


Climate Change Driving Widespread Loss of Coastal Forested Wetlands Throughout the North American Coastal Plain

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ABSTRACT

Coastal forested wetlands support many endemic species, sequester substantial carbon stocks, and have been reduced in extent due to historic drainage and agricultural expansion. Many of these unique coastal ecosystems have been drained, while those that remain are now threatened by saltwater intrusion and sea level rise in hydrologically modified coastal landscapes. Several recent studies have documented rapid and accelerating losses of coastal forested wetlands in small areas of the Atlantic and Gulf coasts of North America, but the full extent of loss across North America's Coastal Plain (NACP) has not been quantified. We used classified satellite imagery to document a net loss of $\sim 13,682 \text{ km}^2$ (8%) of forested coastal wetlands across the NACP between 1996 and 2016. Most forests transitioned to scrub-shrub (53%) and marsh habitats (24%). Even within protected areas,

we measured substantial rates of wetland deforestation and significant fragmentation of forested wetland habitats. Variation in the rate of sea level rise, the number of tropical storm landings, and the average elevation of coastal watersheds explained about 78% of the variation in coastal wetland deforestation extent along the South Atlantic and Gulf Coasts. The rate of coastal forest loss within the NACP ($684 \text{ km}^2/\text{y}$) exceeds the recent estimate of global losses of coastal mangroves ($210 \text{ km}^2/\text{y}$). At the current rate of deforestation, in the absence of widespread protection or restoration efforts, coastal forested wetlands may not persist into the next century.

Key words: Saltwater Intrusion; Sea Level Rise; Coastal Forested Wetlands; Remote Sensing; Climate Change; Land Cover/Land Use Change.

HIGHLIGHTS

- From 1996 to 2016 $\sim 19,480 \text{ km}^2$ of coastal wetlands were deforested in the North American Coastal Plain.
- 77% of these deforested wetlands are now classified as freshwater scrub-shrub or marsh habitats.

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- Sea level rise, tropical storm landings, and topography explain 78% of variation in deforestation.
- Those forested wetland patches that remain are significantly smaller and more fragmented.
- The current rate of loss threatens the future viability of these unique wetland forest ecosystems.

INTRODUCTION

The forested swamps, bogs, and pocosins distributed throughout the Southeastern Atlantic and Gulf coasts of the United States are both prevalent and iconic landscape features that support a unique assemblage of species and provide substantial ecosystem services. These freshwater wetlands are typically dominated by bald cypress and eastern red cedar (*Taxodium distichum*, *Juniperus virginiana*; Brinson and others 1980; Conner and others 1997; Krauss and others 2015) that provide critical habitat to a large number of endemic and endangered species (Coulter and others 1987; Kautz and others 2006; Noss and others 2015). In addition to habitat provisioning, coastal forested wetlands remove excess nutrients, attenuate storm surges, and sequester large amounts of carbon (Engle 2011; Blair and others 2012), a collection of ecosystem services that have been valued at US\$1.5 T y⁻¹ globally (Costanza and others 2014). Further, many indigenous peoples and other communities have longstanding connections to coastal geographies, sometimes spanning centuries or millennia (for example, Bartram and Harper 1943; Martinich and others 2013; Hardy and others 2017; Emanuel 2018), that are being threatened by the present-day loss of these unique coastal forested wetland ecosystems.

Despite their value, the majority of freshwater forested wetlands in North America were deforested and drained between 1780 and 1980. Across the USA, an estimated 53% of wetland habitats were lost, primarily through conversion to agricultural uses (Dahl and Al 1990). These wetland losses were concentrated in coastal watersheds and were most severe for forested freshwater wetlands (Office of Technology Assessment 1984). Recognition of the value of these wetlands and their alarming rate of loss led Congress to pass the Emergency Coastal Wetlands Resources Act of 1986, which brought regulatory action and enabled conservation efforts (Breux 1986).

Unfortunately, while regulations slowed the rate of intentional wetland drainage and deforestation, these valuable ecosystems are now jeopardized by

climate change along the coasts. Rising sea levels, more frequent flooding, more intense hurricanes, more sustained droughts, and increasing salinization of coastal ground and surface waters all threaten the continued existence of trees adapted to life in flooded, but not saline conditions (Tully and others 2019). The current rate of global mean sea level rise (SLR) of 2.8–3.2 mm y⁻¹ (Church and White 2011) already outpaces rates of surface elevation change across many coastal forested wetlands (1.3–5 mm y⁻¹; Doyle and others 2007; Craft 2012, Grieger and others 2020), and the rate of change is expected to accelerate (Nerem and others 2018). The impacts of increasingly frequent and widespread flooding associated with both SLR (Sweet and others 2020) and hurricanes (Knutson and others 2010; Mendelsohn and others 2012; Donnelly and others 2015) are not confined to coastal margins but are propagating upstream through both natural and artificial drainage networks (Bhattachan and others 2018; Tully and others 2019). Without flood-defense structures, a 1-m increase in relative sea level is expected to convert 12,000–49,000 km² of dry land to intertidal land in the conterminous United States alone (Haer and others 2013). This would significantly affect the hydrologic and salinity regimes of coastal forested wetlands situated further inland.

The combined effects of saltwater intrusion and sea level rise (SWISLR) have significant negative effects on both the structure and function of forested wetlands (Williams and others 1999; Middleton and Souter 2016; Grieger and others 2020; Smart and others 2020; Ury and others 2020), with persistent stress from soil salinization and increasing inundation leading to forest mortality and a long-term shift in vegetation (Brinson and others 1995). Increasingly common reports of ‘ghost forests’ in both the scientific literature and the popular press have captured public attention, yet assessments of coastal forested wetland losses due to climate drivers are thus far limited to only a few locations in North America (Figure 1; Kirwan and Gedan 2019; Schieder and Kirwan 2019; Smart and others 2020; Ury and others 2020; White and Kaplan 2021). A national assessment of the modern extent of coastal forested wetlands and their rate of loss is urgently needed given current climate trends.

