Swamp tupelo	<i>Nyssa biflora</i>	13.28	OBL
Water tupelo	<i>Nyssa aquatica</i>	10.52	OBL	Loblolly pine	<i>Pinus taeda</i>	13.25	FAC
Bald cypress	<i>Taxodium distichum</i>	9.78	OBL	Slash pine	<i>Pinus elliotti</i>	12.65	FACW
Swamp tupelo	<i>Nyssa biflora</i>	9.41	OBL	Red maple	<i>Acer rubrum</i>	9.57	FAC
Pond cypress	<i>Taxodium ascendens</i>	6.52	OBL	Sweetgum	<i>Liquidambar styraciflua</i>	9.22	FAC
Green ash	<i>Fraxinus pennsylvanica</i>	5.87	FACW	Pond cypress	<i>Taxodium ascendens</i>	5.84	OBL
Loblolly pine	<i>Pinus taeda</i>	5.56	FAC	Sweetbay	<i>Magnolia virginiana</i>	5.74	FACW
Sweetgum	<i>Liquidambar styraciflua</i>	5.47	FAC	Water oak	<i>Quercus nigra</i>	5.18	FAC
Cabbage palmetto	<i>Sabal palmetto</i>	4.11	FAC	Green ash	<i>Fraxinus pennsylvanica</i>	3.36	FACW
Slash pine	<i>Pinus elliotti</i>	3.91	FACW	Loblolly-bay	<i>Gordonia lasianthus</i>	3.16	FACW
Chinese tallowtree	<i>Triadica sebifera</i>	3.05	FAC	Laurel oak	<i>Quercus laurifolia</i>	2.89	FACW
Redbay	<i>Persea borbonia</i>	3.00	FACW	Blackgum	<i>Nyssa sylvatica</i>	2.33	FAC
Laurel oak	<i>Quercus laurifolia</i>	2.81	FACW	Yellow-poplar	<i>Liriodendron tulipifera</i>	2.29	FACU
Black willow	<i>Salix nigra</i>	2.62	OBL	Sugarberry	<i>Celtis laevigata</i>	1.91	FACW
Pond pine	<i>Pinus serotina</i>	2.54	FACW	Bald cypress	<i>Taxodium distichum</i>	1.76	OBL
Water oak	<i>Quercus nigra</i>	2.24	FAC	American hornbeam	<i>Carpinus caroliniana</i>	1.71	FAC
Sweetbay	<i>Magnolia virginiana</i>	2.21	FACW	Redbay	<i>Persea borbonia</i>	1.58	FACW
Loblolly-bay	<i>Gordonia lasianthus</i>	1.68	FACW	Black willow	<i>Salix nigra</i>	1.49	OBL
American elm	<i>Ulmus americana</i>	1.68	FACW	Chinese tallowtree	<i>Triadica sebifera</i>	1.42	FAC
Atlantic white-cedar	<i>Chamaecyparis thyoides</i>	1.49	OBL	American holly	<i>Ilex opaca</i>	1.37	FAC

%RA = relative abundance. WI = wetland indicator status according to USDA (OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland).

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out of the ten dominant species were classified as obligate wetland (OBL) and two were classified facultative wetland (FACW). In mid elevation plots two of the ten dominant species were classified as obligate wetland (OBL), and four were classified as facultative wetland (FACW, Table 2), suggesting data came primarily from forested wetlands in both elevational zones, which agrees with our initial plot selection to include hydric soils or water features.

There was spatial heterogeneity in changes in forest area (Fig 1), live tree (S1A Fig in S1 Text), standing dead (SD, S1B Fig in S1 Text), and downed dead (DD, S1C Fig in S1 Text) biomass across the eastern coastal plain of the US. Forest area increased by 1.9% in low elevation counties and by 0.3% in mid elevation counties ($X^2 = 0.15$, $p = 0.69$, Table 3). On average, low elevation counties gained 527 ± 372 ha and mid elevation counties gained 91 ± 196 ha of forest (Table 3).

When summed across the region of study, low elevation counties gained 21.8 Tg C and mid elevation counties gained 39.5 Tg C. Live biomass density was 17 to 21% higher in low

Table 3. Forest area (in ha) and estimates of growth, harvest, and mortality (in $\text{Mg ha}^{-1} \text{y}^{-1}$) for low and mid elevation counties.

	Low elevation			Mid elevation		
	Time 1	Time 2	Change	Time 1	Time 2	Change
Forest Area	26892 $\pm$ 3054	27434 $\pm$ 3360	527 $\pm$ 372	30125 $\pm$ 1936	30122 $\pm$ 1969	91 $\pm$ 196
Growth		4.22 $\pm$ 0.19			5.03 $\pm$ 0.13	
Harvest		0.98 $\pm$ 0.15			2.34 $\pm$ 0.18	
Mortality		1.35 $\pm$ 0.11			1.08 $\pm$ 0.07	

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Table 4. Biomass estimates (mean $\pm$ standard error, in Mg ha⁻¹) for live trees, standing dead, and downed dead by size class (cm) and decay class in low and mid elevation counties in the eastern shore of the US.

