Decadal-Scale Vegetation Change Driven by Salinity at Leading Edge of Rising Sea Level

Paul J. Taillie,[1]* Christopher E. Moorman,[1] Benjamin Poulter,[2] Marcelo Ardón,[1] and Ryan E. Emanuel[1]

[1]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina 27695, USA; [2]Biospheric Sciences Laboratory, NASA Goddard Space Flight Center, Greenbelt, Maryland 20771, USA

ABSTRACT

As sea levels rise, low-lying coastal forests increasingly are subject to stressors such as inundation and saltwater exposure. At long timescales (for example, centuries), the extent of inundation and saltwater exposure will increase; however, on a decadal timescale, the role of these drivers may differ in both magnitude and direction. To investigate the drivers of decadal-scale vegetation change, we measured the changes in five metrics of vegetation composition and structure between 2003/2004 and 2016/2017 at 98 plots distributed across a vegetation gradient from coastal forest to brackish marshes (< 0.5–18 ppt). We used elevation as a proxy of inundation vulnerability and soil sodium concentration as a proxy of saltwater exposure, and we investigated relationships between these two variables and the change in vegetation conditions between the two sampling periods. Soil sodium concentration was a significant predictor of vegetation change for all five vegetation metrics, whereas the effect of elevation was not significant for any of the metrics. The one site that was affected by wildfire twice during the duration of the study shifted almost completely from forest to marsh with limited regeneration of woody vegetation observed in 2016/2017. Our results show that salinization in our system is a more important driver of vegetation change than inundation potential. Furthermore, the effects of drought-induced salinization could be amplified by the elevated risk of wildfire during droughts. Forecasting the response of coastal wetlands to rising sea levels will require a better understanding of the individual and combined effects of salinity, droughts, and wildfires on vegetation.

Key words: coastal forest; drought; inundation; marsh migration; salinization; wildfire.

HIGHLIGHTS

- Vegetation change depended on exposure to soil salt, but not elevation.
- Vegetation changes across the forest-marsh gradient reflected marsh migration.
- Wildfire exacerbated the transition from forest to marsh conditions.

INTRODUCTION

As sea level rises, inundation and saltwater exposure have become increasingly important stressors in coastal ecosystems. The landward reach of inundation and saltwater intrusion events has increased, thus increasing the total areal extent of land affected during these events (Poulter and Halpin 2008; Nicholls and Cazenave 2010; Church and others 2013). Because of varying tolerance to inundation and saltwater exposure among plant species, these stressors can cause dramatic changes in vegetation structure and composition (Williams and others 1999; Osland and others 2016). Though inundation and saltwater intrusion can be closely related, for example, occurring simultaneously during a storm, they also may vary independently across space and time (Mulholland and others 1997; Stanturf and others 2007; Herbert and others 2015).

At long timescales (for example, centuries) where global sea level is forecast to rise by a meter or more, chronic inundation and saltwater exposure will increase in both spatial extent and severity. But in addition to chronic inundation and saltwater exposure, discrete severe weather events can have lasting effects on the composition and structure of coastal forests (Williams and others 2003; Krauss and others 2007; Anderson and others 2013; Gabler and others 2017). At decadal timescales, acute inundation and salinization events are driven by a number of factors including precipitation, winds, tides, and coastal geomorphology (Day and others 2007; Manda and others 2014; Herbert and others 2015). In addition to rising sea levels, severe weather events are likely to become more frequent and more severe as a result of anthropogenic climate change (Michener and others 1997; Mulholland and others 1997; Woodruff and others 2013). Therefore, understanding decadal-scale vegetation change will require more specifically considering macroclimatic drivers of vegetation change in addition to rising sea level (Osland and others 2016).

When coastal waters are pushed landward by winds or tides, inundation and salinization may occur simultaneously and thus is difficult to disentangle. In contrast, acute events associated with precipitation may have different effects on each of these stressors. Specifically, high rates of precipitation will increase the likelihood of inundation, but may decrease the likelihood of salinization (Woodruff and others 2013; Herbert and others 2015). Freshwater inputs to estuarine environments increase as rainwater infiltrates and accumulates in the subsurface, raising local water tables, and creating hydraulic gradients that shift the freshwater/saltwater interface downstream (Sklar and Browder 1998). Additionally, saltwater over-wash associated with storm surge is less likely to infiltrate into soils that are already saturated by precipitation (Gardner and others 1991). In contrast, drought conditions can facilitate salinization when both the water table and flooding risk are low (Ardón and others 2013). With reduced freshwater inputs to estuaries, the freshwater/saltwater interface may shift landward, facilitating salinization of previously freshwater environments (Herbert and others 2015). As such, changes in precipitation patterns and the frequency and severity of droughts may have important implications for coastal vegetation dynamics (Desantis and others 2007).