Here we use an analysis of remote sensing data collected by the National Oceanic and Atmospheric Administration (NOAA) Coastal Change Analysis Program (C-CAP; National Oceanic and Atmospheric Administration 2020) to make the first assessment of coastal forested wetland extent, rates

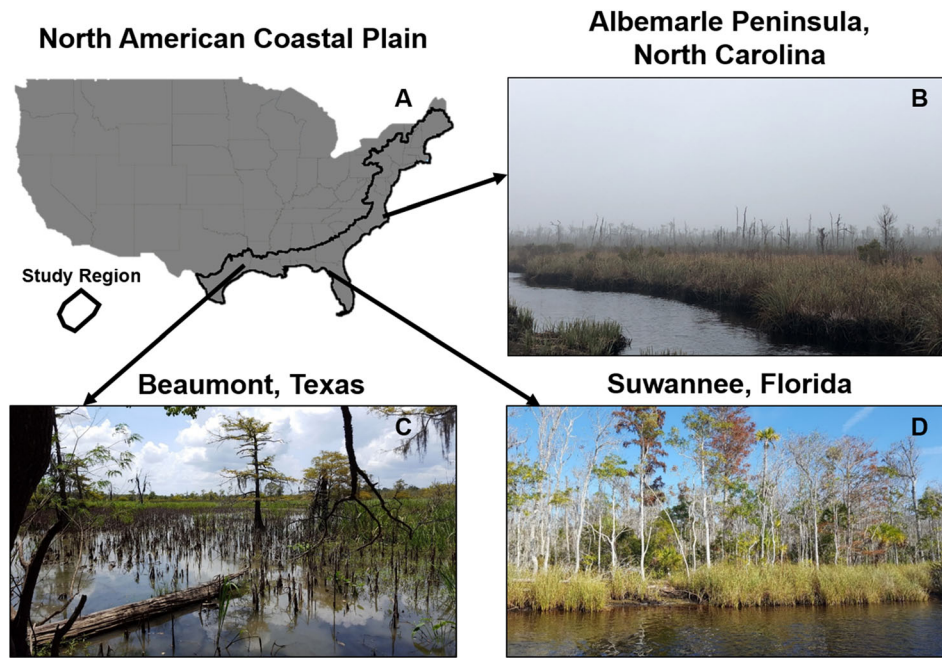


Figure 1. Coastal forested wetlands in highly degraded conditions can be found across the North American Coastal Plain (A), which is our study region. The above examples are all on protected lands, which include the Alligator River National Wildlife Refuge (B), Big Thicket National Park and Preserve (C), and the Lower Suwannee River National Wildlife Refuge (D). (Photo Credit: top right E. Bernhardt, bottom left and right E. White Jr.).

of loss, and fate throughout the entire North American Coastal Plain (NACP) from 1996 to 2016. We leveraged existing long-term datasets and remote sensing products to answer the following questions: (1) What is the current extent of coastal forested wetlands?, (2) Where are the hotspots of coastal forested wetland loss over the last two decades?, (3) How are coastal forested wetlands changing in protected areas? and (4) How is the composition and structure of coastal forested wetland vegetation changing? We were particularly interested in assessing the extent to which coastal forested wetland losses were the result of recent climate change drivers rather than intentional drainage and deforestation. We predicted that if climate drivers are the root cause of forested wetland loss across the coastal plain: (1) the rates of forested wetland loss would be highest in areas of the NACP with the highest rates of local SLR and hurricane landfalls; (2) Most forested wetland loss would be through conversion to coastal shrublands or marsh rather than to agricultural fields or development; and (3) coastal wetlands that remain forested, will have more fragmented canopies due to the spatially heterogeneous effects of SWISLR.

METHODS

Study Region

We chose the North American Coastal Plain, a large geologic region (1.13 million km²) stretching from Massachusetts, USA to Northern Mexico, as our study region. It is recognized as a global biodiversity hotspot (Noss and others 2015), which has been significantly affected by anthropogenic stressors. Across this large coastal region, we have access to consistently derived landcover data available through the NOAA C-CAP dataset. However, despite it being a hotspot there are few studies that seek to understand ecological change across the entire region. In addition, we can use the wealth of long-term data available for the area for a region-wide synthesis. To aid our region-wide analysis, we drew on our previous ground-level knowledge at specific sites in Texas, Louisiana, Florida, and North Carolina and general experience from across the region. We subdivided the NACP into the northern Gulf of Mexico (nGOM), Atlantic Coastal Plain (ACP), and the 51 hydrologic subregions (four-digit hydrologic unit code, HUC). Note that all HUCs in Maine, New Hampshire, and Vermont were included in the ACP and HUC 0309 (Southern Florida) was included in the nGOM due to the location of most of the forest.

Data Sources

Remote Sensing

C-CAP: We used data generated by the NOAA C-CAP to determine the extent of coastal forested wetland in the NACP. Map boundaries, as defined by C-CAP, were based on the Coastal Zone Management (CZM) boundaries, NOAA's Coastal Assessment Framework, and the designation of coastal counties. Additional modification of the extent were made using Omernik EcoRegions, visible natural features, and Landsat imagery path/row boundaries (National Oceanic and Atmospheric Administration 2020). The C-CAP project uses images from Landsat to classify and map the extent of 25 different land cover features throughout the US coastal zone every five years from 1996 to 2016. Images are classified using a mixture of unsupervised/supervised classification, spatial modeling, and manual edits (Jin and others 2019). The product is scaled at the same spatial resolution of Landsat imagery, which is 30 m. The smallest possible feature (minimum mapping unit) that C-CAP could classify would be 30×30 m pixel. However, it is noted that a 60×60 m area, which are four contiguous pixels, would likely be the scale that can be most reliably identified (National Oceanic and Atmospheric Administration 2020). C-CAP seeks to achieve 85% overall accuracy and single class accuracy of 80%. The most recent accuracy assessment occurred for the 2010 data, in which they achieved an 84% overall accuracy (0.83 kappa value), and no class had less than 80% produce and user accuracy (McCombs and others 2016). The C-CAP classification scheme distinguishes six classes of wetlands, based on pre-existing descriptions of wetland classification (Cowardin and others 1979), of which we used their palustrine forested wetland class as our coastal forested wetlands class. The most recent accuracy assessment showed 87.3% and 85.9% user and producer accuracy, respectively, for this class. In the C-CAP Regional Land Cover Classification scheme, palustrine forested wetlands (coastal forested wetland) are defined as tidal and non-tidal wetlands dominated by woody vegetation greater than or equal to 5 m in height, and all such wetlands that occur in tidal areas in which salinity due to ocean-derived salts is below 0.5 percent, with total vegetation coverage is greater than 20 percent.

Landsat: Additional landscape classification was completed using Landsat 5, 7, and 8 imagery. These data were used to address the questions regarding

general change on protected land and fragmentation in the Neuse-Pamlico and Roanoke-Chowan subregions. A more detailed explanation can be found in Ury and others (2021).

Elevation: Elevation data were obtained from the 30-m Shuttle Radar Topography Mission (SRTM) dataset provided by NASA to Google Earth Engine (GEE). Average elevation and slope were calculated for each subregion in the dataset.

Tropical Storm Landfalls

Tropical storm occurrences in each subregion were gathered from the NOAA National Hurricane Center (NHC) Atlantic hurricane catalog in GEE. The dataset was filtered to only capture storms that overlapped with our region of interest between 1996 and 2016. Hurricane occurrence within each subregion was based on the location of the eye. The output from this analysis is a dataframe that includes the name, HUC number, and number of hurricanes that passed through each subregion.