	Low elevation			Mid elevation		
Live trees	Time 1	Time 2	Change	Time 1	Time 2	Change
>20	2.22 $\pm$ 0.09	2.25 $\pm$ 0.08	0.01 $\pm$ 0.07	2.08 $\pm$ 0.07	2.11 $\pm$ 0.06	0.02 $\pm$ 0.08
20–30	4.14 $\pm$ 0.18	4.54 $\pm$ 0.21	0.36 $\pm$ 0.14	3.49 $\pm$ 0.15	4.08 $\pm$ 0.14	0.59 $\pm$ 0.16
30–40	4.02 $\pm$ 0.22	4.75 $\pm$ 0.30	0.70 $\pm$ 0.17	2.78 $\pm$ 0.12	3.55 $\pm$ 0.15	0.77 $\pm$ 0.14
40–50	2.81 $\pm$ 0.19	3.37 $\pm$ 0.21	0.53 $\pm$ 0.14	2.21 $\pm$ 0.13	2.54 $\pm$ 0.13	0.32 $\pm$ 0.11
50–60	1.80 $\pm$ 0.20	1.85 $\pm$ 0.18	0.03 $\pm$ 0.12	1.17 $\pm$ 0.11	1.53 $\pm$ 0.13	0.35 $\pm$ 0.11
60+	1.71 $\pm$ 0.22	2.21 $\pm$ 0.27	-0.01 $\pm$ 0.12	1.36 $\pm$ 0.15	1.78 $\pm$ 0.21	0.39 $\pm$ 0.11
All	18.52 $\pm$ 0.84	21.03 $\pm$ 0.99	2.36 $\pm$ 0.53	14.55 $\pm$ 0.49	17.34 $\pm$ 0.56	2.39 $\pm$ 0.39
Standing dead (SD)						
>20	0.07 $\pm$ 0.006	0.07 $\pm$ 0.006	0.002 $\pm$ 0.006	0.06 $\pm$ 0.005	0.05 $\pm$ 0.006	-0.005 $\pm$ 0.007
20–30	0.13 $\pm$ 0.01	0.11 $\pm$ 0.01	-0.01 $\pm$ 0.01	0.10 $\pm$ 0.01	0.09 $\pm$ 0.01	-0.007 $\pm$ 0.01
30–40	0.10 $\pm$ 0.01	0.09 $\pm$ 0.01	-0.007 $\pm$ 0.02	0.08 $\pm$ 0.01	0.06 $\pm$ 0.01	-0.02 $\pm$ 0.01
40–50	0.08 $\pm$ 0.01	0.06 $\pm$ 0.02	-0.02 $\pm$ 0.02	0.04 $\pm$ 0.01	0.05 $\pm$ 0.01	0.01 $\pm$ 0.01
50–60	0.04 $\pm$ 0.01	0.04 $\pm$ 0.02	0.007 $\pm$ 0.02	0.02 $\pm$ 0.01	0.02 $\pm$ 0.006	-0.002 $\pm$ 0.01
60+	0.07 $\pm$ 0.02	0.03 $\pm$ 0.009	-0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.03 $\pm$ 0.02	0.004 $\pm$ 0.02
All	0.54 $\pm$ 0.04	0.47 $\pm$ 0.04	-0.05 $\pm$ 0.09	0.35 $\pm$ 0.03	0.34 $\pm$ 0.03	-0.01 $\pm$ 0.04
SD/live ratio	0.037 $\pm$ 0.004	0.027 $\pm$ 0.002	-0.006 $\pm$ 0.003	0.028 $\pm$ 0.003	0.021 $\pm$ 0.002	-0.007 $\pm$ 0.003
Downed dead wood (DD)						
>20	1.23 $\pm$ 0.36	0.71 $\pm$ 0.33	-0.19 $\pm$ 0.25	1.55 $\pm$ 0.68	0.69 $\pm$ 0.17	0.02 $\pm$ 0.27
20–30	0.54 $\pm$ 0.34	0.46 $\pm$ 0.11	0.16 $\pm$ 0.23	0.33 $\pm$ 0.14	0.25 $\pm$ 0.06	0.03 $\pm$ 0.10
30–40	0.26 $\pm$ 0.12	0.09 $\pm$ 0.04	-0.13 $\pm$ 0.13	0.02 $\pm$ 0.01	0.22 $\pm$ 0.07	0.31 $\pm$ 0.12
40–50	0.08 $\pm$ 0.07	0.04 $\pm$ 0.03	-0.10 $\pm$ 0.08	0.011 $\pm$ 0.01	0.12 $\pm$ 0.09	0.19 $\pm$ 0.16
50–60	0.10 $\pm$ 0.09	0.09 $\pm$ 0.09	0.06 $\pm$ 0.22	0	0.12 $\pm$ 0.11	0.21 $\pm$ 0.21
60+	0.47 $\pm$ 0.45	0.73 $\pm$ 0.65	0.80 $\pm$ 1.36	0	1.62 $\pm$ 1.62	2.80 $\pm$ 2.80
All	2.99 $\pm$ 0.82	2.36 $\pm$ 0.77	0.66 $\pm$ 1.63	2.11 $\pm$ 0.91	3.37 $\pm$ 1.79	3.96 $\pm$ 2.84
DD/live ratio	0.15 $\pm$ 0.03	0.15 $\pm$ 0.04	0.06 $\pm$ 0.09	0.39 $\pm$ 0.31	0.10 $\pm$ 0.02	0.07 $\pm$ 0.03
Standing dead decay classes						
1	0.12 $\pm$ 0.02	0.18 $\pm$ 0.02	0.005 $\pm$ 0.03	0.08 $\pm$ 0.01	0.07 $\pm$ 0.02	0.02 $\pm$ 0.02
2	0.10 $\pm$ 0.02	0.26 $\pm$ 0.01	0.01 $\pm$ 0.02	0.07 $\pm$ 0.01	1.46 $\pm$ 0.01	0.0007 $\pm$ 0.01
3	0.12 $\pm$ 0.01	0.45 $\pm$ 0.03	0.0005 $\pm$ 0.02	0.10 $\pm$ 0.07	0.85 $\pm$ 0.01	-0.03 $\pm$ 0.02
4	0.09 $\pm$ 0.01	1.07 $\pm$ 0.004	-0.11 $\pm$ 0.04	0.04 $\pm$ 0.01	0.58 $\pm$ 0.004	-0.01 $\pm$ 0.008
5	0.04 $\pm$ 0.005	0.16 $\pm$ 0.003	-0.03 $\pm$ 0.009	0.03 $\pm$ 0.006	0.07 $\pm$ 0.002	-0.01 $\pm$ 0.006
Downed dead Decay classes						
1	0.60 $\pm$ 0.49	0.18 $\pm$ 0.07	-0.55 $\pm$ 0.59	0.13 $\pm$ 0.05	0.07 $\pm$ 0.03	0.001 $\pm$ 0.09
2	0.36 $\pm$ 0.13	0.26 $\pm$ 0.13	-0.03 $\pm$ 0.29	0.30 $\pm$ 0.19	1.46 $\pm$ 1.22	2.38 $\pm$ 2.11
3	0.97 $\pm$ 0.29	0.45 $\pm$ 0.11	-0.28 $\pm$ 0.24	1.12 $\pm$ 0.58	0.85 $\pm$ 0.19	0.52 $\pm$ 0.33
4	0.77 $\pm$ 0.39	1.07 $\pm$ 0.68	1.23 $\pm$ 1.32	0.27 $\pm$ 0.10	0.40 $\pm$ 0.71	0.66 $\pm$ 0.70
5	0.03 $\pm$ 0.003	0.16 $\pm$ 0.06	0.23 $\pm$ 0.10	0.07 $\pm$ 0.03	0.07 $\pm$ 0.05	0.02 $\pm$ 0.10

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elevation plots in both sampling periods ($X^2 = 10.0$, $p = 0.001$, Table 4, S1B Table in S1 Text). Live biomass increased by 13% in low elevation counties, and by 16% in mid elevation counties ($X^2 = 4.69$, $p = 0.03$, Fig 2, Table 4, S1B Table in S1 Text). On average, low elevation counties gained 2.36 ± 0.53 Mg ha⁻¹, while mid elevation counties gained 2.39 ± 0.39 Mg ha⁻¹ of live tree biomass (Fig 2). In terms of different size classes, mid elevation counties accrued 1.6 and 11 times more biomass in smaller (20–30 cm) and larger (50–60 cm) diameter trees ($X^2 = 6.05$, $p = 0.01$, $X^2 = 5.83$, $p = 0.01$, Fig 3, Table 4) than low elevation counties.