Though competition and facilitation have been shown to influence plant species composition in coastal vegetation communities, inundation frequency, and salinity tolerance are the primary drivers of the broader transition from forest to marsh in temperate coastal environments (Pezeshki and others 1990; Ross and others 1994; Williams and others 1999; Pennings and others 2005; Poulter and others 2009). Coastal marsh plants, such as *Spartina alterniflora* and *Juncus romerianus*, can tolerate daily inundation and much higher salinity levels than most trees (Pennings and others 2005; Poulter and others 2008). However, even among woody species, there exists variation in inundation and salinity tolerance (Krauss and others 2007; Desantis and others 2007; Poulter and others 2008). Because inundation and salinity tolerance vary both among plant species and among age classes within a species, changes in forest structure and composition from severe weather events may be realized long before a complete transition to marsh (Williams and others 1999; Field and others 2016).

The implications for vegetation change associated with rising sea level are further complicated by the potential interaction with other forms of disturbance (Myers and Van Lear 1998; Dale and others 2001; Stanturf and others 2007). Storms and fires historically played an important role in shaping coastal forests, but the vulnerability to disturbance may vary over both space and time (Michener and others 1997; Myers and Van Lear 1998; Stanturf and others 2007). For example, as with salinization events, the risk of severe wildfire increases markedly during drought (Frost 1995; Dale and others 2001). In forests maintained by severe, stand-replacing fires, many tree species have evolved

mechanisms to regenerate quickly (Frost 1995). However, salinization could limit post-fire regeneration by preventing seed germination, decreasing seedling survival, and favoring the establishment of more salt-tolerant species (Williams and others 2003; Poulter and others 2008, 2009). As such, salinization may shift the successional pathway following severe disturbance from a regenerative process toward a more permanent transition to marsh (Brinson and others 1995). This interaction between wildfire and salinization could have drastically different implications for coastal vegetation dynamics compared to those associated with inundation.

Previous work has shown that salinity, in both surface water and soil, is a stronger driver of vegetation change than inundation in tidal, herbaceous marshes (Pennings and others 2005; Desantis and others 2007). However, the relative roles of these stressors is less well understood in microtidal systems at the leading edge of rising seas, where forests are less influenced by tidal flooding. In a 4-year study conducted at a microtidal site in western Florida, Williams and others (1999) showed that salinity was more important than inundation to *Sabal palmetto* mortality, but broader vegetation responses are less well understood. We built on these findings by measuring changes in vegetation over a period of 12 years across a gradient of soil salt concentration and elevation at five microtidal sites in eastern North Carolina, a region extremely vulnerable to rising sea level (Hauer and others 2016). Our objectives were to: (1) quantify changes in vegetation composition and structure over a 12-year period; (2) quantify changes in saltwater exposure over the same time frame; (3) compare the relative roles of inundation and saltwater exposure in driving vegetation change; and (4) evaluate the role of other disturbances, namely fire, in driving vegetation change. As sea level continues to rise, potentially at an increasing rate, our relatively long-term results from one of the most vulnerable regions in North America to rising sea level will serve as a model of vegetation change to be expected at other low-lying coastal regions.

METHODS

Study Area

The Albemarle-Pamlico Peninsula (APP) is bounded by the Albemarle Sound to the north, the Croatan Sound to the east, and the Pamlico Sound to the south. Along with the Neuse River Estuary, these water bodies form the second-largest estuary complex in North America. The barrier island geomorphology of the region results in limited influence of astronomic tides (Moorhead and Brinson 1995). Instead, water movement is driven primarily by multi-day wind tides (Manda and others 2014). In combination with low tidal amplitudes, the region is characterized by low sediment loads (Voss and others 2013). The limited number of inlets between barrier islands connecting the sounds to the ocean creates a gradient in salinity from the moderate salinity (10–18 ppt) Pamlico Sound to the largely freshwater (< 5 ppt) Albemarle Sound (Buzzelli and others 2003).

Site Selection

In 2003, we identified five public properties (hereafter referred to as ''sites'') adjacent to the shore of the Albemarle-Pamlico Peninsula: Palmetto-Peartree Preserve, the Mashoes Road section of Alligator River National Wildlife Refuge, the Long Shoal River section of Alligator River National Wildlife Refuge, Gull Rock State Game Land, and Swanquarter National Wildlife Refuge. At each site, 12-m-radius plots were established across the gradient from forest to marsh to serve as experimental units. To distribute the plots evenly across the forest-marsh interface, we used a combination of aerial imagery and qualitative visual assessment to delineate three adjacent vegetation community types in 2003: forest, transition, and marsh. The delineated communities ranged in size from 1.97 to 22.9 ha. The forest community type was defined by living pine trees (*Pinus* spp.), whereas marsh was largely treeless and was dominated by herbaceous vegetation, such as *Juncus romerianus* or *Cladium jamaicense*. The transition community type also was comprised mostly of herbaceous plants, but also had characteristics that indicated the area was recently forested, such as salt-tolerant shrubs (*Myrica* spp. and *Baccharis halimifolia*), standing dead trees, and some persisting live trees. The Palmetto-Peartree Preserve site did not have marsh, so only forest and transition types were delineated at this site. Within each community type at each site, we established seven 12-m-radius plots, for a total of 98 vegetation plots (Figure 1). All plots were within 1.25 km of the APP shoreline.