Sea Level Rise Trends

SLR trends were gathered from the NOAA tides and currents website (NOAA 2020). Gages were selected based on their proximity and relevance to each subregion. For each gage, the relative sea level trend was used as the rate of SLR. For subregions with multiple relevant gages, the SLR rate used is an average of SLR trends.

Drainage Density

Drainage network data were only calculated for the 14 subregions with 1996 coastal forested wetland area greater than 5000 km^2 . HUC 4 level drainage maps were downloaded from the National Hydrography Database (NHD, U.S. Geological Survey 2020). The following was done in R using the packages *rgdal* and *rgeos* (Bivand and others 2020,2021). 'gArea()' was used to calculate the area of the catchment. 'Flowlines' was used to determine total drainage length in the catchment. We combined the NHD classes of flowlines into artificial (558, artificial path; 336, canal/ditch), coastline (566), natural (460, river/stream), and other (334, connector; 428, pipeline; 420, underground conduit). The sum of each subset was calculated. Drainage density was calculated as the total length of drainage features (artificial, natural, and other) divided by the total area of the subregion.

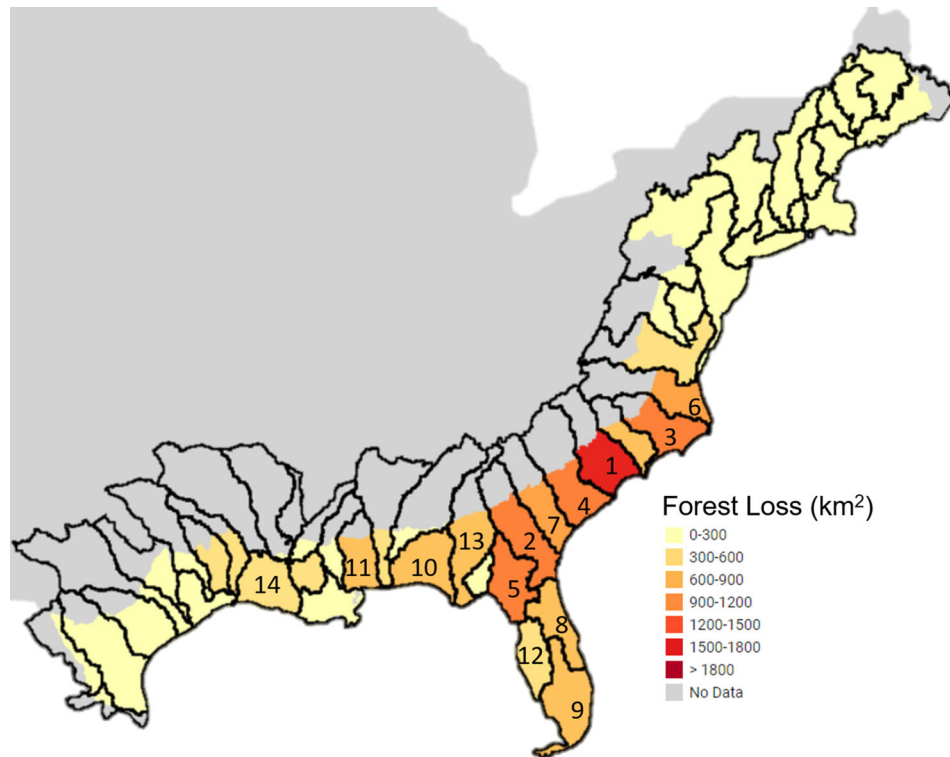


Figure 2. The area of coastal forested wetlands deforested within every hydrologic subregion (4-digit HUC codes) across the North American Coastal Plain is shown above. Subregions with forested coastal wetland area greater than 5000 km² in 1996 were ranked based on cumulative loss from 1996 to 2016, which is indicated by the number within a subregion (on the map and Table 1). Observed losses are concentrated in the Southeastern US (Louisiana to North Carolina). Subregions West of Louisiana and North of the Delmarva Peninsula had relatively few losses.

Landscape Change Analysis

Quantifying Areal and Rates of Loss

To address questions 1 and 2, we used C-CAP land cover images for years 1996 and 2016. These images were used to generate two different sets of products: a change image and a dataframe of coastal forested wetland areal coverage. A binary change image (0, no change; 1, change) for coastal forested wetlands was created using the 1996 and 2016 image. The change image was cropped to the HUC 4 level boundary in GEE so that only the subregions where data occur were retained. From the HUC 4 level change image, five metrics were generated for each HUC: total area of coastal forested wetland in 1996, area of coastal forested wetland loss, gain, and net change from 1996 to 2016, and percent change from 1996 to 2016. A dataframe was created that lists the following: HUC Geographic Names Information System (GNIS) name, HUC Number, Area of Change, Total Coastal Forested Wetland Area, and Percent Change. The dataframe was exported to R (rjson package; Couture-Beil 2018) for further analysis. We then cre-

ated a second image based on the total area changed within each HUC. That image was then discretized to visualize subregion level changes, which can be seen in Figure 2.

Modeling Drivers of Change

We used a generalized linear model (Stagg and others 2017; Taillie and others 2019a; Matos and others 2020; “glm”, stats package, R Development Core Team 2019) to analyse the predictive power of our hypothesized climate drivers and basin topography in explaining variation in the rates of coastal forested wetland area loss. The terms in the model were additive with no interaction between terms. Net forest area change was the response variable, with the rate of sea level rise, drainage density, number of tropical storms, average elevation, and average slope as potential predictor variables (SM Table 1). The coefficient of determination (R^2) was determined using the “rsq” function (rsq package; Zhang 2020). The best fit model was found using the “step” function (stats package) with forwards and backwards predictor variable removal (direction = “both”), which minimizes Akaike’s Infor-

Table 1. Change in Coastal Forested Wetland (CFW) Areal Coverage From 1996 to 2016.