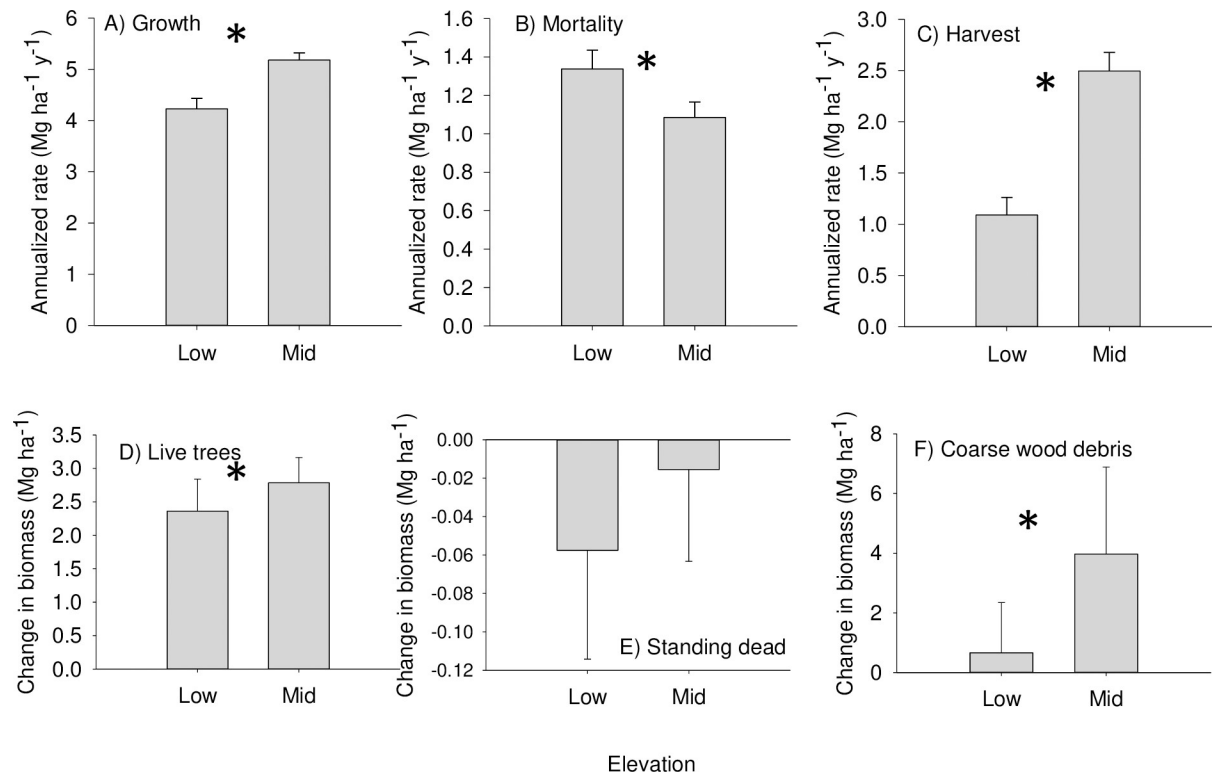


Fig 2. Change in annualized growth (A), mortality (B), harvest (C), and changes in live tree (D), standing dead (E), and downed dead (F). Asterisks denote significant differences from Kruskal Wallis.

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When summed across the study region, low elevation counties lost 0.48 Tg C, and mid elevation counties lost 0.82 Tg C in standing dead biomass over the study period. Standing dead biomass was 27–35% higher in low elevation plots than in mid elevation plots ($X^2 = 11.52$, $p = 0.0006$ in time 1, $X^2 = 13.46$, $p = 0.002$ in time 2, Table 4, S1B Table in S1 Text). Between survey periods, SD decreased in low elevation counties by 9.2% and by 2.8% in mid elevation counties ($X^2 = 0.78$, $p = 0.37$, Fig 2, Table 4, S1B Table in S1 Text). In time 1, low elevation counties had higher standing dead biomass in all size categories, except the largest (>60 cm, Table 4, S1B Table in S1 Text), but the differences mostly disappeared in time 2 (Table 4). Low elevation counties lost more SD in the most decayed classes (decay classes 4 and 5) than mid elevation counties ($X^2 = 8.58$, $p = 0.0033$, and $X^2 = 10.32$, $p = 0.001$, respectively, Fig 4, Table 4, S1B Table in S1 Text). The mean ratio of SD to live tree biomass was higher in low elevation counties in time 2 ($X^2 = 8.48$, $p = 0.003$), but the change in both elevation classes was similar ($X^2 = 0.82$, $p = 0.36$, S1B Table in S1 Text).

When summed across the study region, low elevation counties gained 6.1 Tg C and mid elevation counties gained 9.1 Tg C in DD over the study period. During the first survey, DD was 29% higher in low elevation counties ($X^2 = 6.06$, $p = 0.01$), but that switched in the second survey when DD was 29% higher in mid elevation counties ($X^2 = 0.88$, $p = 0.34$, Table 4, S1B Table in S1 Text). On average, DD decreased by 22% in low elevation counties and increased by 39% in mid elevation counties from ($X^2 = 3.06$, $p = 0.07$, Fig 2, Table 4). However, the low elevation county DD numbers are strongly affected by a county (parish) in LA (Saint John the Baptist) which gained 40.9 Mg ha^{-1} between the sampling periods. If that low elevation county is removed, the mean biomass in DD in time 2 is $2.09 \pm 0.54 \text{ Mg ha}^{-1}$, which would mean that

