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ARTICLE

Coastal and Marine Ecology

The resistance of Georgia coastal marshes to hurricanes

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Abstract

Ecosystems vary broadly in their responses to disturbance, ranging from highly impacted to resilient or resistant. We conducted a large-scale analysis of hurricane disturbance effects on coastal marshes by examining 20 years of data from 10 sites covering 100,000 ha at the Georgia Coastal Ecosystems Long-Term Ecological Research site distributed across gradients of salinity and proximity to the ocean. We analyzed the impacts of Hurricanes Matthew (in 2016) and Irma (in 2017) on marsh biota (plants, crabs, and snails) and physical attributes (erosion, wrack deposition, and sedimentation). We compared these variables prior to the storms (2000–2015) to years with storms (2016, 2017) to those after the storms (2018–2020). Hurricanes generated storm surges that increased water depth and salinity of oligotrophic areas for up to 48 h. Biological variables in the marsh showed few effects of the hurricanes. The only physical variable affected was creek bank slumping; however, slumping had already increased a year before the hurricanes, suggesting that slumping could have a different cause. Thus, our study uncovered only minor, ephemeral impacts on Georgia coastal marshes, highlighting their resistance to hurricane disturbance of the lower magnitude that typically confronts this region of coastline.

KEYWORDS

climate change, coastal protection, disturbance ecology, GCE-LTER, resilience, salt marshes, storm surge

INTRODUCTION

Disturbances can alter the structure and functions of ecosystems (Bernhardt & Leslie, 2013). However, ecosystems can also be resistant or resilient to disturbance, experiencing few persistent negative impacts (Elsey-Quirk, 2016; O'Leary et al., 2017; Patrick et al., 2022). Resilient systems are affected but recover rapidly, whereas resistant systems experience minimal effects. In both cases, the system maintains function, structure, and feedbacks in the face of disturbance (Folke et al., 2004). Ecologists are increasingly interested in the resilience or resistance of systems to understand the mechanisms that minimize impact, especially because some disturbances are increasing due to climate change (Dale et al., 2001; Holland & Bruyere, 2014).

Hurricanes are a notable disturbance whose intensity and perhaps frequency are increasing (IPCC, 2021; Knutson et al., 2020; Kossin et al., 2020). Hurricanes can profoundly affect ecosystems by changing abiotic conditions and killing or damaging organisms (Boose et al., 1994; Greening et al., 2006; Tanner et al., 1991). However, hurricane effects can depend on the characteristics of the recipient system (Hogan et al., 2020; Patrick et al., 2022; Sousa, 1984). For example, although hurricanes can destroy the structure of terrestrial forests and coral reefs (Gardner et al., 2005; Scoffin, 1993), not all ecosystems are strongly affected. Grassland ecosystems with short-stature, flexible vegetation may not be affected by storm-generated wind, and sheltered habitats may not be affected by waves (Leonardi et al., 2018). Documenting hurricane effects across a range of ecosystem types is important to fully understand their impacts, especially in coastal systems that often receive the most intense hurricane exposure as the storm comes ashore (Sheng et al., 2022).

In coastal systems, hurricanes can cause strong wind and waves, substantial precipitation, and increased sea level. These factors can directly affect coastal ecosystems by altering salinity, depositing or eroding sediment, enhancing flooding, or destroying biotic structure. These direct effects can induce attendant, indirect effects on biota as the effects interact and magnify through species interaction networks (Lugo, 2008).

Hurricane effects can also be spatially complex and heterogeneous, even within the same system (Hu et al., 2018). In estuaries, subtidal and intertidal habitats are likely differentially affected. In subtidal habitats, hurricanes can drastically change water quantity and quality (Walker et al., 2021), with cascading impacts on vertical stratification, bottom water hypoxia, and increases in algal biomass and fish disease (Burkholder et al., 2004; Paerl et al., 2001). In contrast, intertidal habitats such as salt marshes have shown modest effects and quick recovery from hurricanes. Salt marshes dissipate wave energy and storm surges, especially when the marsh is highly elevated and continuous (Leonardi et al., 2018). Marsh vegetation is often pliable and can flatten during powerful storms. Although flattening may not dissipate storm energy, this process could make marshes more resistant to structural damage and help protect the marsh surface from erosion (Conner et al., 1989; Leonardi et al., 2018). For example, during Hurricane Harvey in 2017, salt marsh plants in Texas were generally resistant to hurricane effects, whereas stiffer mangroves suffered leaf loss and branch breakage (Armitage et al., 2020).