Region/Subregion (HUC)	1996 CFW Area (km ²)	Area Lost (km ²)	Area Gain (km ²)	Net Change (km ²)	Net Change (%)
North American Coastal Plain	172,147	19,480	5796	13,682	8
Atlantic Coastal Plain	95,788	11,624	2760	8863	9
Northern Gulf of Mexico	76,359	7856	3036	4819	6
1 Pee Dee (0304)	10,370	1935	293	1642	16
2 Altamaha-St. Mary's (0307)	9304	1477	355	1122	12
3 Neuse-Pamlico (0302)	6120	1372	270	1102	18
4 Edisto-Santee (0305)	7934	1309	250	1059	13
5 Suwannee (0311)	10,010	1389	462	927	9
6 Chowan-Roanoke (0301)	6834	936	154	782	11
7 Ogeechee-Savannah (0306)	5893	915	160	755	13
8 St. John's (0308)	6129	861	233	628	10
9 Southern Florida (0309)	7005	854	333	521	7
10 Choctawhatchee-Escambia (0314)	8005	785	289	496	6
11 Pascagoula (0317)	5856	751	306	445	8
12 Peace-Tampa Bay (0310)	5308	574	185	389	7
13 Apalachicola (0313)	7093	677	305	372	5
14 Louisiana Coastal (0808)	7896	469	239	230	3
Total for 14 Subregions	103,757	14,304	3834	10,470	10

The table is ordered by the Area Lost column

mation Criterion (AIC; Akaike 1974) value. We also calculated the AICc (Akaike's Information Criterion-Corrected; Burnham and Anderson 2002), which corrects for small sample sizes (and too many parameters that may cause overfitting), using the "AICc" function (MuMIn package; Barton' 2020). The model only used data from the fourteen subregions that had greater than 5000 km² coastal forested wetland area in 1996.

Protected Area Classification

We used these data to address question 3, which seeks to understand how changes occurring in protected areas compare to their local setting. Critically, the area classified has been well studied by the authors, thus allowing for more detailed explanations of the observations. Classification of land cover for the North Carolina protected areas in the Chowan-Roanoke (0301) and Neuse-Pamlico (0302) subregions was conducted using the classification schema from Ury and others (2021). Their classification scheme has six land cover types, which include pine, deciduous, shrub, marsh, and ghost forest, which was developed using a random forest decision tree classifier trained by ground truthed analysis of imagery collected from Landsat (5, 7, and 8) and very high-resolution airborne images. This approach had a land use classification

overall accuracy is 86%. Additional details can be found in Ury and others (2021).

Landscape Fragmentation

Question 4 was addressed using landscape fragmentation analysis. We chose the Chowan-Roanoke (0301) and Neuse-Pamlico (0302) subregions and Palmetto-Peartree Preserve, which is a protected area in the Neuse-Pamlico subregion, to understand fragmentation. These areas were chosen because they were recently classified and analyzed by Ury and others (2021). Additionally, Palmetto-Peartree Preserve's status as a protected area ensures that the observed changes are not due to direct human intervention. This allows us to compare changes and understand potential drivers based on the difference, if any, between the local protected and unprotected lands. The classified rasters for 1996 and 2017 were imported into ArcGIS Pro (version 2.4) and reprojected from WGS 84 to NAD 1983 UTM Zone 18 N. The forest pixels were extracted, and we used "Region Group" to give each pixel a unique ID for later steps. Finally, forest patches were assessed for area and perimeter using "Zonal Geometry as Table". In R, we calculated the total numbers of patches for each year and generated the perimeter to area ratio (P:A) statistic. For each year, we calculated the mean, median,

and max patch perimeter, area, and P:A. The Kolmogorov–Smirnov and Mann–Whitney U tests (stats package; R Development Core Team 2019) were used to determine statistical difference between the two time periods. This process was repeated for the area within the Palmetto-Peartree Preserve boundaries.

RESULTS

Net Loss of Coastal Forested Wetland area and Rates of Change

Based on satellite image analysis, we quantified a loss of ~ 19,480 km² of coastal forested wetlands to other habitat types in the NACP between 1996 and 2016, representing an 11% reduction of the 172,147 km² of coastal forested wetlands present in 1996 (Table 1). Over the same period, conservation efforts and natural recovery led to the conversion

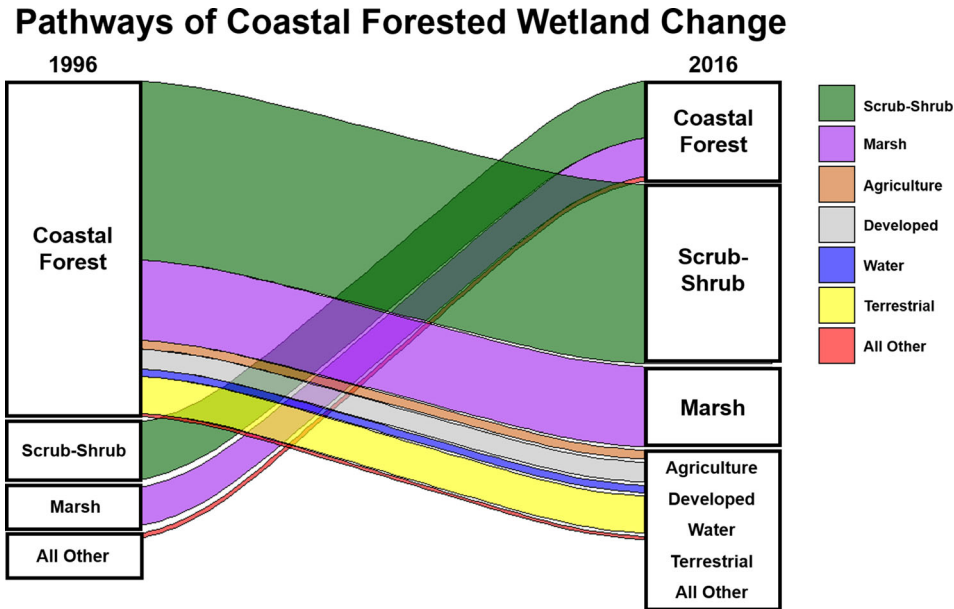


Figure 3. The alluvial diagram shows the transition to and from coastal forested wetlands from 1996 to 2016 for all subregions in the North American Coastal Plain. Freshwater scrub-shrub and marsh represent the primary pathways to (57 and 39%, respectively) and from (53 and 24%, respectively) the coastal forest. Other pathways make relatively minor contributions to either the gain or losses (Table 2).

Table 2. Land Cover/land Use Change Frequencies for Coastal Forested Wetlands Between 1996 and 2016.

Cover Class in 1996	Cover Class in 2016	Percent (%)
Loss		
Coastal Forested Wetland	Freshwater Scrub-Shrub	53.3
	Freshwater Marsh	23.9
	Agriculture	2.6
	Developed	5.9
	Water	2.2
	Terrestrial	11.1
	Unvegetated	0.9
	Other Wetlands	< 0.1
Gain		
Freshwater Scrub-Shrub	Coastal Forested Wetland	56.7
	Freshwater Marsh	38.5
	All Other	4.8

of 5,799 km² from other land cover types to coastal forested wetlands for the entire NACP, with the ACP and nGOM contributing 2760 and 3036 km², respectively. Accounting for both the gains and losses, the NACP experienced a net decline of 13,682 km² (~ 8%) in total forested wetland area. Similarly, the ACP and nGOM experienced net declines of 8863 km² (~ 9%) and 4819 km² (~ 6%), respectively. A disproportionately high fraction of coastal forested wetland loss occurred within 14 subregions, which each had greater than 5000 km² forested coastal wetland in 1996 (Figure 2). Though they contained 60% of all coastal forested wetlands in the entire NACP in 1996, those 14 subregions accounted for 77% of total losses. Within these subregions between 3 and 18% of all coastal forested wetlands detected in 1996 were permanently deforested by 2016.