Over the course of the study, the five sites varied in terms of disturbance history and soil type. The soils at both Palmetto-Peartree Preserve and Swanquarter consisted of mineral-based soils, whereas the other three sites had primarily organic soils (Poulter 2005). Palmetto-Peartree Preserve experienced substantial mechanical removal of
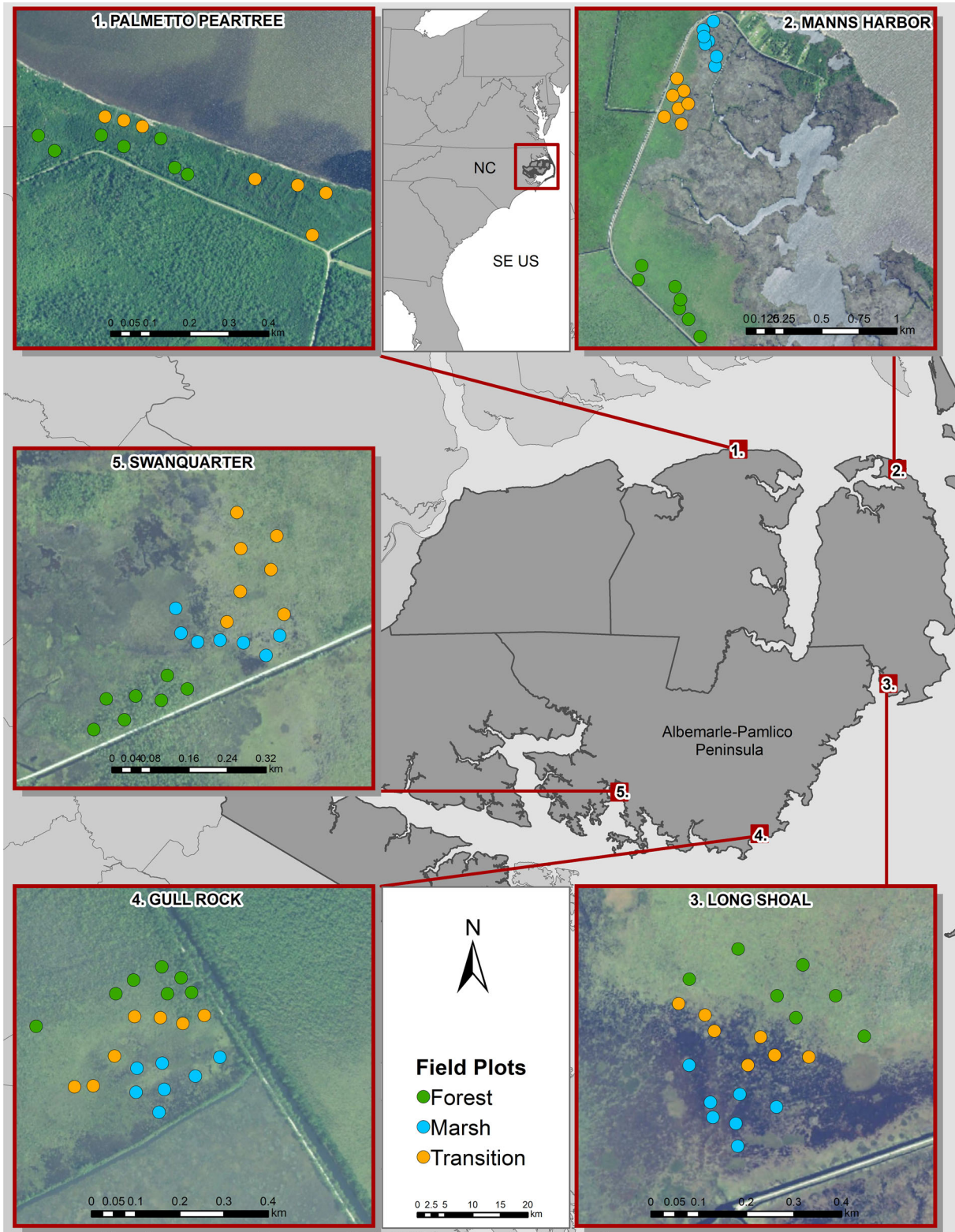
Figure 1. Map of study sites with inset maps of each to show the locations of vegetation plots in each of three vegetation community types (forest, transition, and marsh) in eastern North Carolina, USA.

trees preceding the first sample period to control an outbreak of southern pine beetle (*Dendroctonus frontalis*), and the distinction between forest and transition was determined primarily by the harvest intensity. Specifically, the canopy was completely removed in the transition plots, whereas individual trees and snags were removed in the forest plots, leaving a mostly intact canopy (Poulter 2005). The Mashoes Road site burned in a wildfire shortly after the 2004 sampling, but only two of the forest plots were affected and no mortality of pond pine was observed following the fire (Poulter 2005). The Long Shoal site burned in a large wildfire in 2011, and again 1 month prior to sampling vegetation in 2016. The Swanquarter transition plots burned in the years prior to this study, but not during the duration of the study. Gull Rock had no history of fire since 2000, when reliable monitoring of fire began (Poulter 2005).

