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ECOSYSTEMS

The Effect of Marsh Age on Ecosystem Function in a Rapidly Transgressing Marsh

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ABSTRACT

Sea-level rise is leading to the migration of marshes into coastal forests throughout North America. Marsh migration represents a primary mechanism for marsh survival in the face of sea-level rise and leads to a fundamental reorganization of vegetation communities. Yet, the ecological implications of these changes remain unknown. To evaluate the effect of marsh migration on ecosystem function, we compared habitat, primary production, vertical accretion, nutrient cycling, and carbon accumulation between new and old salt marsh on Goodwin Island (Virginia, USA) where salt marsh is migrating landward into rapidly retreating coastal forest. Using historical imagery and radioisotopic dating of sediment cores, we determined marsh age (< 3 to approximately 616 years) across the landscape. We found that salt marsh functions generally depended more on elevation and/or landscape position than marsh age. Primary production and nutrient cycling (%C and %N soil content) did not vary significantly with marsh age. Accretion and carbon accumulation rates varied predictably with elevation in old marsh but not in new marsh. Instead, trends in soil formation were controlled by the colonization of *Phragmites australis*, a dominant plant in migrating marsh-forest boundaries along the Atlantic Coast. Vegetation zonation patterns were more clearly defined in old marsh, indicating that habitat types take time to develop. However, these vegetation differences did not translate to consistently different ecological functions. These observations suggest that marsh migration does not lead to permanent differences in ecological functions between new and old marsh, rather ecological functions will converge as new marsh ages.

Key words: carbon accumulation; climate change; community reassembly; habitat; nutrient cycling; primary production; sea level rise.

HIGHLIGHTS

- Vegetation zonation across elevation in salt marsh takes time to develop.

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- Transgressing marsh driven by organic processes rather than mineral processes.
- Ecological functions of new and old marsh converge as new marsh ages

Introduction

Sea-level rise is transforming coastal regions around the world as increased flooding and salinization lead to land submergence, landward migration of ecosystems, and ecosystem replacement (Scavia and others 2002; Harley and others 2006; IPCC 2013; Gabler and others 2017; Schuerch and others 2018). The extent to which coastal regions will change largely depends on the resilience of coastal ecosystems to the effects of sea-level rise. For example, freshwater and brackish systems like freshwater wetlands and tidal swamps are especially vulnerable to saltwater intrusion, whereas increased flooding and salinity threaten upland coastal forests, and erosion and migration create lateral instability for beaches and coastal dunes (Williams and others 1999; Zhang and others 2004; Feagin and others 2005; Shaffer and others 2009; White and Kaplan 2017; Kirwan and Gedan 2019). Other systems, like salt marshes, can be more resilient to the effects of sea-level rise. Salt marshes can maintain vertical stability via feedbacks between sediment deposition, organic matter accumulation, and sea level, and they can also respond laterally via landward migration. (Kirwan and Megonigal 2013; Kirwan and others 2016a; Schuerch and others 2018).

Marsh migration can be a primary mechanism for marsh survival in the face of sea-level rise (Reed 1995; Donnelly and Bertness 2001; Kirwan and Megonigal 2013; Kirwan and others 2016b; Borchert and others 2018; Fagherazzi and others 2019). Tidal flooding of adjacent uplands creates growing conditions that support salt marsh vegetation and delivers mineral sediments that help build up marsh soil. Where landward migration is not restricted by anthropogenic or topographic barriers (that is, steep slopes, infrastructure, shoreline protection structures), marshes can preserve or even expand their spatial extent under accelerated rates of sea-level rise, offsetting areal loss from edge erosion (Kirwan and Megonigal 2013; Enwright and others 2016; Kirwan and others 2016b, 2016a). For marshes that are subject to high rates of erosion or are unable to maintain vertical stability (for example, due to limited sediment inputs or effects on vegetation that limit their productivity), landward migration is critical for their survival.

Changes in the composition of coastal landscapes due to the varied resilience of ecosystems to sea-level rise will likely have large-scale ecological repercussions. Anticipated consequences include habitat loss, decreases in biodiversity, and potentially altered or diminished ecosystem functions (Craft and others 2009; Gedan and others 2011; Pecl and others 2017). Marsh migration into vulnerable upland forests, for example, leads to a fundamental reorganization of vegetation communities; this phenomenon has become one of the most pronounced transformations in low-lying coastal regions of North America (Williams and others 1999; Raabe and Stumpf 2016; Langston and others 2017; Kirwan and Gedan 2019; Schieder and Kirwan 2019). Sea-level rise creates flooding conditions that prevent forest regeneration and over time, leads to a turnover of plant communities in which trees give way to more salt tolerant shrubs, that are replaced by herbaceous salt marsh species via landward migration (Langston and others 2017). This reorganization, or community reassembly, results not only in a change of species composition to species more adapted to flooded, saline conditions, but fundamental changes in the growth forms represented by plants and overall habitat structure.

Though previous work has investigated transitions from upland and freshwater coastal communities to salt marsh, the ecological implications of these changes remain largely unknown. Moreover, the quality of new marsh replacing coastal forest has been called into question, as it often supports high densities of *Phragmites australis*, a non-native species prevalent along the Atlantic Coast of North America in high elevations of marsh and in transition zones between marsh and adjacent uplands (Chambers and others 1999; Orson 1999; Rice and others 2000; Silliman and Bertness 2004). Here we evaluate the effect of landward marsh migration on ecosystem function by comparing habitat, primary production, vertical accretion, nutrient cycling, and carbon accumulation between new and old salt marsh in a coastal landscape where salt marsh is migrating rapidly into retreating coastal forest. We expected marsh age to be the predominant influence on ecological functions; however, our findings demonstrated that ecological functions were driven by vegetation and soil characteristics across gradients of age and elevation.