The predominant ecosystem state change that we measured across the entire NACP in the period 1996–2016, was a shift from forested to scrub-shrub and herbaceous wetlands (Figure 3, Table 2). Most coastal forested wetlands were converted to low stature, freshwater scrub-shrub habitats (53%), or freshwater marsh (24%). In contrast to historic drivers of coastal forested wetland loss, agricultural conversion accounted for only about 3% of the total coastal forested wetland losses observed since 1996. Direct losses to inundation by sea level rise and increased inland flooding were a minor pathway, which accounted for only about 2% of coastal forested wetlands converting to open water. Of the areas that converted to coastal forested wetland by 2016, freshwater scrub-shrub (57%) and marsh (39%) were the largest contributors. Reclamation from agricultural development (0.6%) was a minor component of the total re-growth of forested wetlands.

Drivers of Change

Over three-fourths (adjusted $R^2 = 0.78$) of the variation in forest loss for the 14 subregions are driven by the rates of sea level rise, drainage density, storms incidences, slope, and elevation. In the full model, we found that the subregion drainage density and number of tropical storm impacts were significant predictors of forest loss (SM Table 2). Through model selection, the AICc score was reduced from 26.29 to 17.91. The reduced model explained a marginally greater proportion of variation (adjusted $R^2 = 0.80$), without elevation as a predictor. Another round of model selection starting with the reduced model did not produce a better model. Model performance, as visualized in

Figure 4, was similar for all sites with the number on plot corresponding to the ordering on Table 1.

To further examine the hypothesis that climate change is the primary driver of recent deforestation, we measured the rates of loss within protected, unmanaged coastal protected areas and compared them to those estimated for the subregion that they are nested within. The extent of coastal forested wetlands within protected areas of the Neuse-Pamlico (#3 on Table 1) and Chowan-Roanoke (#6 on Table 1) were 1421 km² and 1988 km², respectively. Coastal forested wetlands in protected areas lost 13.6% of their forest area between 1996 and 2017. Forest within the Neuse-Pamlico and Roanoke-Chowan protected areas declined at 1.3% and 0.4% per annum, respectively (Figure 5). The loss rates within protected areas are similar to rates estimated for all coastal forested wetlands within the subregions each are embedded within (− 1.1% and -0.7% per annum, respectively) and are similar in magnitude of loss rate estimated for the entire NACP (0.6% per annum).

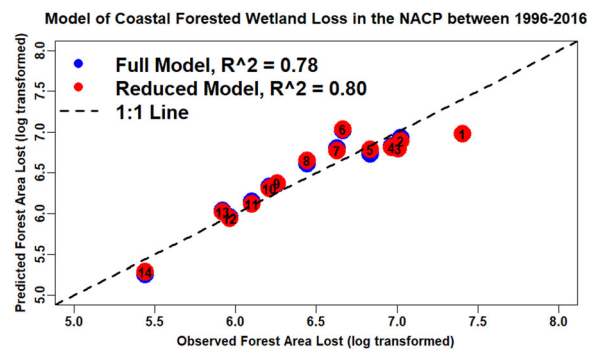


Figure 4. Generalized linear models were developed to understand the relationship between forest drivers of change and total coastal forested wetland (CFW) area loss. Only subregions with 1996 CFW area greater than 5000 km² were used in the model. The potential predictor variables used for each model were the relative rate of sea level rise, the number of storm incidences, landscape slope and elevation, and drainage density for each subregion. The Full Model contains all five predictor variables. Elevation was dropped as a predictor variable, based on model fitting and selection using AIC scores, which resulted in the Reduced Model. Both models explained a large, and similar, portion of variation (adj. $R^2 = 0.78$, and 0.80) within the data. Additional rounds of model fitting and selection did not produce a better model.

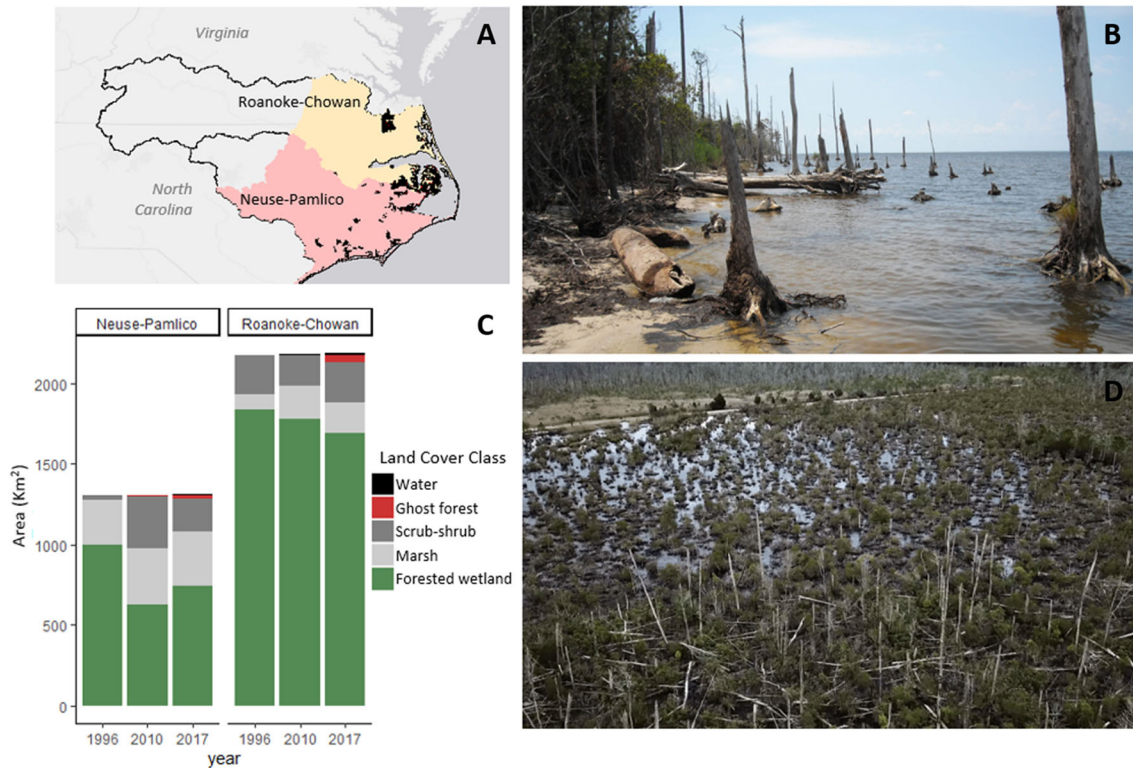


Figure 5. Protected lands (**A**; shown in black in the inset) of the Roanoke-Chowan and Neuse-Pamlico coastal plain subregions are both experiencing rates of coastal forested wetland decline that are consistent with rates at larger scales. From 1996 to 2017, forests in protected areas of the Neuse-Pamlico and Roanoke-Chowan subregions (**C**) were most likely to transition to scrub-shrub or marsh habitat (**D**). Transitions into open water are far less common (**B**). (Photo Credit: top right M. Ardon, bottom right L. Groskin).