Elevation

We used elevation as a proxy for inundation vulnerability. To calculate elevation, we used a LiDAR-derived 3-m-by-3-m resolution, bare earth digital elevation model. Multiple return LiDAR data were collected in 2014 by the State of North Carolina as part of its statewide floodplain mapping program (http://www.ncfloodmaps.com/lidar.htm). These data were collected during leaf-off season, had a nominal post spacing of 0.7 m, a point density of 2.0/m², a vertical accuracy (RMSEz) of 0.12 m, and were categorized according to ground/non-ground. To generate a smoothed elevation surface, we extracted the ground points and applied a regularized spline with tension interpolation followed by a spline smoothing algorithm to remove noise (Mitasova and others 2009). We checked for systematic errors in the LiDAR data by comparing the derived DEM along stable features and geodetic benchmarks in open areas gathered from the National Geodetic Survey and determined minimal difference between the derived elevation surface and the NGS benchmarks (mean = 0.23 m). Within each 12-m plot, we extracted the elevation at six randomly selected locations spaced at least 4 m apart, and averaged these values to get an average bare earth elevation for each plot.

We acknowledge that hydrological connectivity and other factors may also influence inundation vulnerability. In an attempt to explain variation in vegetation change related to these processes, we also investigated the distance to the shoreline as a predictor of vegetation change. However, preliminary analysis revealed that this variable was not significant for any of the five vegetation metrics and thus did not explain any additional variation in vegetation change.

Soil Cation Concentration

To quantify saltwater exposure, we collected soil from the center of each vegetation plot in February of both 2004 and 2017. We first cleared undecomposed organic matter from the soil surface, and then collected at least 30 g of soil from the top 20 cm using a small shovel. In both sampling periods, samples were sent to Brookside Labs in New Bremen, OH to be analyzed using a Mehlich III extraction. We used base cation concentrations as metrics of previous saltwater exposure. Preliminary analysis revealed a high degree of correlation between cations, so we report results for sodium only. Although soil was collected only once during each sampling period and salinity can vary within a given year, comparison with monthly groundwater sampling in 2004 suggested that the soil measurements were representative of annual salinity levels (Poulter 2005).

Vegetation

From November to February of 2003/2004 (that is, first sampling period), and May to June of 2016/2017 (that is, second sampling period), we inventoried all woody plants within the 12-m vegetation plots. For every woody stem with a diameter at breast height (DBH) greater than 2.5 cm, we measured the DBH, estimated the height, recorded the species, and recorded whether the stem was alive or dead. For individual plants that branched below breast height, we considered each branch that was greater than 2.5 cm DBH a separate stem.

To quantify herbaceous vegetation, we established five 1-m² subplots within the larger vegetation plot. We placed a 1-m² PVC quadrat 10 m from the plot center in each of the cardinal directions, and 2 m from the plot center in the north direction. The percent cover of vegetation less than 1 m tall within the quadrat was recorded for all plant species, as well as dead plant material and unvegetated ground. Unvegetated open water was lumped with bare ground as unvegetated ground.

We summarized vegetation observations into five characteristics of vegetation structure and composition: tree density, snag density, sapling density, shrub density, and herbaceous cover. Snags were defined as any standing dead woody stem greater than 2.5 cm DBH and greater than 1.3 m tall. Shrubs were defined as all live stems of species that typically do not exceed heights of about

Table 1. Parameter Estimates, Standard Errors, and *p* Values for the Effects of Soil Sodium Concentration and Elevation on the Change in Five Metrics of Vegetation Composition and Structure Between 2003/2004 and 2016/2017 at 98 Vegetation Plots in Eastern North Carolina, USA

	Soil sodium concentration			Elevation		
	Estimate	SE	Pr($>$ |*t*|)	Estimate	SE	Pr($>$ |*t*|)
Trees	− 0.29	0.12	0.02	0.13	0.12	0.26
Saplings	− 2.62	1.02	0.01	0.02	1.02	0.99
Snags	− 0.69	0.33	0.04	− 0.56	0.33	0.10
Shrubs	− 2.26	0.89	0.02	− 1.11	0.89	0.23
Grass	− 8.16	3.96	0.04	5.37	3.96	0.18

5 m (for example, *Baccharis hamifolia*, *Ilex* spp., *Lyonia* spp., *Myrica* spp.). Trees and saplings included all non-shrub woody species and were classified as saplings if DBH was less than 20 cm and trees if DBH was at least 20 cm. Herbaceous cover at each plot was calculated by combining the percent cover of the four dominant marsh plants: *Juncus romerianus*, *Cladium jamaicense*, *Schoenoplectus* spp., and *Spartina patens*, then averaging across the five subplots within each of the larger vegetation plots. Although sampling during different seasons between the two sampling periods could influence herbaceous cover, these differences would be minimal for the four species of marsh plants that comprise the metric of herbaceous cover. Because the Long Shoal site burned in a wildfire 1 month prior to vegetation sampling in 2016, substantially reducing herbaceous cover, we resampled the herbaceous cover in May 2017 and used the 2017 observations only. Despite this difference from the other sites, we still refer to these observations as the second sampling period. At all sites, the other four vegetation structure and composition metrics were calculated from measurements in 2016 only.