Hurricanes also influence the water depth and salinity of coastal marshes, but these effects are likely minimal. Increased water depth from hurricanes likely will not affect intertidal biota because they are already submerged for many hours a day and may experience flooded conditions as an extended high tide. Moderate changes in salinity are common in estuaries, and organisms such as halophytic plants and euryhaline animals tolerate these shifts (Li & Pennings, 2018; Torres et al., 2011). However, extended periods of freshening, which may occur with heavy rains, can kill or displace organisms used to saline conditions (Zedler, 1983).

Potentially the largest hurricane impact on coastal marshes is changes in sediment distribution. Hurricanes can deposit or erode sediments in marshes (Donnelly et al., 2001; Hu et al., 2018). The most extreme sediment effect occurs when barrier islands and their associated marshes are entirely reshaped from a hurricane. Examining 700 years of storm-related sediment events revealed that storm surges from category 2 hurricanes or greater often overtopped barrier islands, removing sediments from the beach and depositing overwash as sediment fans across adjacent back-barrier marshes (Donnelly et al., 2001). However, marshes farther from the ocean may be less susceptible to such depositional events (Donnelly et al., 2001). Therefore, hurricane-related effects of sedimentation likely vary spatially.

Hurricane characteristics, including their intensity, duration, and proximity, influence their impacts (Ayala & Matyas, 2016; Claudino-Sales et al., 2008). The frequency of direct hurricane strikes varies along the southeastern US coast, with hotspots in southeastern Louisiana, southern Florida, and eastern North Carolina (Muller & Stone, 2001). In contrast, much of the southeastern US coast has historically had fewer direct hurricane strikes (Muller & Stone, 2001). The Georgia coast, the location of this study, is typical of the southeast and is primarily subject to passage of hurricanes offshore and tropical storms from hurricanes that have made landfall elsewhere.

High spatial variation in hurricane impacts in coastal ecosystems requires well-replicated and well-distributed sampling over broad temporal and spatial scales to examine a hurricane's net influence. Because hurricanes are episodic, unexpected events, their effects rarely can be systematically documented except in cases where they come ashore near long-term monitoring efforts (Smith et al., 2009). The Georgia coast was affected by hurricanes in both 2016 and 2017 (Hurricanes Matthew and Irma, respectively). The timing of the hurricanes allowed us to use a Before–After design with long-term monitoring data from the Georgia Coastal Ecosystems Long-Term Ecological Research (GCE-LTER) program to assess storm effects on estuarine water conditions and coastal marsh biological and physical attributes. To evaluate hurricane impacts in coastal Georgia marshes, we compared data from 16 years prior to these storms (2000–2015), two years in which sampling occurred immediately following hurricanes (2016 and 2017), and three years post-storms (2018–2020). Our study combines four aspects that support a holistic examination of hurricane effects on coastal marshes, including (1) multiple biological and physical response variables, (2) a 20-year data record that puts the hurricanes into temporal context, (3) 10 replicated monitored sites covering 100,000 ha across gradients of salinity and proximity to the ocean, and (4) two hurricanes in consecutive years, which replicates the natural experiment and intensifies the signature of the hurricanes' impact.

METHODS

Hurricanes

In October 2016, Hurricane Matthew moved from the tropical Atlantic up the east coast of the southeast Atlantic United States, remaining 90 km offshore of the Georgia coast on October 7–8 (Stewart, 2017; Figure 1B). The storm brought category 2 hurricane-force wind gusts to the Georgia barrier islands, peak water levels over 1.5 m above mean higher high water (MHHW), and rainfall accumulations up to 44 cm (Stewart, 2017). In September 2017, Hurricane Irma made landfall in southwest Florida and passed across central Florida up to southern Georgia on September 11 (Figure 1A). The storm brought sustained winds of 93 km/h to coastal Georgia, peak water levels over 1.4 m above MHHW, and rainfall accumulations of up to 25 cm (Cangialosi et al., 2021). Automated water column sampling by the GCE-LTER sondes continued throughout the hurricanes' passage. Annual biological and physical measurements of monitored sites by the GCE-LTER program in the two hurricane years occurred 2–4 weeks after the storms.