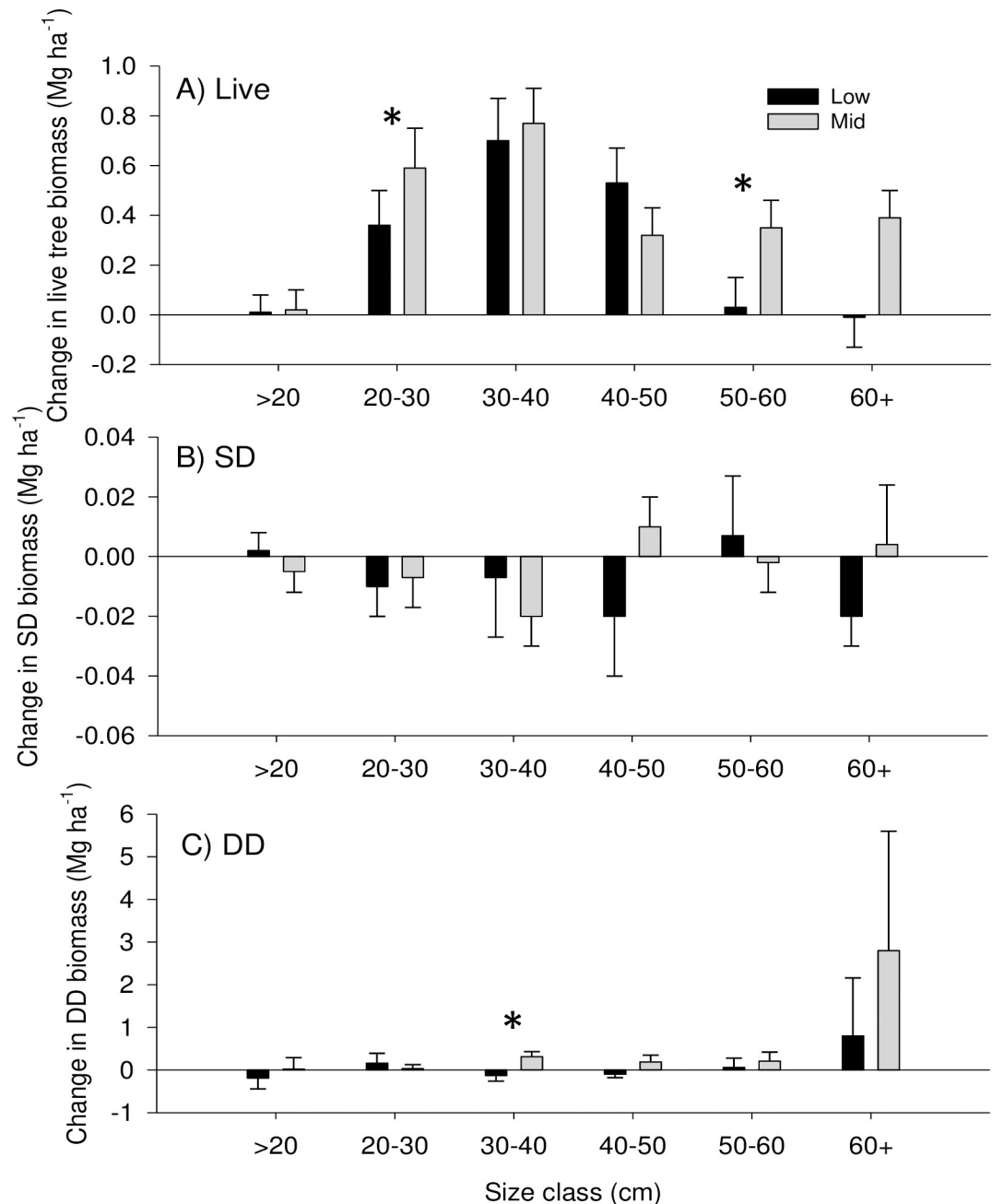


Fig 3. Changes in size class categories (cm) in biomass of live trees (A), standing dead (B), and downed dead (C). Asterisks denote significant differences from Kruskal Wallis.

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the low elevation counties lost DD ($0.48 \pm 0.98 \text{ Mg ha}^{-1}$). Similarly, the mid elevation counties are strongly influenced by another parish in LA (Ouachita), which gained 105 Mg ha^{-1} of DD between time 1 and time 2. If that county is removed, the time 2 mean was $1.60 \pm 0.71 \text{ Mg ha}^{-1}$, and mid elevation counties gained on average $1.07 \pm 0.40 \text{ Mg ha}^{-1}$. Low elevation counties lost DD in mid-size classes (30–40 cm), while mid elevation counties gained in that size class ($X^2 = 8.14$, $p = 0.004$, Fig 3). In terms of decay classes, the low elevation counties gained more biomass in the most decayed class (class 5, $X^2 = 3.63$, $p = 0.05$, Fig 4), while mid elevation