Analysis

We first standardized both elevation and soil sodium concentration by subtracting the mean and dividing by the standard deviation. Because we expected that lower elevation sites were more vulnerable to saltwater intrusion, we tested for correlation between soil sodium concentration and elevation in either sampling period by calculating the Pearson's Correlation Coefficient using the *cor* function in the stats package of program R version 3.5.1 (R Core Team 2018). We investigated differences in soil sodium concentrations among sites and between the two sampling periods using a two-way analysis of variance (ANOVA). Sampling period and site were treated as categorical variables with two and five levels, respectively. We also evaluated the effect of the interaction between site and sampling period.

We modeled the relationships between elevation and soil sodium concentration on vegetation change using the *glm* function in R. We fit a separate model for each of the five metrics of vegetation composition described previously, and used the change in a given metric between the two sampling periods as the response variable. Specifically, for the four metrics of woody vegetation density, we calculated the proportional change by subtracting the second sampling period value from the first sampling period value, then dividing that difference by the first sampling period value. As such, the minimum value of vegetation change for these density metrics was − 1. For each metric, we omitted all plots for which the change in the given metric was 0. Because grass cover was measured as a percent, we calculated the change in grass cover as simply the difference in percent cover between the two sampling periods. We included the standardized values of elevation and the soil sodium concentration (averaged between the two sampling periods) as dependent variables. We also investigated an interaction between these predictors; however, in order to conserve statistical power, we did not include these interactions in the results reported below because the effect was not significant for any of the vegetation metrics.

RESULTS

We observed vegetation change was more strongly related to soil sodium concentration than elevation. The effect of soil sodium concentration was significant for all vegetation metrics (Table 1). These effects were negative for all vegetation metrics, reflecting that vegetation density was more likely to decrease at sites with greater concentrations of
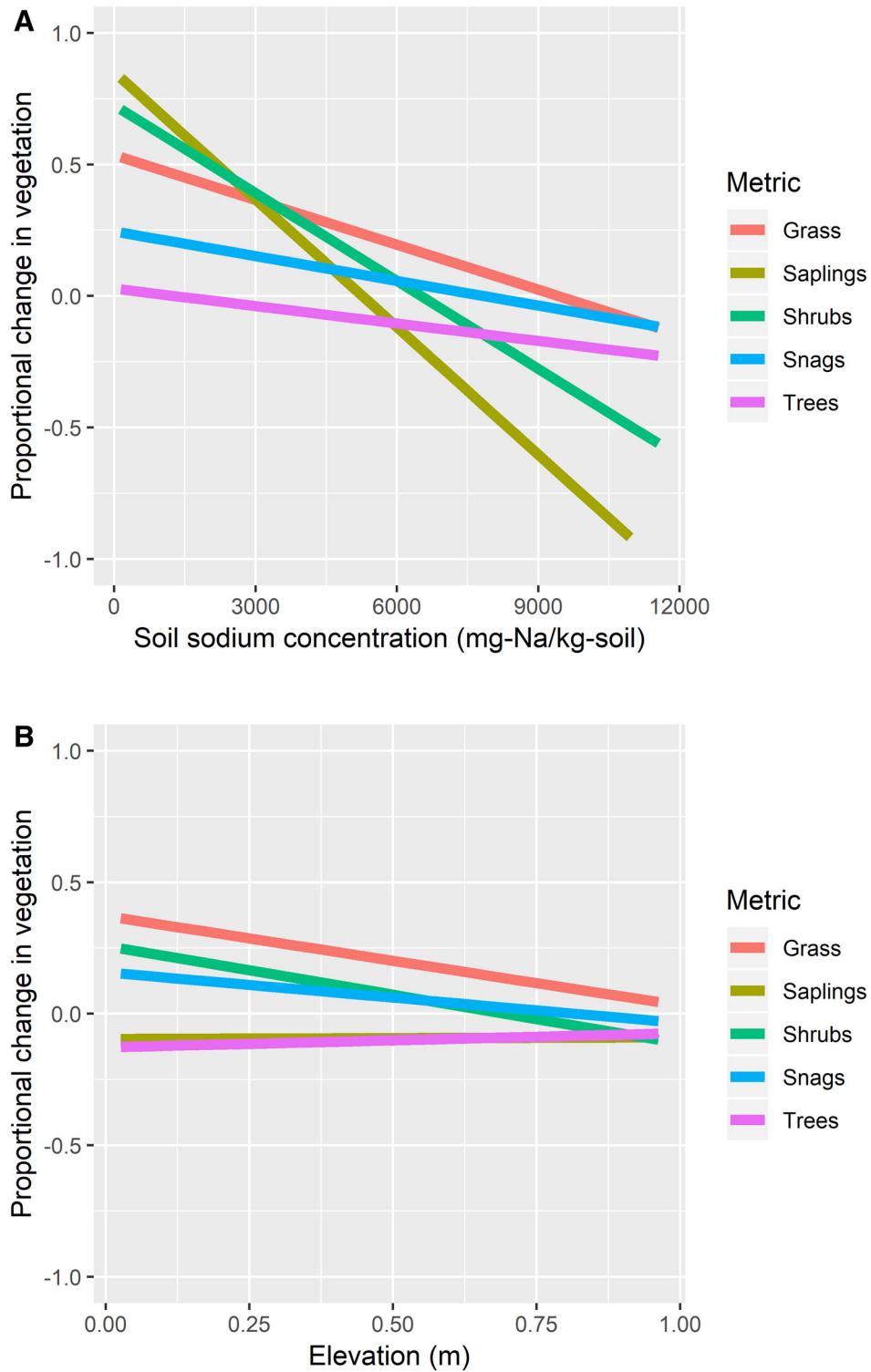
Figure 2. Linear relationships between the change in each of five metrics of vegetation composition and soil sodium concentration (**A**) and elevation (**B**) between 2003/2004 and 2016/2017 in eastern North Carolina, USA.

soil sodium (Figure 2).The effect of elevation was not significant for any of the vegetation metrics (Table 1).