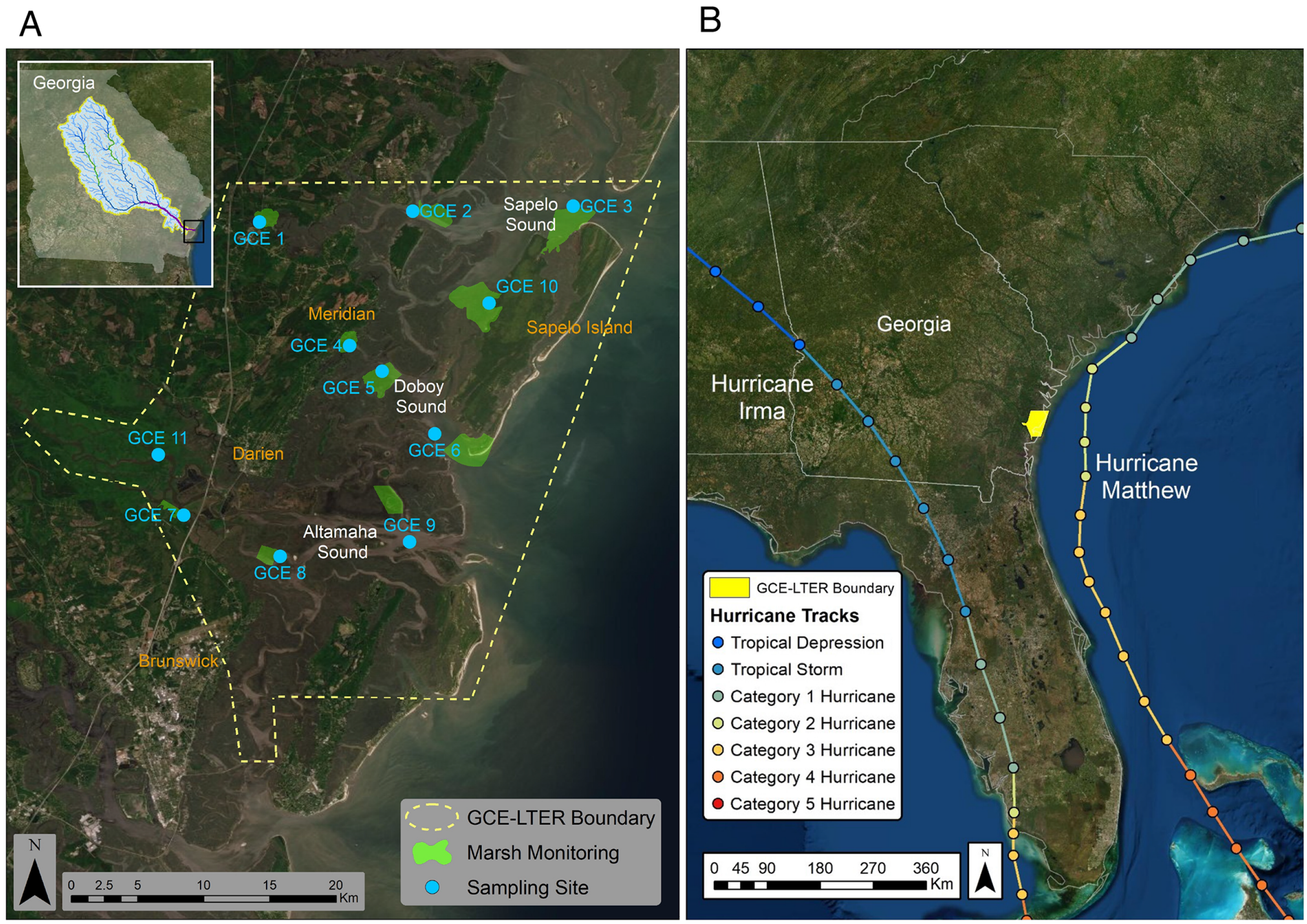

FIGURE 1 (A) Location of 11 Georgia Coastal Ecosystems (GCE) Long-Term Ecological Research (LTER) study sites in the Sapelo, Doboy, and Altamaha Sounds of Georgia, USA. The marsh sites are at GCE 1–10; GCE 11 is a tidal freshwater forest. Each sound has landward, mid-estuary, and seaward sites. Sites span a range of salinity conditions, including fresh (11), oligohaline (7), mesohaline (1, 8, 9), and polyhaline (2–6, 10) sites. Blue dots are the sonde locations measuring water variables; the green shading is the corresponding marsh area for each site. Coordinates of each sampled marsh site are in Appendix S2: Table S1. (B) Storm tracks of Hurricane Matthew (2016) and Hurricane Irma (2017) in the southeastern United States. Hurricane intensity is color-coded. GCE-LTER domain is shown as yellow polygon.

Hurricane effects on water conditions

A network of Sea Bird sondes measures salinity and water depth at nine locations throughout the GCE-LTER domain (GCE 1–3, 6–11) (Figure 1A; Appendix S2: Table S1; Di Iorio, 2020). To assess the effect of hurricanes on marsh attributes and water conditions (salinity and water depth), we analyzed these measures before and after Hurricane Matthew and Hurricane Irma. For water salinity (practical salinity units, PSU) and water depth (meters), we calculated mean, maximum, and minimum summary statistics for the period before the hurricanes (2000–2015) and compared deviations from these patterns for the 48 h encompassing the hurricane's acute influence in coastal Georgia (10/07/2016–10/09/2016 for Hurricane Matthew; 09/11/2017–09/13/2017 for Hurricane Irma). We also compared salinity changes among sites with different baseline salinities (e.g., oligohaline, mesohaline, or polyhaline) for the 48 h before, during, and after each hurricane. We fit a linear model for the relationship between the most extreme change (maximum or minimum) for each site relative to the mean salinity of the month prior to each hurricane using R version 4.1.2 (R Core Team, 2021). Model residuals met model assumptions of normality and heterogeneity.

Hurricane effects on coastal marsh attributes