Fragmentation of Remaining Coastal Forested Wetlands

When looking at the protected areas in the Neuse-Pamlico and Chowan-Roanoke subregions from 1996–2017, we found that the remaining areas of coastal forested wetland have become more fragmented, and the largest forest patches are shrinking. The number of forest patches increased from 3605 to 5580 and the increase in the total number of patches led to a significant decline in the median (MWU $p < 0.05$; Figure 6, Table 3) perimeter and area across the subregions, as well as their distributions (KS $p < 0.05$). The mean, median, and maximum P:A ratio increased between 1996–2017. Additionally, the sign and magnitude difference between the mean and median P:A ratio became more strongly negative (0.96 to -10.99), which correlates with the increase in small patches. The largest patch size decreased from 388 km² to 373 km² (– 4%) between the two periods and the number of forest patches over 25 km² decreasing from 18 to 14. The area held by these patches de-

creased from 1840 km² to 1460 km² (– 26%) from 1996 to 2017. Palmetto-Peartree Preserve, a protected area of land in the Neuse-Pamlico subregion, experienced similar amounts of fragmentation (Table 4). The increase in P:A can be seen in Figure 7 with the none uniform loss patterns across the landscape. Importantly, the total number of patches increased by almost five-fold (32 to 148).

DISCUSSION

Between 1996 and 2016, 13,682 km² of the coastal forested wetlands in the North American Coastal Plain were deforested. As we anticipated, the rates of coastal wetland forest loss were highest for subregions with more frequent tropical storms, higher rates of sea level rise, and lower average surface elevations. As we predicted, forested wetlands were primarily lost via conversion to scrub-shrub or freshwater marsh rather than conversion to agricultural or urban development. We documented substantial forested wetland loss and fragmentation within protected areas in two study

watersheds over the period of record. Each of these findings is consistent with our prediction that climate drivers are the root cause of recent coastal forested wetland loss across the coastal plain.

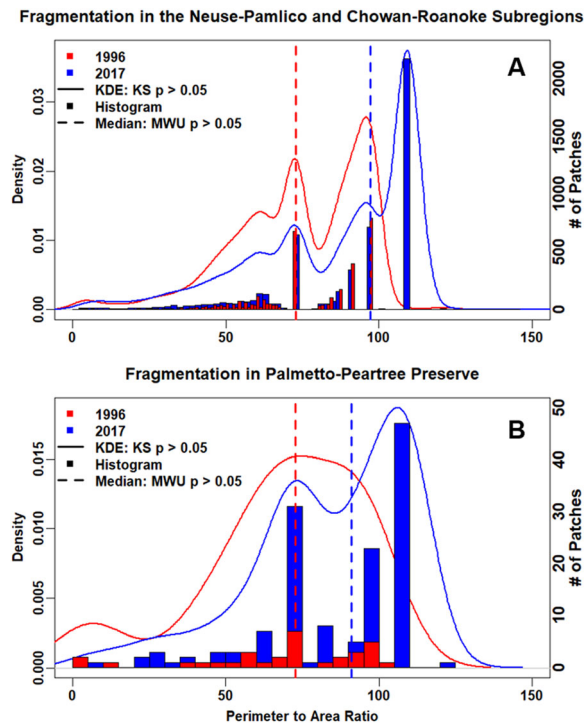


Figure 6. Forest fragmentation has increased within the Neuse-Pamlico and Roanoke-Chowan subregions from 1996 to 2017 (A). The number of patches has increased over time, which has led to a significant increase in the perimeter to area ratio have increased during this period. Interestingly, the same patterns of change can be seen when only looking at Palmetto-Peartree Preserve, which is a protected area in the Neuse-Pamlico subregion (B). The similarity in results indicate the driver of change is likely not due to direct human intervention on the landscape.

The State of Coastal Forested Wetlands

Our estimates of both coastal forested wetland extent and loss are far higher than reported by the most recent U.S. National Wetlands Status Report (Stedman and Dahl 2008; Dahl and Stedman 2013). They report an estimated total coastal forested wetland area of only about 63,000 km² (37% of our 1996 estimate) and a loss of only 1800 km² between 2004 and 2009 (360 km²/y), whereas we estimate an annual loss rate of 684 km² annually (Dahl and Stedman 2013). In contrast to our approach, the US Fish and Wildlife Service’s (FWS) national assessment of coastal wetlands is a plot-based study, with estimates scaled up from repeated image analysis of 2614 plots of 10.4 km² (accounting for only 0.01% of the total land area of the NACP). The difficulty of scaling plot level assessments of land cover and land use change to a landscape scale makes this broader, remotely sensed-based approach more comprehensive (Marceau and Hay 1999).

In addition to coming to quite different conclusions about both the extent and the magnitude of the threats to coastal forested wetlands, our analysis also comes to different conclusions about the strongest driver of coastal forested wetland loss in the NACP. Analysis based on the FWS dataset have estimated that conversion to plantation forestry as a dominant driver of coastal forested wetland loss in North America (Lang and others 2020), while we see little evidence in support of this conclusion from our full coverage analysis. There are similar rates of coastal forested wetland loss across the entire Southeastern coastal plain despite differences in timber production. Additionally, the rates of coastal forested wetland loss within protected, unmanaged areas are similar to loss rates detected for the region as a whole. Each of these pieces of evidence strongly support a mechanism other than direct intervention (for example, logging or inten-

Table 3. Patch Statistics for the Neuse-Pamlico (0302) and Chowan-Roanoke (0301) Subregions.