Vegetation changes varied among the five sites and the three community types. At Palmetto-Peartree Preserve, the mechanical treatment to
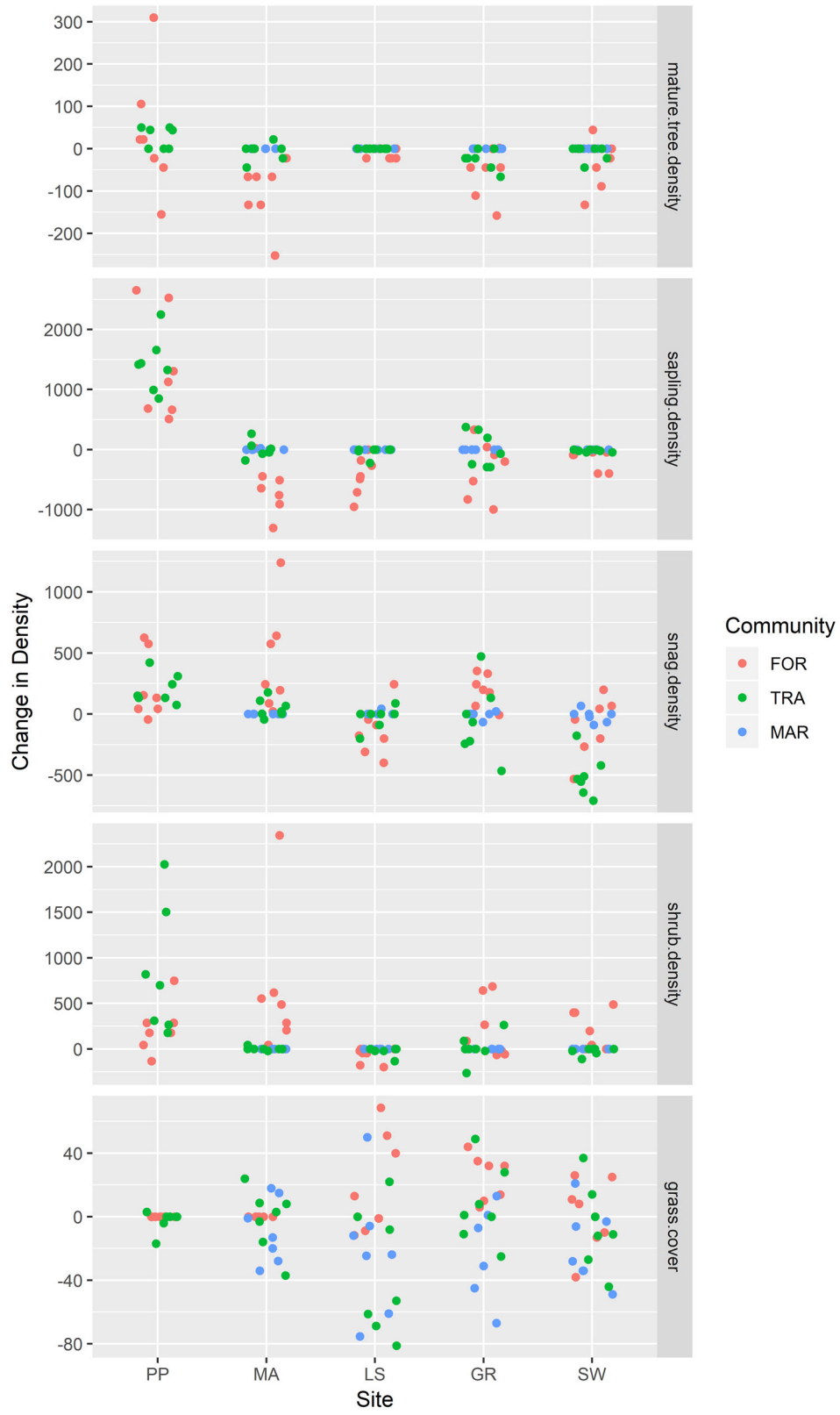
◀**Figure 3.** Change in five vegetation metrics at 98 vegetation plots at five sites (*PP* Palmetto-Peartree, *MA* Mashoes, *LS* Long Shoal, *GR* Gull Rock, and *SW* Swanquarter) in eastern North Carolina, USA, from 2003/2004 to 2016/2017. Plots are colored according to three vegetation community types (*FOR* forest, *TRA* transition, and *MAR* marsh) delineated at the start of the study. The *y*-axis units for the top four panels are stems/ha, whereas the units for the bottom panel are percent cover.