METHODS

Study Site

To determine how ecological functions change with marsh age in a transgressing system, we evaluated habitat, productivity, vertical accretion, nutrient cycling, and carbon accumulation across elevation gradients of new and old marsh on Goodwin Island, which is located near the mouth of the York River in the Chesapeake Bay (Virginia, USA). Goodwin Island (0.8 km^2) is located in a sea-level rise hot spot that has a long-term (1950–2019) mean rate of relative sea-level rise of 4.86 mm year^{-1} (Yorktown, Virginia US Coast Guard tide station #8637689), which exceeds the current global mean rate of sea-level rise (3.2 mm year^{-1} since 1993; IPCC 2013). In response to sea-level rise, new salt marsh on Goodwin Island is rapidly migrating into upland coastal forest dominated by *Pinus taeda* at a long-term rate of 0.5 m year^{-1} (1937–2011; Kirwan and others 2016b). Marsh migration is accelerating with the rate of sea-level rise and is occurring at roughly twice the rate of edge erosion, resulting in an overall increase in marsh area and a loss of coastal forest through time (Kirwan and others 2016b; Schieder and Kirwan 2019). In general, low marsh on Goodwin Island is dominated by *Spartina alterniflora*, and high marsh is dominated by *S. patens* and *Distichlis spicata*. *Phragmites australis* is common in the highest elevations of marsh as well as in the transition zone from high marsh to forest, where it co-occurs with native high marsh species and shrubs (*Iva frutescens* and *Morella cerifera*).

In a transgressing marsh, marsh age generally increases with distance from the current marsh-upland boundary. However, the rate of migration depends on upland slope; migration occurs slowly or not at all near steeper slopes and faster near gentler slopes (Kirwan and others 2016b; Schieder and others 2018). These differences in upland slope result in marsh on Goodwin Island that is more than centuries old immediately adjacent to marsh that is only decades old. Thus, our comparisons between new and old marsh account for both elevation and landscape position.

Imagery Analysis and Elevation Transects

To determine the age of the marsh at different positions across Goodwin Island, we used historical maps, aerial imagery, and radioisotopic dating. We manually delineated the marsh-forest boundary between the years 1853–1906 using 1:20,000 scale US Coast Survey topographic maps (T-sheets; (NOAA 2016). The T-sheets were previously georeferenced to modern aerial imagery with a root mean square error (RMSE) of approximately 5 m (Schieder and others 2018). We also delineated the marsh-forest boundary in orthorectified aerial mosaics from 1937, 1953, 1960, and 1994 (VIMS Shoreline Studies Program), in aerial imagery from 1982 and 2005 with 0.5 m resolution (USGS 2016), and in orthoimagery from 2013 (ArcGIS server gismaps.vita.virginia.gov). All images were adjusted to match the scale of the T-sheets. We estimated marsh age by subtracting the marsh extent in each image from the previous image, in descending order, and grouped marsh extent into age classes. Thus, marsh ages inferred from historical maps and photographs refer to the period of time since marsh, rather than forest, was first visible.

Based on the imagery analysis, we established four elevation transects on Goodwin Island from which we collected field data on marsh age, vegetation composition and biomass, vertical accretion, nutrient cycling, and carbon accumulation. Transects extended from the seaward edge of the marsh to the marsh-forest boundary. Elevations were measured along each transect using an RTK GPS and were converted from NAVD88 to MHW using a conversion factor derived from the Yorktown US Coast Guard tide station. Three transects (T1, T2, T3) were placed in ‘‘new marsh’’, and one transect was established as a reference transect and placed entirely within an area of old marsh (‘‘old marsh’’). Transects in new marsh spanned age classes identified from the imagery analysis. The reference transect of old marsh was located in the oldest marsh identified from the imagery analysis.

Vegetation Composition and Biomass

We compared habitat and productivity between new and old marsh across elevation gradients by identifying plant species composition and measuring aboveground biomass. We mapped vegetation on Goodwin Island manually in ArcGIS based on aerial and drone imagery. We did not differentiate between tall and short form *S. alterniflora*, nor did we differentiate between *S. patens* and *D. spicata*, which are co-occurring species that occupy the same elevation range. All other plants identified in the GIS analysis were described to species level. We layered marsh age zones over the vegetation layer to determine marsh age across vegetation types. To determine whether vegetation type was a function of marsh age, we calculated the area of each vegetation type in each age class.

We used aboveground biomass as an estimate of aboveground productivity in new and old marsh. We measured aboveground biomass in five 0.0625-m^2 quadrats positioned along the four marsh elevation transects in Summer 2016. Live and dead vegetation were clipped at the marsh surface from each quadrat, washed, and separated by species, then dried at 60 °C to constant mass ($\sim$ 48 h) before weighing. Biomass of *S. patens* and *D. spicata* were not separated because they are co-occurring high marsh species. We used a multiple linear regression to test the effects of age and elevation on aboveground biomass. We also applied a logistic regression to compare vegetation type across marsh age and elevation. We estimated the elevation at which vegetation type shifted by calculating the inflection point of each logistic curve. For this analysis, marshes were categorized as new ($<$ 110-years-old) and old ($>$ 110-years-old), based on the imagery analysis.

Vertical Accretion and Radioisotopic Dating

To compare accretion rates in new and old marsh, we estimated vertical accretion by measuring the thickness of organic rich sediment in sediment cores collected along the four marsh transects and using ^{210}Pb geochronology. Sediment cores were collected in 2016 from different age classes along T1, T2, and T3 and along the transect of old reference marsh in locations of similar elevation and vegetation type as those along the new marsh transects. Six cores were taken along T1, seven along T2, and five cores each were taken along T3 and the reference transect of old marsh. Cores were collected using a 5-cm-diameter Russian Peat Corer. Depths of cores varied depending on the depth of organic matter. The position and elevation of each core location were recorded using an RTK GPS; elevations were converted from NAVD88 to MHW. We estimated organic matter thickness in the field by identifying the transition from pre-marsh, upland sediment to marsh sediment within each core based on visual and tactile cues: pre-marsh sediment on Goodwin Island is gray, lacks fibrous organic content, and has higher bulk density; marsh sediment is brown, has visible organic matter, and lower bulk density (Schieder and Kirwan 2019). Organic matter thickness was measured as the length from the top of the core to the depth of the pre-marsh-to-marsh transition. Accretion rates were then calculated as organic matter thickness divided by marsh age estimated from the imagery analysis.