The GCE-LTER program monitors permanent plots at 10 intertidal marsh sites located on or near the three sounds (GCE 1–10, Figure 1A). Permanent plots at each site are located on transects in creekbank ($n = 8$) and mid-marsh ($n = 8$) habitats, for a total of 16 plots per site ($n = 10$ sites). In mid-October of each year (starting in 2000, 2001, or 2002 depending on the variable, and running through 2020), we measured plant biomass, crab burrow density, snail density, percent creekbank slumping, percent cover of wrack, and sediment elevation at each site (Alber, 2020a, 2020b; Craft, 2020; Pennings, 2020a, 2020b). See Appendix S2 for detailed methods.

For each of these attributes, we calculated the mean and SD across sites for each year over the monitoring period. To determine whether measured marsh values were anomalous during each hurricane year (2016, 2017) and post-hurricane year (2018, 2019, 2020) relative to the pre-hurricane period (2000–2015) for each site, we used the pre-hurricane period to define the "normal" distribution for each variable and calculated the z score $(x - \mu)/s$ based on this distribution for responses measured in hurricane years and post-hurricane years. Here, x is the mean for each site for the focal year, μ is the population mean for each site from the pre-hurricane period, and s is the population SD for each site from the pre-hurricane period. We considered z-score values greater than 2 SDs from the mean (~5% of the distribution) as a significant deviation from the pre-hurricane period. Because we examined two zones (creekbank and mid-marsh) at 10 sites in two hurricane years and three post-hurricane years, we evaluated 100 z-score responses (40 in hurricane years; 60 post) for each biological variable. For physical variables, which were only measured at the creekbank, we had 50 z-score responses (20 in hurricane years; 30 post). Given these numbers of z scores, at an overall level of $\alpha = 0.05$, we expect ~5 significant results for each biological variable and 2–3 for each physical variable due to chance alone. For sediment elevation, with the exception of one missing value, we had measurements from seven sites from one zone for a total of 34 z scores (13 in hurricane years; 21 post) and would expect approximately two significant results due to chance alone. At oligohaline site GCE 7, two variables—snails and wrack—were not present pre-hurricane; therefore z scores were not calculable, and we considered hurricane effects there as negligible on those variables.