control the outbreak of southern pine beetle left little standing woody vegetation in the transition community in the first sampling period (Table S1). By 2016/2017, however, woody vegetation density increased dramatically at these plots, particularly for saplings and shrubs (Figure 3). In contrast, mature trees and saplings decreased or stayed the same at the other four sites in both the forest and transition communities (Figure 3). This decline in woody vegetation was particularly clear at Long Shoal, where all plots decreased or stayed the same in woody vegetation density. In the first sampling period, snag density was greater at the three sites on the Pamlico Sound than on the sites on the Albemarle Sound (Table S1). Over the course of the study, snags largely increased in density in the forest plots, but decreased or stayed the same at Long Shoal and in the transition plots at the other two sites on the Pamlico Sound: Gull Rock and Swanquarter (Figure 3). In the first sampling period, shrub density was generally greater in the forest communities at the Albemarle Sound sites, whereas the transition communities had much greater shrub densities than the forest communities at the Pamlico Sound sites (Table S1). At all sites other than Palmetto-Peartree Preserve, shrub density increased between the two sampling periods in the forest communities, but tended to remain constant in the transition communities. The grass cover in the marshes in the first sampling period at Long Shoal and Gull Rock was approximately half that observed at Mashoes and Swanquarter (Table S1). There was little change in grass cover at Palmetto-Peartree and the forest plots at Mashoes (Figure 3). At the remaining sites, grass cover tended to increase in the forest plots and decrease in the marsh plots (Figure 3).

We did not observe a high degree of correlation between soil sodium concentration and elevation. There was some correlation between elevation and the 2017 soil sodium concentration ($r = - 0.45$), but correlation between elevation and the 2004 soil sodium concentration was substantially lower
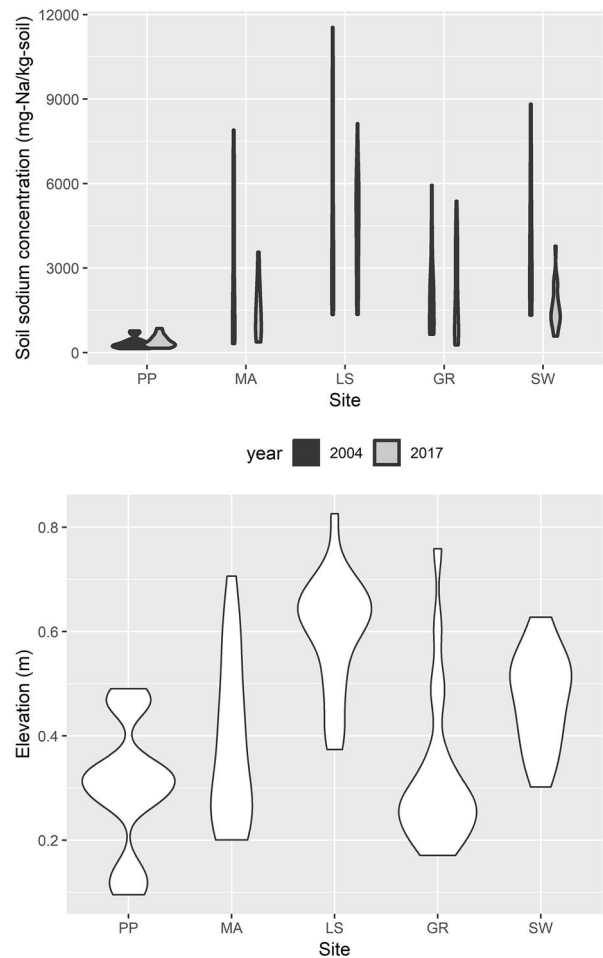
Figure 4. Violin plots of the soil sodium concentration (top) measured during two sampling occasions at 98 plots distributed across the coastal forest-marsh transition at five sites in eastern North Carolina, USA. Lower panel shows elevations across the same plots at the same sites. A wider violin corresponds to a greater density of points in the associated range of the *y*-axis.

($r = - 0.09$). The Palmetto-Peartree Preserve site was the lowest elevation, but also had the lowest levels of soil sodium concentration (Figure 4). In contrast, the Long Shoal site was the highest elevation, and had the greatest levels of soil sodium (Figure 4). We observed a significant difference in soil sodium concentrations between years across all sites ($F = 9.06$, $p = 0.003$); however, soil sodium concentrations were on average lower in the second sampling period than in the first (Figure 4).

DISCUSSION

The strength of dependence of vegetation change on soil sodium concentrations and lack of dependence on elevation suggest that salinization is a

more important driver of vegetation change than inundation at the leading edge of rising sea level. This work builds on prior research from the US Gulf Coast, which reported that salinity was more important than inundation or competition as a driver of *Sabal palmetto* mortality in coastal hydric hammocks (Williams and others 1999), suggesting that non-inundation salinization is a widespread phenomenon capable of driving land cover change in advance of permanent inundation by rising seas. Furthermore, this phenomenon may be an example of a broader pattern of ''freshwater salinization syndrome'' that is becoming more widespread across North America (Kaushal and others 2018). Along with these previous studies, our results help to reveal the important contribution of salinization to decadal-scale vegetation change in coastal regions as sea levels rise.