We also estimated accretion rates using ^{210}Pb geochronology. ^{210}Pb accretion rates were calculated for sediment samples collected from five push cores (16-cm-diameter, 21–60 cm deep) in new and old marsh. Three cores were taken along T3 in new marsh, and two cores were taken from the reference transect in old marsh. Cores were sectioned into 1-cm intervals and oven-dried at 60 °C until a constant weight was achieved. Sediment was then homogenized, weighed, packed in 25 mL petri dishes, and sealed to retain radon gas for ^{226}Ra isotopic measurements. The samples were equilibrated for $\geq$ 30 days and measured for ^{137}Cs and ^{210}Pb gamma emissions on a Canberra Low Energy Germanium gamma detector for 24 h. Unsupported ^{210}Pb (^{210}Pb$_{ex}$) was determined by subtracting estimated ^{226}Ra radioactivity (calculated as the mean activities of ^{214}Bi and ^{214}Pb) from total ^{210}Pb radioactivity. Accretion rates were calculated using the Constant Initial Concentration (CIC) model (Goldberg 1963). Accretion rates based on organic matter thickness and ^{210}Pb analysis were summarized as mean rates (± standard deviation) for new and old marsh.

We also used the ^{210}Pb sediment samples for radioisotopic dating. We estimated marsh age along T3 and along the reference transect of old marsh by dividing the depths of organic matter by accretion rates estimated from ^{210}Pb profiles.

Nutrient Cycling and Carbon Accumulation

To compare soil nutrient characteristics in new and old marsh, we analyzed weight percent carbon (% C) and percent nitrogen (% N) from sediment cores collected along the four elevation transects. Cores were taken from the same locations as cores used for measuring accretion rates based on organic matter thickness (six cores from T1, seven cores from T2, and five cores each from T3 and the reference transect of old marsh). Cores were divided by depth into the following sections: 0–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm. Samples from each section were dried at 60 °C, then ground with a mortar and pestle. Subsamples were then analyzed from each core for C and N content using a Perkin-Elmer 2400 CHN elemental analyzer. We calculated means and standard deviations of % C and % N by age class and across elevation.

We evaluated carbon storage capacity as a function of marsh age by calculating carbon accumulation rates from each sediment core. To get a consistent depth across age zones of the marsh, including in newer marsh with shallow organic soils, we measured C accumulation to depths of 10 cm. Carbon accumulation was calculated as the product of the carbon content of the sample, accretion rate, and bulk density. Bulk density was calculated by dividing the mass of oven-dried sediment by sediment sample volume. We summarized C accumulation as a mean rate (± standard deviation) for each age class.

RESULTS

Marsh Age

We identified 8 age classes from historical maps and aerial imagery: < 3-years-old, 3–11-years-old, 11–22-years-old, 22–34-years-old, 34–56-years-old, 56–79-years-old, 79–110-years-old, and > 110-years-old (Figure 1a). The oldest age range was not confined by a maximum age because the T-sheets revealed the presence of marsh in 1906 but not the year it formed. The three transects across new marsh spanned an age range > 110-years-old at the seaward edge to < 3-years-old at the marsh-forest boundary. Marsh along the old transect was also present in the 1906 T-sheet, confirming it was also > 110-years-old.

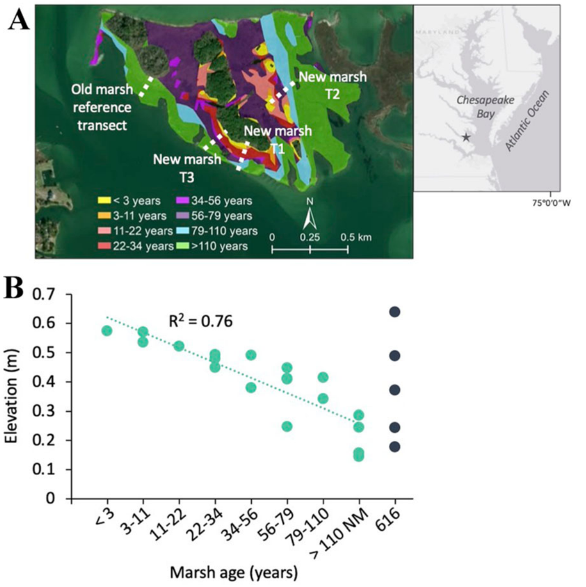

Figure 1. Marsh age **A** spatially distributed across Goodwin Island based on historical imagery analysis and the **B** elevational distribution along new marsh ('NM'; green) and old marsh (blue) transects. Transects located along new marsh (T1, T2, T3) span a marsh age gradient of < 3 years to > 110 years. The reference transect of old marsh was entirely within marsh > 110-years-old. Note that the historical imagery analysis could only identify the oldest marsh on Goodwin as > 110 years; radioisotopic dating revealed marsh along the old marsh reference transect to be approximately 616-years-old.

Marsh age was estimated using radioisotopic dating for two of the three cores along T3. Sediment from core 1 was estimated as 109-years-old and occurred in marsh identified in the historical imagery analysis as > 110-years-old. Sediment from core 2 was estimated as 204-years-old and occurred in marsh identified in the historical imagery analysis as 56–79-years-old. Sediment from core 3, which was collected from marsh in the 22–34 age class, showed two periods of accretion based on its ^{210}Pb profile and could not give a reliable age estimate. We determined that results from radioisotopic dating in new marsh were not useful and instead used the age classes identified from imagery analysis for evaluating ecological functions in new marsh. Marsh along the reference transect of old marsh was estimated as 616-years-old based on radioisotopic dating of one sediment core. No age was estimated from the second core because an accretion rate could not be determined from the ^{210}Pb profile.