RESULTS

Hurricane effects on water conditions

Hurricanes Matthew (2016) and Irma (2017) altered water column salinity during the 48 h of each storm's closest approach relative to the 48 h before and after (Figure 2). The direction of salinity effects varied with local salinity (Figure 2). In both years, salinity declined ~4 PSU at polyhaline sites (Figure 2A,B), likely due to fresh rainfall. In contrast, salinity increased sharply (10–25 PSU) at the oligohaline sites due to salty storm surge (Figure 2E,F). At the mesohaline sites, salinity initially increased, then decreased; this pattern occurred against a backdrop of large pre-storm fluctuations in salinity due to the tidal cycle (Figure 2C,D). The change from baseline salinity decreased with increasing mean baseline salinity in both 2016 ($F_{1,7} = 7.13$, $p = 0.032$, $R^2 = 0.50$) and 2017 ($F_{1,7} = 29.19$, $p = 0.001$, $R^2 = 0.81$; Figure 2G,H). Although changes in salinity were rapid and anomalous relative to the months before and after the storms (Appendix S2: Figure S3), oligohaline sites showed the greatest changes relative to the pre-hurricane period (2001–2015; Appendix S2: Table S2).

All sonde locations increased in water depth during the hurricanes' 48-h period of influence (Appendix S2: Figure S2). Water depth exceeded, often by >1.5 m, the