The spatial and temporal dynamics of future vegetation change in low-lying coastal areas will likely depend on factors that facilitate salinization, including severe and persistent drought. Though the implications of anthropogenic climate change for global precipitation patterns are uncertain, some studies project that droughts may become more frequent or severe (Trenberth and others 2013; Pfahl and others 2017). In addition, local sea level rose by approximately 40 mm over the course of our study, and this rate may accelerate in the future (NCDENR 2010). This combination of rising sea level and increasing frequency and severity of droughts could result in much greater rates of vegetation change than those we measured, as well as increasing the spatial extent of these changes. Continued efforts to monitor and forecast changing precipitation patterns will be crucial to fully understanding the implications of rising sea level for coastal ecosystems.

The shift in vegetation conditions toward more salt-tolerant shrubs and herbaceous vegetation over the course of this study likely represents the landward movement of coastal marshes, a process known as marsh migration. Coastal marshes are of high conservation value as a result of the varied ecosystem services they provide (Barbier and others 2011). However, these ecosystems are vulnerable to rising sea level because they occur along a narrow range of environmental conditions near the shoreline, and marsh migration has been identified as one of the primary mechanisms by which they may persist as sea level continues to rise (Craft and others 2009; Stralberg and others 2011; Enwright and others 2016; Anisfeld and others 2017). Though previous studies have investigated the potential future role of marsh migration in the conservation of coastal marshes, ours is one of the first to document this process at multiple sites at a decadal timescale. This process of marsh migration will be of particular importance in areas with low tidal amplitude and sediment supply where vertical accretion of coastal marshes is slow, such as the APP.

Given the vegetation changes that we observed and their apparent relationship to soil sodium, combined with the rise in sea level over the duration of the study, the fact that soil sodium concentrations actually decreased over the duration of the study may seem counterintuitive. However, this observation simply illustrates the complex nature of salinization dynamics. Salinity in estuarine environments is driven by several factors, including winds, precipitation, and evapotranspiration not only in the estuary, but also throughout the associated watersheds, resulting in high spatial and temporal variation (Herbert and others 2015). Though evidence of salinization may persist longer in soils compared to surface waters (Chagué-Goff and others 2012), it is possible that soil cation concentrations may not accurately reflect the history of saltwater exposure over multiple years. Long-term monitoring of salinity on the APP revealed acute pulses of salinity associated with late-summer droughts in multiple years between our two sampling periods (Ardón and others 2013). Thus, widespread salinization during drought conditions could drive the vegetation changes we observed in the second sampling occasion, but not be reflected in soil measurements due to non-drought conditions at the time of sampling. Furthermore, high temporal resolution in salinity monitoring often comes at the cost of spatial coverage, and the spatial distribution of drought-induced salinization remains poorly understood. A better understanding of the spatial and temporal variation in salinity in terrestrial estuarine environments is needed to more explicitly link vegetation changes to salinization dynamics.

The dramatic vegetation shifts we observed at Long Shoal suggest that fire may interact with salinization to promote marsh migration. The forests of the South Atlantic Coastal Plain historically were maintained by fire (Frost 1995; Bailey and others 2007), and species like *Pinus serotina* often regenerate quickly following fire via serotinous cones and stump-sprouting. However, saltwater exposure may limit regeneration of many tree species, even at levels tolerated by mature trees (Williams and others 2003; Poulter and others 2008). Pine seedling establishment may be further limited by competitive exclusion from encroaching

marsh grasses (Poulter and others 2009). Our observations of increased grass cover and limited woody regeneration at the burned Long Shoal plots that were forested in 2004 may indicate an altered successional trajectory following fire in salt-affected forests. Previous work has identified fire as a catalyst for transition between alternative stable states (Fletcher and others 2013; Ross and others 2009), and the coastal forest/marsh interface may reflect such a scenario where feedbacks inhibit forest regeneration following fire, even after a saltwater intrusion event has subsided (Brinson and others 1995). If so, consideration of these interactions between drought, salinization, and fire will become increasingly important to understanding vegetation change as sea levels continue to rise, patterns of disturbance change, and the effects of salinization become more widespread.

In addition to variation in vulnerability to saltwater exposure and disturbance history among the five sites in our study, the among-site variation in vegetation change that we observed could result from several factors that we did not consider. For example, the orientation of the shoreline could affect the exposure to storm surge from tropical cyclones. Additionally, the five sites differed in the degree to which the hydrology has been modified by the use of drainage ditches and canals (Bhattachan and others 2018). As such, extension of our results to other sites should be done with caution. Future studies of coastal vegetation change related to rising sea level should aim to identify mechanistic drivers of vegetation change in order to provide specific recommendations for ecological management and restoration.

A better understanding of how coastal environments are changing and the interacting factors driving vegetation changes are requisite to effective coastal management. As sea level continues to rise, possibly at an increasing rate, and severe weather events become more frequent, managing coastal environments will require novel strategies to adapt to these changing conditions (Wigand and others 2017). Our results from one of the most vulnerable regions of North America to sea level rise serve as a model of the vegetation changes expected to become more widespread in low-lying coastal regions.

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Data Accessibility Statement The data reported in this study are permanently archived at the Pangaea Online Data Repository and can be found at https://doi.pangaea.de/10.1594/PANGAEA.896941.

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