Marsh age was correlated with elevation, with the newest marsh occurring at higher elevations than older new marsh, which occurred at subsequently lower elevations (Figure 1b).

Vegetation Composition and Biomass

Vegetation composition varied with marsh age. *Phragmites australis* made up > 90% of plant cover in the newest marsh and rapidly declined with marsh age (Figure 2). *Spartina patens* and *D. spicata* cover quickly increased with time in marsh < 50-years-old and replaced *P. australis* as the dominant species in marsh aged 56–110-years-old. *Spartina*

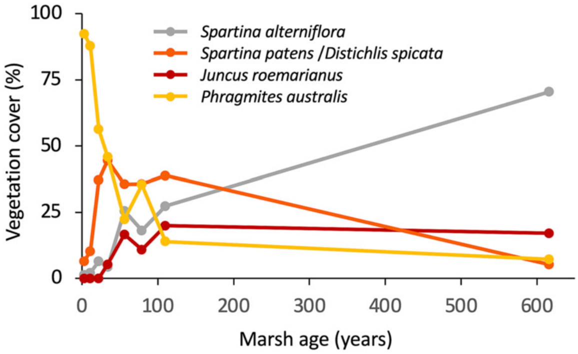

Figure 2. Relative percent cover of plant species occupying marsh over time based on GIS analysis for all of Goodwin Island.

alterniflora cover increased over time. It was the dominant species in marsh > 110-years-old, and made up > 70% of plant cover in the oldest marsh.

In new marsh, *S. alterniflora* co-occurred with *J. roemarianus*, *S. patens*, *D. spicata*, and *Salicornia virginica* along elevations ranging from 0.2 to 0.6 m (Figure 3a). *Phragmites australis* co-occurred with *S. alterniflora*, *S. patens*, and *D. spicata* from 0.5–0.6 m. In old marsh, sharp transitions in vegetation composition occurred across an elevation gradient. *Spartina alterniflora* exclusively occupied lower elevations of old marsh (0.1–0.3 m). From 0.3 to 0.4 m, species composition included *S. alterniflora*, *J. roemarianus*, *S. patens*, *D. spicata*, and *S. virginica*. These marsh species were replaced by *P. australis* at elevations above 0.4 m.

In new marsh, the transition from low to high marsh species occurred gradually (Figure 3b). In old marsh, the transition from low marsh dominated by *S. alterniflora* to high marsh dominated by *S. patens* and *D. spicata* occurred sharply at 0.3 m. The elevation at which native high marsh plants transitioned to *P. australis* was higher in new marsh than old marsh (0.53 m compared to 0.4 m).

Aboveground biomass significantly increased with elevation in both new and old marsh (p value < 0.0001; Figure 4a). For a given elevation, biomass was similar in new and old marsh (p value = 0.43), though a significant interaction between elevation and age effects (p value = 0.009) showed that biomass increased with elevation more quickly in old marsh than in new marsh (Figure 4a). Biomass in the newest (< 3 years) and oldest marsh (616 years) was primarily composed of *P. australis* (1187 g m^{-2} and 1519 g m^{-2}, respectively; Figure 4b). In marsh between 11 and 110-years-old, biomass was primarily composed of *S. alterniflora*, *S. patens* and *D. spicata*.

Vertical Accretion

Vertical accretion in old marsh decreased with elevation but increased with elevation in new marsh (Figure 5). Mean vertical accretion in new marsh based on organic matter thickness was 5.6 ± 6.3 mm $year^{-1}$ and was 1.01 ± 0.83 mm $year^{-1}$ in old marsh. The mean ^{210}Pb accretion rate in new marsh was 2.0 ± 1.4 mm $year^{-1}$. ^{210}Pb accretion rates in cores 1 and 2 along T3 were 1.92 mm $year^{-1}$ and 1.13 mm $year^{-1}$, respectively (Figure 6). Two periods of accretion were identified in core 3, shown by two distinct slopes of excess ^{210}Pb activity. The ^{210}Pb accretion rate of core 1 along the old marsh reference transect was 1.15 mm $year^{-1}$. A ^{210}Pb accretion rate could not