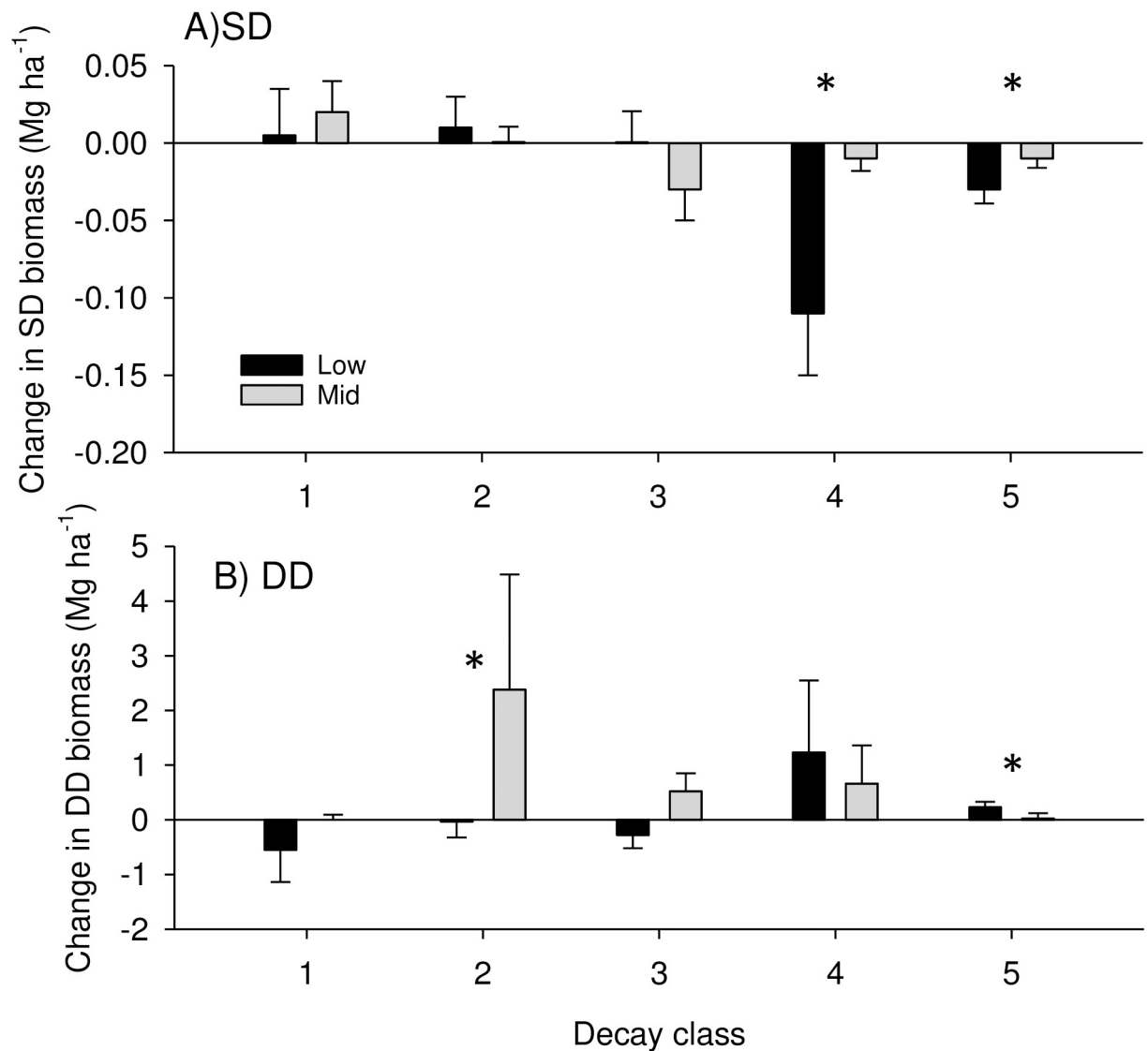


Fig 4. Changes in decay classes in biomass of standing dead (A) and downed dead (B). Asterisks denote significant differences from Kruskal Wallis.

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counties gained more biomass in decay class 2 ($X^2 = 3.47$, $p = 0.06$, Fig 4). The DD to live tree ratio did not differ between low and mid elevation counties (Table 4).

Annualized growth and harvest were both higher in mid elevation counties than low elevation counties ($X^2 = 19.3$, $p < 0.001$, $X^2 = 41.69$, $p < 0.001$, respectively, Fig 2, S1C Table in S1 Text). Mortality was higher in low elevation counties than in mid elevation counties ($X^2 = 5.77$, $p = 0.01$, Table 3, S1C Table in S1 Text). Climate change drivers varied across the region (S1A Table in S1 Text). In low elevation counties annualized growth rates were negatively correlated to sea level rise rate ($r = -0.39$, $p < 0.005$) and positively correlated to number of storms ($r = 0.28$, $p < 0.01$, Figs 3 and 4). In mid elevation counties, annualized growth was positively correlated to number of storms ($r = 0.25$, $p < 0.05$). In low elevation counties, mortality was positively correlated to number of storms ($r = 0.19$, $p < 0.1$, Fig 5), while in mid elevation counties mortality was negatively correlated to average temperature ($r = -0.17$, $p = 0.05$), change in

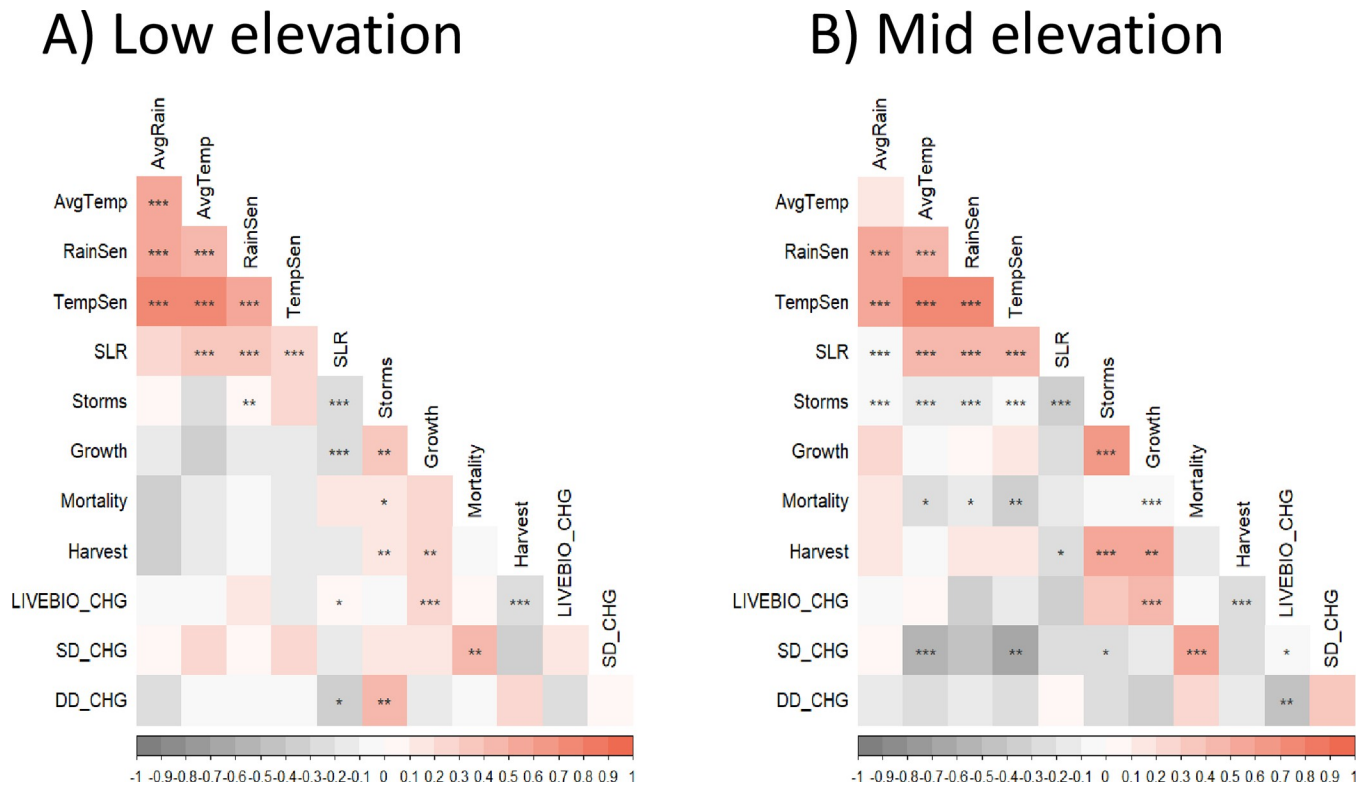


Fig 5. Pearson correlation coefficients of growth, mortality, harvest, change in live biomass (Livebio_chg), standing dead (SD_chg), and downed dead (DD_chg) in low (A) and mid (B) elevation counties. Significance levels include 0.1 (*), 0.05 (**), and 0.01 (***).