Year, Metric	Mean (\pm sd)	Median (\pm mad)	Max
1996: n = 3,605 patches			
Perimeter (km)	2.75 \pm 33.44	0.33 \pm 0.16*	1303.4
Area (km ²)	0.64 \pm 10.42	0.005 \pm 0.003*	387.84
P:A Ratio	73.8 \pm 21.3	72.84 \pm 27*	127.47
2017: n = 5,580 patches			
Perimeter (km)	2.12 \pm 30.31	0.22 \pm 0.08	1546
Area (km ²)	0.35 \pm 7.6	0.002 \pm 0.001	373.13
P:A Ratio	86.13 \pm 26	97.12 \pm 18	145.67

sd standard deviation, mad median absolute deviation, P:A perimeter to area. (*) denotes a significant difference ($p < 0.05$) between 1996 and 2017 using the Mann–Whitney U test.

Table 4. Patch Statistics for the Palmetto-Peartree Preserve.

Year, Metric	Mean (\pm sd)	Median (\pm mad)	Max
1996 n = 32 patches			
Perimeter (km)	15.82 \pm 59.98	0.36 \pm 0.2*	280
Area (km ²)	4.11 \pm 17.09	0.004 \pm 0.002*	89
P:A Ratio	68.69 \pm 23.66	72.84 \pm 25.86*	102
2017 n = 148 patches			
Perimeter (km)	5.93 \pm 47.83	0.22 \pm 0.08	469
Area (km ²)	0.89 \pm 8.37	0.003 \pm 0.002	97
P:A Ratio	84.29 \pm 25.54	91.05 \pm 27	121

sd standard deviation, *mad* median absolute deviation, *P:A* perimeter to area.

(*) denotes a significant difference ($p < 0.05$) between 1996 and 2017 using the Mann-Whitney U test.

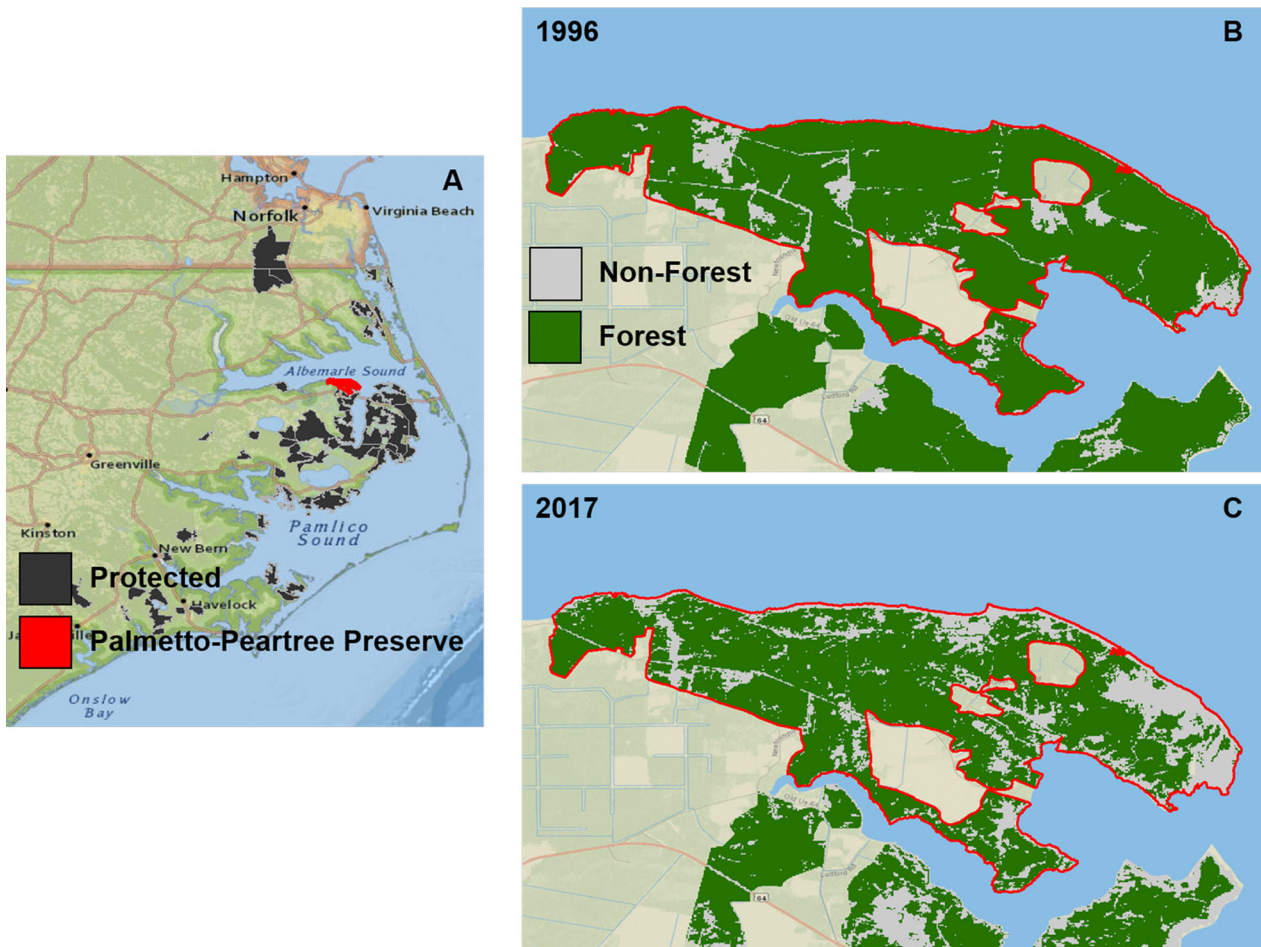


Figure 7. Coastal forested wetlands patches in Palmetto-Peartree Preserve, North Carolina (**a**; outlined in red) have become more fragmented between 1996 (**b**) and 2017 (**c**). Although deforestation due occur in areas closest to saline bodies of water, it can be observed that there is also deforestation occurring in more entire regions of the protected area. This deforestation is associated with anthropogenic hydrologic features, which can facilitate the quickening of saline water into entire areas. The result is increased fragmentation as patches are broken into smaller parts.

tional hydrologic alteration) as a primary driver of coastal forested wetland loss.

Understanding the Drivers of Forest Loss

The climatic and topographic drivers of forest loss used in our model, which are well understood in the literature, explained a large proportion of the variation in deforestation. Across both models, the drainage density and number of tropical storms that impacted a subregion were the only significant predictors. Coastal forested wetlands are populated by species that can tolerate temporary high winds, flooding, and saltwater intrusion associated with tropical storms (Conner 1994). However, successive storms may have an additive, ratcheting effect that leads to more deforestation (Fagherazzi and others 2019). There is strong evidence that climate change driven increases in sea surfaces temperatures are leading to the increase in Atlantic hurricane activity since 1995, our data start in 1996 (Goldenberg and others 2001; Mann and Emanuel 2006; Saunders and Lea 2008). We were surprised by the negative coefficient for drainage density (-0.31), however it is likely driven by data from two subregions (Apalachicola, 0313 and Louisiana Coastal, 0808). These two subregions had the least amount of forest lost, but substantially higher drainage densities (SM Table 1). There is strong literature support for increased connectivity to saline waterbodies as a driver of inland, freshwater habitat salinization (Herbert and others 2015; Bhattachan and others 2018). Additionally, the rate of local SLR, average elevation, and average also drive or contribute to increases in coastal forested wetland deforestation (Doyle and others 2007; Strauss and others 2012; White and Kaplan 2017), though they were not significant in either of our models.