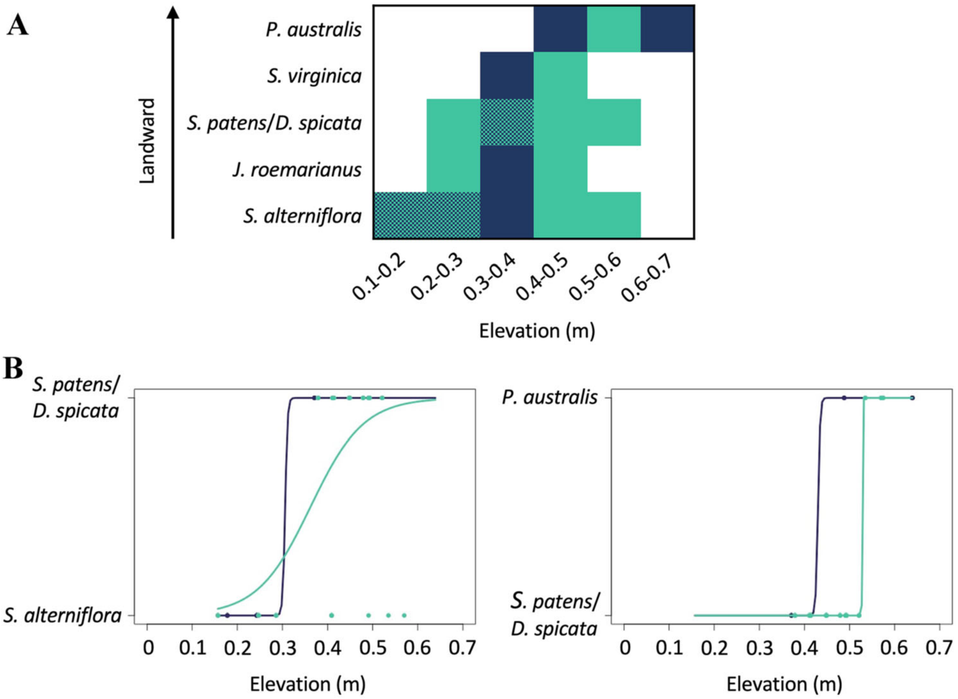

Figure 3. Species composition across elevation based on biomass field data showing **A** presence of marsh species across elevation in new marsh (green), old marsh (blue), or both (stippled) and **B** transitions from dominant low and high marsh species in new (green) and old (blue) marsh.

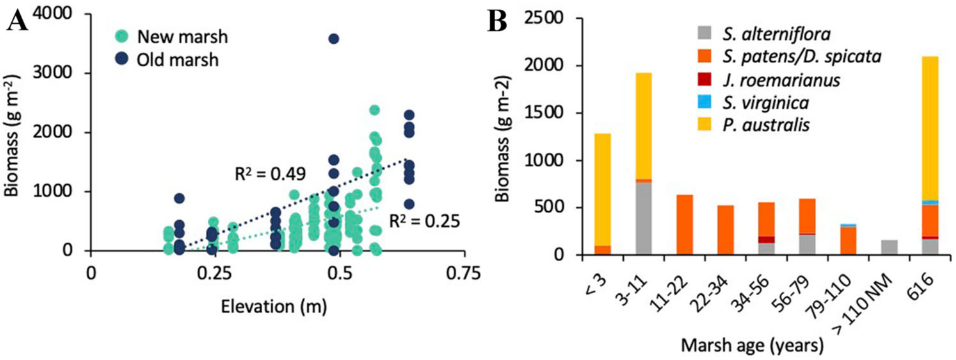

Figure 4. Aboveground biomass across **A** elevation in new (green) and old (blue) marsh, and **B** marsh age. Biomass in **B** is presented as average biomass of each species in each age class.

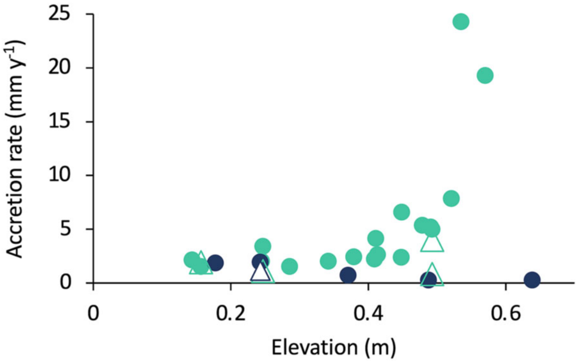

Figure 5. Marsh accretion rates based on organic matter thickness and ^{210}Pb analysis (CIC model). Green = new marsh; blue = old marsh; circles = organic matter thickness method; triangles = ^{210}Pb analysis. *Note that the outlying accretion rate estimated for the newest marsh (< 3-years-old; 113 mm year^{-1}) is not shown here.

be calculated for core 2 because the excess ^{210}Pb values fell below the supported values for all samples below 2 cm.

Nutrient Cycling and Carbon Accumulation

Neither C nor N content in marsh soil was correlated with marsh age or elevation (Figure 7). Percent C and % N followed similar patterns; both were highest in marsh aged 3–11 years (% C: 7.8 ± 6.1; % N: 0.49 ± 0.39) and lowest in marsh aged 79–110 years (% C: 3.6 ± 0.7; % N: 0.29 ± 0.06; Figure 7a). In the newest marsh (> 3 years), % C was 6.9 ± 1.3, and % N was 0.49 ± 0.07. Both % C and % N were higher in the oldest region of new marsh (> 110-years-old; % C: 7.0 ± 5.4; % N: 0.45 ± 0.33) than in old marsh dated 616-years-old (% C: 4.2 ± 4.9; % N: 0.30 ± 0.28). Percent C varied more within elevations than across elevations and ranged from 1.3 ± 0.2 to 10.3 ± 5.4 (Figure 7b). Percent N did not change with elevation and ranged from 0.13 ± 0.02 to 0.68 ± 0.40.

Carbon accumulation rate was highest at high elevations of new marsh (965 g C m^{-2} year^{-1}) and decreased with marsh age (Figure 8). Carbon accumulation rate was lowest in marsh dated 79–110-years-old (10 ± 0.4 g C m^{-2} year^{-1}), which was only slightly lower than the rate of carbon accumulation in old reference marsh (13 ± 16 g C m^{-2} year^{-1}).

Bulk densities ranged from 0.04 to 0.33 g cm^{-3} in new marsh and from 0.16 to 0.33 g cm^{-3} in old marsh. Mean bulk density across both new and old marsh was 0.20 ± 0.08 g cm^{-3}.