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rainfall (sen slope, $r = -0.16$, $p = 0.07$) and change in temperature (sen slope, $r = -0.18$, $p = 0.04$, Fig 5). In low elevation counties harvest rates were positively correlated to number of storms ($r = 0.23$, $p = 0.03$) and growth rates ($r = 0.23$, $p = 0.04$, Fig 5). In mid elevation counties harvest rates were negatively correlated to sea level rise ($r = -0.17$, $p = 0.06$) and positively correlated to number of storms ($r = 0.25$, $p = 0.004$) and growth rate ($r = 0.18$, $p = 0.04$, Fig 5). In low elevation counties changes in live tree biomass were positively correlated to growth ($r = 0.46$, $p < 0.001$) and sea level rise rate ($r = 0.25$, $p = 0.05$), and negatively related to harvest rates ($r = -0.37$, $p < 0.001$, Fig 5). Similarly, in mid elevation counties live biomass change was positively correlated to growth ($r = 0.56$, $p < 0.001$) and negatively correlated to harvest ($r = -0.31$, $p < 0.001$). In both low and mid elevation counties, change in SD was positively correlated to mortality ($r = 0.23$, $p = 0.04$, $r = 0.47$, $p < 0.001$, respectively, Fig 5). In mid elevation counties change in SD was also negatively correlated to average temperature ($r = -0.25$, $p = 0.008$), change in temperature ($r = -0.21$, $p = 0.02$), and number of storms ($r = -0.16$, $p = 0.09$). In low elevation counties changes in DD were negatively correlated to sea level rise rate ($r = -0.35$, $p = 0.08$) and positively correlated to number of storms ($r = 0.45$, $p = 0.02$, Fig 4). In mid elevation counties, change in DD was negatively correlated to change in live tree biomass ($r = -0.46$, $p = 0.03$).

Discussion

We found partial support for our initial hypotheses. First, we hypothesized that low elevation counties experienced more areal forest and biomass loss than mid elevation counties, due to more frequent disturbances. Contrary to our hypothesis, we found that both low and mid

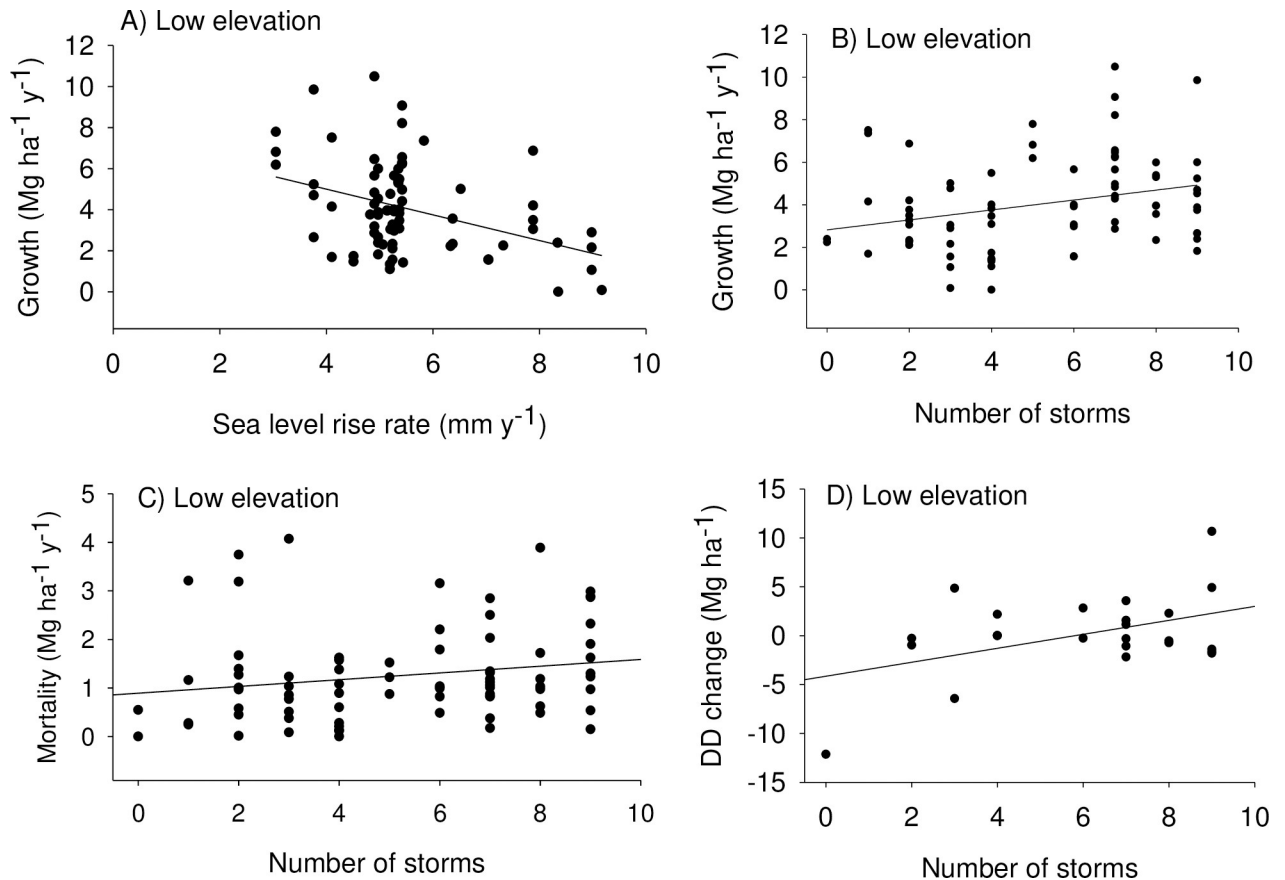


Fig 6. Relationships between annualized growth and sea level rise rate (A) and number of storms (B) in low elevation counties. And relationship between number of storms and mortality (C), and change in downed dead wood (D) in low elevation counties.

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elevation counties gained forest area (527 ± 372 ha and 91 ± 196 ha, respectively) and live tree biomass (2.36 ± 0.53 Mg ha⁻¹ and 2.39 ± 0.39 Mg ha⁻¹, respectively, Fig 2). The gain in forest area and biomass in both elevations agrees with previous estimates of change in forests for the conterminous US [33, 34]. It is interesting that while low elevation counties gained more forest area (increased by 1.9%) than mid elevation counties (increased by 0.3%), the gain in biomass was very similar between low and mid elevation counties (increased by 13–16%), suggesting that changes in spatial extent of forest area do not directly translate into more biomass (or more stored C). Our second hypothesis was that low elevation counties would have lower biomass of live and dead trees, compared to the mid elevation forests. Contrary to our hypothesis, we found higher biomass of live and standing dead trees in low elevation plots (Table 4). There was no clear pattern in terms of downed dead wood between elevation categories. Annualized growth and harvest were higher in mid elevation counties, while mortality was higher in low elevation counties (Fig 2). Our third hypothesis was that climate change drivers would explain changes in biomass, growth, and mortality in low elevation counties, but not in mid elevation counties. We found that sea level rise and number of storms can impact growth, mortality, and changes in biomass in both low and mid elevation counties (Fig 5). In low elevation counties, greater rates of sea level rise were negatively correlated with growth (Fig 6). However, the direction of the relationships between climate change drivers and biomass change was sometimes opposite to what we expected. For example, in both low and mid elevation counties the

number of storms was positively correlated with annualized growth (Fig 6), suggesting that forests respond to more frequent disturbances with increased biomass growth, which aligns with forest biometrical growth principles (e.g., mean versus annual increment [35]). To our knowledge, this study is the first to use repeated, on-the-ground surveys (FIA) to provide evidence that sea level rise rates and storms can impact the biomass accumulation, growth, and mortality of coastal plain forests over a large area. Overall, our results suggest that coastal forests are vulnerable to climate change drivers, with climate change potentially already altering the structure of forests on the Eastern shores of the US.