Long-term Fate of Coastal Forested Wetlands

The forest loss and conversion patterns that we document are consistent with recent field-based studies of coastal forested wetland losses due to climate change drivers (Schieder and Kirwan 2019; Ury and others 2020). Concerning the transition to scrub-shrub habitat, there is no consensus on whether this is a new, self-sustaining habitat, or a transitional habitat that leads to freshwater marsh. The scrub-shrub habitat can be a mixture of immature canopy species (for example, *Taxodium distichum*, *Juniperus virginiana*, and *Nyssa* spp.) that have varying salinity tolerances, encroaching species (for example, *Sabal palmetto* and *Myrica cerifera*) that are more salt tolerant, or unhealthy and

stunted individuals of the canopy species. The transition to freshwater marsh has been theorized (Brinson and others 1995) and supported in the literature in places such as the Florida Gulf Coast, Georgia, and the Delmarva Peninsula (Williams and others 1999; Craft and others 2009; Fagherazzi and others 2019). Although our dataset does not allow us to ascertain whether the conversion of forested coastal wetlands to shrublands results from direct management or climate change for the entire area of NACP, the widespread and parallel trends across the entire NACP are consistent with the hypothesis that coastal climate change is driving this rapid deforestation of coastal wetlands. Draining and land clearance for agriculture were the primary drivers of deforestation historically (Okey 1918; Norgress 1947), but only account for less than 3% of all forest loss in our study period. Although there was recovery of 37 km² of forest from agricultural land, these forests are less mature. Thus, they likely won't offer the same capacity for ecosystem services and will likely be less resilient to future drivers of change (Sutherland and others 2016; Jonsson and others 2019).

Dangers of a Fragmented Landscape

In addition to the negative consequences of reduced habitat area and connectivity, "edge-effect" theory posits that habitat edges are more vulnerable to change (Benítez-Malvido and Arroyo-Rodríguez 2008). We documented an increase in perimeter to area ratio for forest within and outside of protected areas from 1996 to 2017. As the extensive, contiguous coastal forested wetlands are altered into disconnected patches of forested wetland in a matrix of low stature shrub/scrub or marsh, the trees that remain may become more susceptible to subsequent hurricane and drought disturbances (Haddad and others 2015; Ehlers Smith and others 2018). The now fragmented forest landscape will provide a smaller proportion of ecosystem services compared to a similar sized area that is still intact (Ferraz and others 2014). The decrease in forest area and increase in fragmentation will have a negative impact on regional biodiversity (Liu and others 2019; Taillie and others 2019b). For example, the Florida panther and wood stork, which are endangered and threatened, respectively, may be in greater jeopardy with these continued changes (Coulter and others 1987; Kautz and others 2006).

Replacing the Irreplaceable

Our analyses suggest that accelerating climate change is further reducing the spatial extent of an already threatened, floristically unique and biodiverse coastal habitat throughout the North American Coastal Plain (Noss and others 2015). If the rate of coastal forested wetland decline observed here continues, coastal forested wetlands will be drowned and salted out of existence throughout the NACP within 100 years. When we consider that the rate of SLR now has accelerated relative to the period of study 1996–2016 (Sallenger and others 2012), this point of no return may arrive within the century. The loss of coastal forested wetlands will lead to a reduction or disappearance of ecosystem services, which include carbon sequestration and habitat provisioning. Carbon sequestration is an important ecosystem service provided by coastal forested wetlands. It is estimated that the loss of carbon held by coastal forest will take 130 to 760 to be replaced during the climate change driven forest to marsh transgression (Smith and Kirwan 2021). Critically, the transition of coastal forested wetlands to ghost forests in the North American Coastal Plain contributes to about a 4 Tg C y^{-1} decline in aboveground biomass, which is 2% (200 Tg C y^{-1}) of what is released by all forests in North America (Williams and others 2016; Smart and others 2020). However, the contributing area of forested coastal wetlands is 0.62% of North American forest, resulting in about a $3 \times$ greater loss per unit area. The release of carbon dioxide from the decomposition of dead trees may limit the ability of coastal ecosystems to counteract rising atmospheric CO_2 levels (Edwards and others 2019; Smart and others 2020). A global remote sensing-based study found that coastal mangrove coverage declined by 3363 km^2 from 2000 to 2016, with anthropogenic drivers being the largest cause of their decline (Goldberg and others 2020). Comparatively, the NACP alone has seen almost four times as much deforestation as mangroves globally over a similar period. Beyond the ecosystem effects and potential global reverberations that losing these forests may have, there is also a direct effect on the peoples that have significant cultural connections to them (de Oliveira; Emanuel 2018). The climate driven deforestation of coastal forested wetlands must now be added to other better publicized issues for coastal regions, as losses are on par or exceed rates of salt marsh and mangrove loss (Craft and others 2009; Goldberg and others 2020).

Our efforts to understand climate driven deforestation coastal forested wetlands have added a

critical spatiotemporal component that was needed to understand region-wide changes. While the current analysis was restricted to the North American coastal plain, we know that coastal forested wetlands are critically important ecosystems across the globe. Despite their inclusion among critically protected ecosystems listed as Ramsar sites, there is no scientific literature reporting the current status of CFWs within Brazil's Baixada Maranhense Environmental Protection Area, the Ukraine's Kyliiske Mouth, or Mozambique's Zambezi Delta. It is reasonable to expect that these and other coastal forested wetlands are similarly threatened by climate change driven increases in sea levels and freshwater salinization, which ultimately leaves their survivability threatened. However, coastal forested wetlands are not studied in the same capacity around the world as they are in the US. The scale and magnitude of our work, documenting change across a $1.13 \text{ million km}^2$ region of North America, were only possible because of the well-produced maps and consideration of coastal forested wetlands as a unique habitat of interest by NOAA C-CAP. Efforts to expand these analyses globally are badly needed to assess the global vulnerability of these diverse and carbon rich ecosystems.

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DATA AVAILABILITY

URL links to data repositories and code are available at: <https://github.com/ElliottWhiteJr/C-CAP>

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