DISCUSSION

Habitat and Productivity

In general, newly formed marsh on Goodwin Island inhabited high elevations toward the interior of the island and subsequently older marsh generally occupied lower elevations nearer the seaward edge (Figure 1). However, old marsh also occurred at high elevations adjacent to newly-formed marsh at the marsh-forest boundary due to differences in upland slope. Vegetation composition among age classes of marsh varied with elevation and landscape position, reflecting differences in environmental, edaphic, and biotic factors that influence the distributions of marsh plants (Bertness 1991; Pennings and Callaway 1992; Edwards and Proffitt 2003; Silvestri and others 2005). For example, new marsh at the marsh-forest boundary that formed within the past 34 years and occupied the highest elevations of the marsh (~ 0.45–0.6 m) was dominated by *P. australis* (Figure 2). This region most likely has lower concentrations of toxic soil sulfides

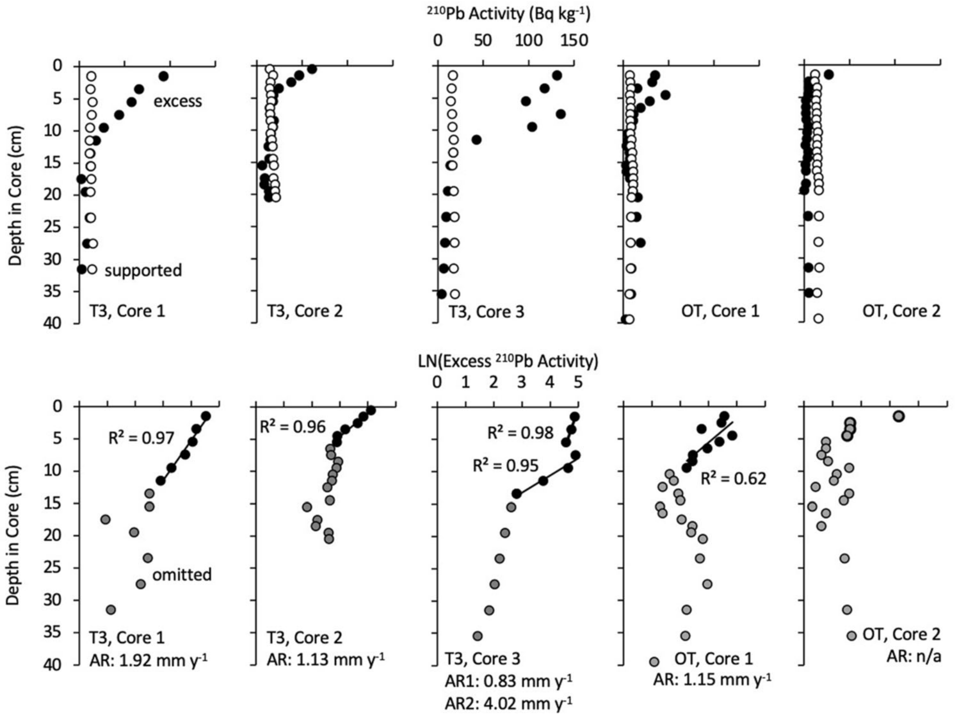

Figure 6. Accretion rates calculated from cores collected along new marsh transect T3 and along the transect of old reference marsh (OT) using ^{210}Pb profiles (CIC model). The top row shows ^{210}Pb activity (Bq kg^{-1}) across core depth for supported ^{210}Pb (open circles) and excess ^{210}Pb (closed circles). The bottom row shows the natural log of excess ^{210}Pb activity from which accretion rates (AR) were determined (solid black circles). Excess ^{210}Pb values that fell below supported values were omitted from accretion rate estimates (gray circles). Note that two accretion rates were estimated for T3, core 3 (AR1, AR2) based on the presence of two distinct slopes of excess ^{210}Pb.

and greater rhizosphere oxidation that promote *P. australis* establishment compared to lower elevations (Chambers and others 2003). Marsh in older age classes (35–110 years) occupied mid elevations (~ 0.3–0.5 m) dominated by high marsh species, *S. patens* and *D. spicata*, which are more flood and salt tolerant than *P. australis* (Smith 2013). Marsh > 110-years-old, which supported *S. alterniflora* in more frequently flooded regions and *P. australis* near the marsh-forest boundary, most clearly demonstrated that plant composition on Goodwin Island was a function of growing conditions influenced by factors other than marsh age.

Distinct vegetation zonation between low and high marsh plants, as observed in the old marsh, is a prevailing characteristic of salt marsh landscapes (Adams 1963; Bertness and Ellison 1987; Bertness 1991; Pennings and Callaway 1992; Pennings and others 2005; Smith 2014). *Spartina alterniflora* routinely dominates low elevations of marsh because it is better adapted than other marsh plants to anoxic soils and high salinity in frequently flooded marsh. In high marsh elevations, where less flooding and lower salinity create less stressful growing conditions, *S. alterniflora* is outcompeted by *S. patens* and other marsh plants (Bertness 1991). In new marsh on Goodwin Island, *S. alterniflora* and high marsh plants overlapped across most of the elevation profile and a gradual shift from *S. alterniflora* to *S. patens*/*D. spicata*-dominated marsh blurred the transition from low to high marsh zones (Figure 3). This suggests it takes time for vegetation zonation patterns to develop in a marsh, which likely depends on how quickly wetland soils develop (Hill and Anisfeld 2015), and the role different plant species play in engineering their physical environment (Marani and others 2013). Consistent with previous work (Marani and others 2013), our findings suggest that it takes centuries for vegetation zonation to fully develop.

Phragmites australis played a prominent role in several ecological functions in the highest elevations of marsh on Goodwin Island, including primary production. *Phragmites australis* was introduced to Goodwin Island in the 1990s (Perry and Atkinson 1997); less than 30 years later, we found it accounted for most of the aboveground biomass in both new and old marsh near the