Forest area change

Our findings of forest area gain in both low and mid elevation counties contrast with recent papers that have reported loss of forests along the eastern coast of the US [4, 13, 21]. Most of these studies have been based on remote sensing, which measures land cover change. Our study uses the FIA data, which measures forest land use. As a result, FIA data might count areas as forest when trees are relatively small following a disturbance, such as a harvest, which would not be classified as forest using remote sensing approaches. For example, White et al. [13] found that a large portion of forested wetlands were transformed to scrub-shrub vegetation (53.3%), and thus were no longer classified as forests. Based on the height and elevation of those scrub-shrub vegetation, those could have still been considered as forests in the FIA methodology. Recently abandoned agricultural land could also be considered forests in the FIA methodology but missed using remote sensing. Agricultural land abandonment is one of the main ways that forests have recovered in the southeastern US [36]. The higher forest gain observed in the low elevation counties compared to mid elevation counties could be due to increased flooding and saltwater intrusion leading to agricultural land abandonment [37]. Agricultural land abandonment due to increased flooding and saltwater intrusion could lead to increased forest area in the near term, with forest losses in the long-term due to sea level rise [12].

Live tree biomass change

In terms of size classes of live trees, mid elevation counties had higher biomass in both small and larger size classes (Fig 3, Table 2). Mid elevation counties tended to gain more biomass in larger size classes (50–60 and 60+ cm, Fig 3). This increase in larger size classes could explain the fact that even though low elevation counties gained more forest area (1.9% vs 0.3%), the gain in biomass was very similar between elevation classes (Fig 2). The lack of increases in larger diameter size classes (>50 cm), could be due to low elevation counties experiencing more frequent disturbances, such as wind events from hurricanes, or increased flooding, which lead to losses of older and larger trees [38]. Frequent disturbances lead to thinning of forests and canopy mortality [39]. Studies all along the East coast of the US have reported higher disturbance and more tree mortality in low elevation forests [9, 11, 19, 21, 40]. Despite this research, we still don't have a good understanding of changes in size structure of remaining trees, and changes in stocks of dead wood (both standing and downed) in response to disturbances.

Harvest rates were higher in mid elevation than in low elevation counties (Fig 2C), suggesting that harvests were not driving the increased mortality in low elevation counties. Harvest rates were positively correlated to annualized growth and number of storms in both low and mid elevation areas (Fig 5). It makes sense that areas with more growth were also areas where more trees were harvested. The positive relationship with number of storms could be due to harvesting after storms. Wood harvesting has been shown to lead to younger forests [41]. Our

results agree with this, with mid elevation forests having slightly more of the biomass (35–37%) in the smaller size classes ($>30\text{cm}$), than low elevation forests (31–33%). However, frequent disturbances can also lead to younger forests, making it challenging to separate the effects of harvest from natural disturbances. As soils become wetter, it becomes more challenging to harvest forests, as has been seen in northern forests due to lack of snowpack [42]. More frequent flooding due to sea level rise and storms could lead to less harvesting of coastal forests.

Dead wood dynamics

Despite much research on the changes in the spatial extent of coastal forests [12], changes in the stocks of dead wood have not received as much attention in coastal forests. Our results build on previous analyses of large-scale changes in dead wood. In the Eastern US, small increases in dead wood (standing and downed (0.02 and 0.11 Mg ha^{-1})) were reported over a 5-year period using the US FIA plot network, as used here [30]. Similarly another study using the same data, over the conterminous US with a time period of about 10 years, also found increases in live tree biomass (3.8%), standing dead (14.7%), and downed dead (18.3%, 0.22 Mg ha^{-1} , [33]). In contrast, we found losses of SD in both low (9.2% , $0.05 \pm 0.09\text{ Mg ha}^{-1}$) and mid (2.8% , $0.01 \pm 0.04\text{ Mg ha}^{-1}$) elevation counties. In terms of DD, we found losses in low elevation (22%) and gains (39%) in mid elevation counties. The period covered here (Table 1) was slightly longer than the time period covered by Woodall et al. [33] (which ended in 2019). They also considered a much larger area (conterminous US), so it is not surprising results differ. However, they did report increases in DD in the East coast and Gulf coast, which agrees with our results, potentially due to disturbances such as hurricanes. Hurricanes can lead to tree mortality [39], which can cause shifts from live trees to dead biomass. We found a positive correlation between the number of storms and increase in DD in low elevation counties (Fig 6). On the other hand, changes in temperature and flooding frequency can alter the decomposition of dead wood (both standing and downed) [17, 43]. We found negative correlations between SD change and average temperature and change in temperature in mid elevation counties (Fig 5), illustrating the complex interactions between drivers and changes in stocks, and the challenges to disentangle the different factors driving dead wood dynamics over space and time [30, 33].

The increase in DD in the larger size class for both elevation classes (Fig 3) was mostly driven by one county in each elevation (Saint John the Baptist and Ouachita, both in Louisiana). The largest change in DD between sampling intervals occurred in Ouachita Parish, LA, a mid-elevation county which gained 105 Mg/ha and had a ratio of DD to live trees of 6.04. The second largest change in DD occurred in Saint John the Baptist Parish, which gained 40.9 Mg ha^{-1} and had a ratio of DD to live trees of 2.5. Given the location of both parishes and the timing of plot measurements, these increases in DD could have been caused by Hurricane Isaac (2012), Harvey (2017), or other major storms that hit the region during the study period. Given the large interval between sampling periods, it is challenging to link changes in structure to specific disturbances. As stronger storms become more common, pulse events of DD might become more common, which make it challenging to model and assess [43].

Changes in the decay classes of dead wood can also provide insights into how these systems are responding to disturbances. We observed higher losses of the most decayed classes of SD in the low elevation counties, compared to the mid elevation counties (Fig 4). These losses of more decomposed SD wood could be due to disturbances causing the falling of SD, which could then lead to increases in DD. DD can accelerate the decomposition of other dead wood [44], thus higher disturbances and lower SD pools can lead to more vulnerable pools of C.