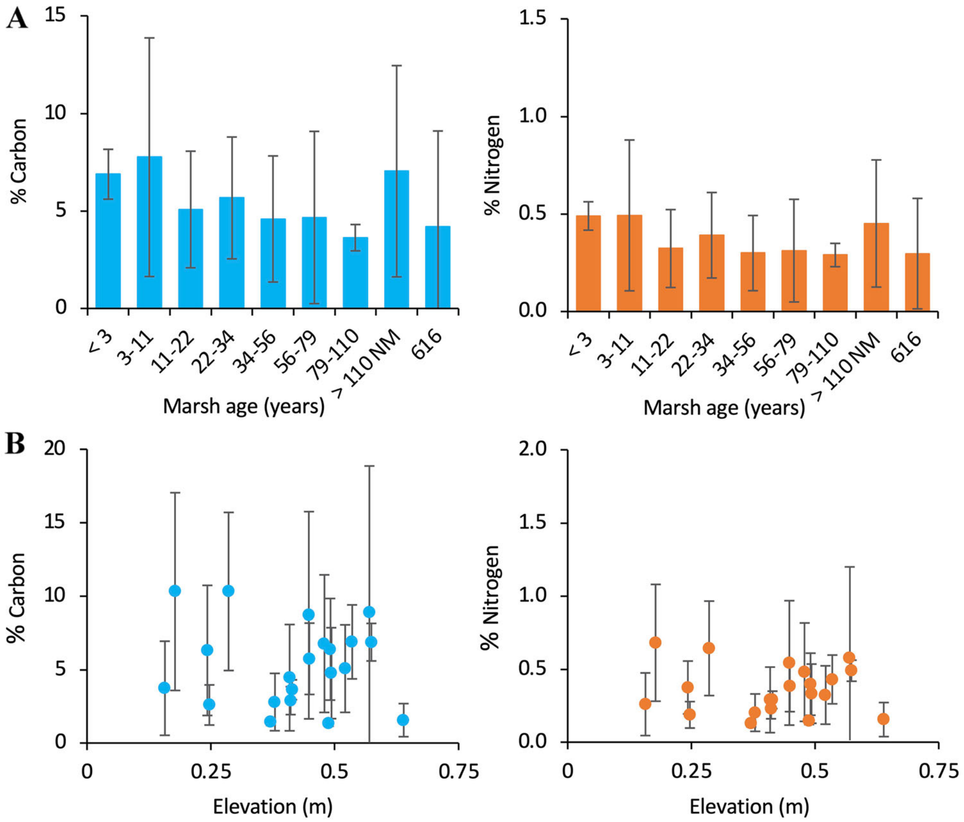

Figure 7. Percent soil carbon and percent soil nitrogen content as measures of nutrient cycling across gradients of **A** age and **B** elevation for the top 30 cm of soil. Carbon and nutrient content were measured from sediment cores collected along transects in new and old marsh; values shown as means ± 1 SD within age classes and elevation.

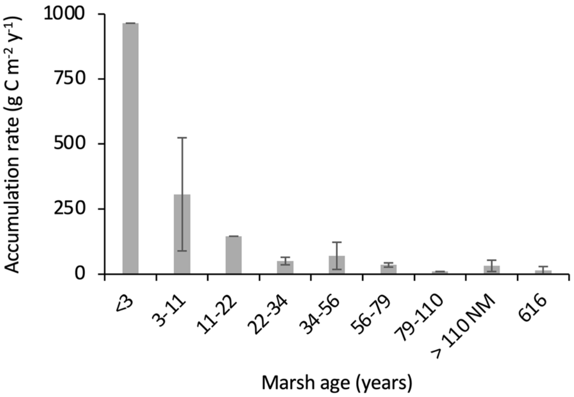

Figure 8. Carbon accumulation across a gradient of marsh age within the top 10 cm of soil; values shown as means ± 1 SD.

marsh-forest boundary (Figure 4). A prevalent species in transition zones between marsh and upland, *P. australis* relies on clonal integration to quickly colonize upper elevations of adjacent marsh (Chambers and others 1999; Orson 1999; Amsberry and others 2000; Rice and others 2000; Silliman and Bertness 2004). Clonal integration allows *P. australis* growing at the marsh-forest boundary to send rhizomes into adjacent marsh and share water, oxygen, nutrients, and photosynthates with new shoots, enabling *P. australis* to colonize upper elevations of both new and old marsh (Amsberry and others 2000).

Though *P. australis* occurred in both new and old marsh, it transitioned to *S. patens* and *D. spicata*-dominated marsh at a higher elevation in new marsh than in old marsh. The presence of *P. australis* in old marsh demonstrated that new marsh was no more susceptible to colonization by *P. australis* than old marsh near the marsh-forest boundary and indicates that *P. australis* will continue migrating into lower elevations of new marsh over time. However, sensitivity to flooding, salinity, and soil sulfide will likely limit the spread *P. australis* (Chambers and others 2003; Smith 2013). Over time, as sea-level rise increases flooding frequency in elevations currently supporting *P. australis*, *P. australis* may be replaced by marsh species better adapted to anoxic, saline soils (Wijte and Gallagher 1996b, 1996a).

Vertical Accretion

Despite *P. australis* dominating high elevations and overall plant biomass increasing with elevation across Goodwin Island, vertical accretion rates were much different in new and old marsh (Figure 5). Accretion steadily decreased with elevation in old marsh, consistent with the typical pattern of soil build up in marshes. Generally, accretion rates decrease with increased elevation because higher elevations of marsh are flooded less frequently and receive less sediment than lower elevations of marsh (Friedrichs and Perry 2001; Morris and others 2002; Kirwan and Megonigal 2013). However, accretion rates in old marsh may be underestimated due to the lack of clear ^{210}Pb profiles that could not be confirmed by ^{137}Cs profiles (Figure 6). Depleted sediments at the top of the profile suggest a well-mixed sediment column possibly from bioturbation or other physical mixing. Nonetheless, all measures of accretion rates (organic matter thickness, ^{210}Pb profiles, and ^{137}Cs profiles) were similar in old marsh and were consistently lower than accretion rates in new marsh.

In new marsh, accretion rates dramatically increased in elevations above 0.4 m, suggesting that contributions of organic material from *P. australis* outweighed potentially low rates of sediment deposition. Previous studies have found that *P. australis* biomass not only contributes to high rates of organic accretion, but also traps more sediment than marsh plants such as *Spartina* spp. (Harrison and Bloom 1977; Rooth and Stevenson 2000; Rooth and others 2003). Contributions of *P. australis* to vertical accretion in recent decades have a much greater influence on new marsh formed since the 1990s, where *P. australis* has been the dominant plant species during new marsh formation, than on long-term accretion rates in old marsh on Goodwin Island. A spike of increased sedimentation from *P. australis* in old marsh would be muted against centuries of slower accretion rates in high marsh dominated by native plant species.

Nutrient Cycling and Carbon Accumulation

Our findings indicated no clear relationship between soil nutrient content and marsh age or elevation on Goodwin Island (Figure 7), which is inconsistent with other studies. We would expect C and N content to be higher in older marsh compared to new marsh because soil nutrients build up as organic matter decomposes and is buried over time. For example, C and N concentrations were lower in new naturally-formed sandbar marshes than in more mature marshes in Georgia, USA (Krull and Craft 2009). Similarly, it was estimated it would take an average of 24 years for soil % C and 13 years for soil % N in newly constructed marshes around the Chesapeake Bay to reach % C and % N levels found in paired old marsh (Chambers and others 2021). A long-term study comparing two sets of constructed and natural marshes in North Carolina, USA, also found C and N concentrations were lower in a constructed marsh compared to a natural marsh that had formed 2500 years prior (Craft and others 1999). However, unlike constructed marshes built using low-nutrient, sand-dominated substrates, new marsh on Goodwin Island formed on forest soils already containing carbon and nitrogen. Soil nutrient content is also typically greater in low elevation marsh compared to high marsh, because low marsh is flooded more frequently. This trend has been observed previously in created marshes in North Carolina and Texas, USA (Lindau and Hossner 1981; Craft and others 2002). On Goodwin Island, however, newly formed marsh ($<$ 3 and 3–11 years) occupying high elevations had the highest % C and % N content, potentially corresponding with high aboveground biomass and high accretion rates from *P. australis*.

Carbon accumulation rates on Goodwin Island were much faster in the youngest marsh ($<$ 3 and 3–11-years-old; Figure 8) than in older marsh, and also exceeded the global mean rate (245 g C m^{-2} $year^{-1}$) and the mean rate along the Atlantic Coast (172 g C m^{-2} $year^{-1}$; Ouyang and Lee 2014). Short-term measures of carbon accumulation tend to be higher than long-term measures because over time, decomposition, compaction, and increased inundation from sea-level rise slow carbon accumulation rates. Indeed, similar trends were observed in a restored English marsh where new marsh less than 20-years-old supported much higher rates of carbon accumulation compared to low, consistent rates in older marsh (Burden and others 2019), in created and natural marshes in Louisiana (Abbott and others 2019), where short-term rates of carbon accumulation were higher than long-term rates, and in a natural marsh in North Carolina, USA, where the 11-year carbon accumulation rate was higher than the long-term (100 y) rate (Craft and others 1999). However, carbon accumulation is also a function of the accretion rate, soil carbon content, and soil bulk density. Given that soil bulk density was relatively low in new and old marsh, carbon accumulation in newer marsh may also be explained by high rates of organic accretion and soil organic carbon from *P. australis*.

Maturation of a Transgressing Marsh

Trends observed on Goodwin Island, where new, high elevation marsh is forming via transgression, differ somewhat from trends observed in newly restored and constructed marshes, which generally occupy low elevations near the seaward edge (Craft and others 1999, 2002). In those marshes, vertical accretion is driven by mineral deposition from frequent tidal inundation. Over time, they become more influenced by organic processes as community structure develops and biomass increases. Nutrient reservoirs grow and carbon accumulates as the marshes mature. Similar trends occur via primary succession in natural marshes that have developed from intertidal sand flats (Osgood and Zieman 1993; Osgood and others 1995). On Goodwin Island, transgressing marsh is driven by organic processes largely influenced by *P. australis* and ecological functions and attributes are typical of high marsh rather than low elevation new marsh. Over time, as new marsh becomes increasingly flooded and farther removed from the marsh-forest boundary, it becomes more influenced by mineral processes. Just as successfully restored and created marshes become increasingly similar to natural reference marshes as they mature, our results suggest new marsh on Goodwin Island will eventually resemble lower elevations of old reference marsh.

This study evaluated the ecological attributes and functions of salt marsh migrating into upland coastal forest. The primary difference between new and old marsh on Goodwin Island was related to habitat: sharp transitions between vegetation zones observed in old marsh had not yet developed in new marsh. Differences in accretion rates (decreasing with elevation in old marsh, increasing in new marsh) and carbon accumulation (low in old marsh, high in new marsh) as well as similarities in primary production and nutrient cycling appear to be driven more by vegetation and soil characteristics influenced by landscape position and elevation rather than marsh age. These findings potentially contrast with work in other ecosystems showing a tight relationship between ecosystem age and function (Odum 1969; Ballantine and Schneider 2009; Osland and others 2020). The presence of *P. australis* had potentially large influences on all ecological functions, particularly in new marsh. Concerns have arisen that migrating marsh facilitates the expansion of non-native species like *P. australis* and consequently, that new marsh provides diminished ecological functions compared to old marsh (Smith 2013). However, we found *P. australis* was a function of elevation and landscape position rather than a defining characteristic of new marsh replacing coastal forest. As high marsh on Goodwin experiences more flooding, contributions of *P. australis* to biomass, accretion rates, and soil nutrients may facilitate the eventual transition to native marsh species. We expect the ecological functions in newly formed marsh eventually to resemble those of older, lower elevation marsh on Goodwin Island as increased tidal flooding creates conditions more suitable for marsh species such as *S. patens*, *D. spicata*, and *S. alterniflora*. Hence, our observations suggest that marsh migration does not lead to permanent differences in ecological functions of the marsh, rather ecological functions converge as the marsh ages.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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