Episodic increases in DD changes the structure of forests for decades to centuries, referred to as ecological memory [45]. It is important to understand the fate of dead wood, both standing and downed, because the decomposition of that C will lead to release of C to the atmosphere [30]. Understanding the fate of that dead C in coastal forests is still not as complete as in upland forests. For example, numerous studies have reported release of CO₂ from downed wood [43, 46] and standing dead wood [44] in upland forests. To our knowledge, only a few studies have examined CO₂ emissions from SD in coastal forests [47, 48].

The ratio of SD and DD to live tree biomass has been proposed as a way to examine downed dead wood dynamics [33]. While we did not find significant differences in those ratios between low and mid elevation counties, regions with different ratio values might provide insights into disturbances. Research in Georgia and South Carolina that has followed forests along the Waccamaw and Savannah rivers has documented increases in the SD/live tree ratio, from 0.007 in a healthy forest to 0.46 in a forest experiencing saltwater intrusion (Krauss et al. 2018). Similarly, the DD ratio increased from 0.006 in a healthy forest to 0.40 in a salt degraded forest (Krauss et al. 2018). We hypothesize that forests with higher SD/live tree ratios might be experiencing more chronic stressors (such as increased flooding and salinity), while forests with higher DD/live tree ratios might have recently experienced episodic stressors (such as hurricanes or other storms). In low elevation forests, DD biomass increased more in areas that experienced more storms (Fig 6). Future research should further examine SD and DD dynamics in coastal forests.

Climate change drivers

Our results suggest that climate change drivers can impact the growth, mortality, and biomass accumulation of low and mid elevation forests. Previous studies have found that low elevation forests are more vulnerable to flooding, storms, and saltwater intrusion [21, 49, 50]. Chen and Kirwan (2022) reported that forests surrounding Chesapeake Bay lower than 5m elevation experienced loss of biomass due to sea level rise and flooding, while forests in elevations higher than 5m gained C due to higher temperatures and precipitation. We found that sea level rise was negatively correlated with growth in low elevation counties, with areas with sea level rise rates lower than 4 mm yr⁻¹ having double the growth of areas with the higher rates of SLR (8 mm yr⁻¹, Fig 6). Surprisingly, growth was positively correlated to number of storms in both low and mid elevation forests (Fig 5). This might be due to storms increasing successional change and releasing species from competition. As different climate change factors can have both positive and negative effects on different parts of coastal landscapes, it is important to go beyond single location and ecosystem studies to understand the overall effect on landscape C dynamics. We found that sea level rise rates can decrease growth of coastal forests across the eastern shore of the US, suggesting that rates of sea level rise should be incorporated into management of coastal forests. Recent increases in rates of sea level rise for the southeastern US [31] indicate that these effects are likely to become exacerbated.

Carbon balance

When summed across our study region, our results suggest that forests can play an important part in the C balance of coastal ecosystems. For example, over our study period low elevation forests gained 21.8 Tg C and mid elevation counties gained 39.5 Tg C. A recent study combined remote sensing and on the ground soil C measurements to estimate the amount of C lost from coastal marshes in the period 2000–2019 globally [51]. They estimated that the US lost 9.54 (range 1.5 to 30.5) Tg C due to salt marsh soil loss to increased flooding and storms. Our results suggest that forest tree growth can compensate for the loss of marsh soil C, and

that more frequent storms can stimulate growth in coastal forests (Fig 5). Storms are known to lead to marsh erosion [52], suggesting that climate change drivers can have contrasting effects on different components of the coastal landscape [20, 24, 50]. Moreover, our results suggest that the changes in pools of SD and DD (range 0.48 to 9.1 Tg C) are on the same order of magnitude as marsh soil C loss, even though changes to SD and DD pools have not received nearly as much attention as marsh soil loss due to sea level rise. Understanding the drivers of SD and DD will be important to manage this important C store in the face of climate change and sea level rise.

Study limitations

Our results must be taken with caution, as they are documenting only about a decade of change. It is a decade that has experienced some of the highest rates of sea level rise [31] and very severe storms, but changes in forests are slow [33]. While the FIA data are very valuable, due to standardized techniques within a national statistical design, the low frequency of sampling (every 5–7 years) makes it challenging to examine the impacts of individual disturbance events. We also only use the two most recent survey periods (to account for more standardized dead wood sampling methods), which make it challenging to capture the non-linear dynamics of forest change [41]; however, the expected future resampling of these sites will further empower change detection especially if aligned with less latent remotely sensed observations.

Conclusions

An examination of forest change, both structurally and by carbon pools, across coastal areas of the southeastern US subject to inundation events and hurricanes indicate complex changes that may accelerate as climate change and associated social responses such as land use change continue. We found that live tree biomass may be increasing, but with declines in stocks of standing dead and downed dead wood. These changes to dead wood stocks and sensitivity of growth and mortality estimates highlight that these forests are vulnerable to climate change drivers and sea level rise which may require integration of national monitoring programs (e.g., FIA), remotely sensed observations, and site intensive studies to adequately estimate how this population of “forest sentinels” to change are evolving.

Supporting information

S1 Text. Fig A. Map of change between sampling intervals in live biomass (Mg/ha) for low and mid elevation (crossed) counties derived from the FIA. Vector shapefiles were retrieved from the U.S. Census Bureau (<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>) and ESRI (<http://www.ArcGIS.com>). The map was created using ESRI Arc GIS Pro 3.2.0. Fig B. Map of change between sampling intervals in standing dead biomass (Mg/ha) for low and mid elevation (crossed) counties derived from the FIA. Vector shapefiles were retrieved from the U.S. Census Bureau (<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>) and ESRI (<http://www.ArcGIS.com>). The map was created using ESRI Arc GIS Pro 3.2.0. Fig C. Map of change between sampling intervals in downed dead biomass (Mg/ha) for low and mid elevation (crossed) counties derived from the FIA. Vector shapefiles were retrieved from the U.S. Census Bureau (<https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>) and ESRI (<http://www.ArcGIS.com>). The map was created using ESRI Arc GIS Pro 3.2.0. Table A. List of NOAA sea level gauges along with climatic variables. Table B. Kruskal Wallis results (X^2 and p value) of comparisons between mid and low elevation counties for live, standing dead (SD), downed dead (DD) biomass across size classes and decay classes. Size classes are in cm, decay classes

from 1 (least decayed) to 5 (most decayed). Bold number denotes $p < 0.1$. Table C. Kruskal Wallis results (X^2 and p value) of comparisons between mid and low elevation counties for annualized mortality, growth, and harvest rates. Bold numbers denote $p < 0.1$. (DOCX)

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