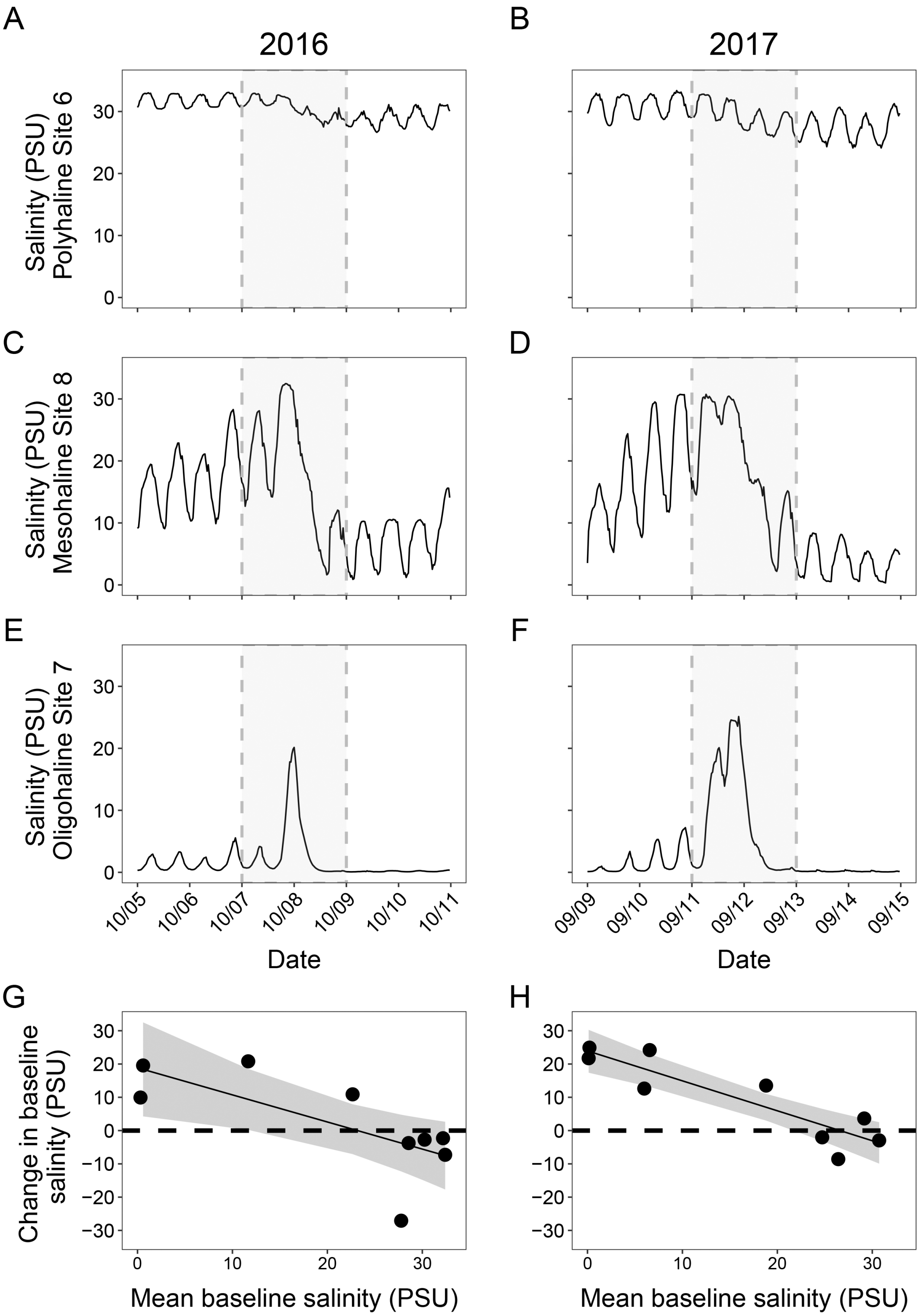

FIGURE 2 Salinity (in PSU) measurements taken at 30-min intervals for the 48 h before, during, and after Hurricane Matthew in 2016 at (A) polyhaline site 6, (C) mesohaline site 8, and (E) oligohaline site 7, and after Hurricane Irma in 2017 at (B) polyhaline site 6, (D) mesohaline site 8, and (F) oligohaline site 7. These sites are meant to be representative; other sites within the same salinity group showed similar patterns. The most extreme change in salinity (maximum or minimum) at all sites within a 48-h period of each hurricane is compared against the mean baseline salinity for the month prior to (G) Hurricane Matthew in 2016 and (H) Hurricane Irma in 2017.

mean pre-hurricane values at all sites, and exceeded pre-hurricane maximum values at two of the eight sites in 2016 and at six of the eight sites in 2017 (Appendix S2: Table S2). Water depth increases were greater relative to pre-hurricane values during Hurricane Irma (2017) than during Hurricane Matthew. Changes in water depth during the hurricanes were rapid and anomalous relative to the months before and after the storms (Appendix S2: Figure S4) and the pre-hurricane period (2001–2015; Appendix S2: Table S2).

Hurricane effects on coastal marsh attributes

In contrast to the strong short-term effects of hurricanes on water conditions, we observed few substantive effects of the two hurricanes on the biological (Figure 3A,C,E) or physical attributes (Figure 3B,D,F) of coastal marshes. Biological attributes of plant biomass, crab burrow density, and snail density during the two hurricane years generally remained within 2 SDs of responses measured during the pre-hurricane period (Appendix S2: Figures S6, S8, and S10). Plant biomass significantly increased in 2 cases and decreased in 3 cases out of 40 total responses (Appendix S2: Table S3). Crab burrows never differed during hurricane years. Snails increased significantly in 5 out of 40 total responses (Appendix S2: Table S3). Biological attributes did not differ consistently across sites as a function of salinity or landscape position (Appendix S2: Figures S5, S7, and S9).

For physical attributes, percent wrack disturbance positively exceeded two SDs for the pre-hurricane period in 2 out of 20 (10%) responses (Appendix S2: Table S3, Figure S14). Percent slump disturbance increased during hurricane years relative to the pre-hurricane period in 12 out of 20 (60%) responses (Appendix S2: Table S3, Figures S1 and S12). However, creekbank slumping began increasing at most sites a year before the hurricanes (Figure 3, Appendix S2: Figure S11), suggesting that slumping was initiated by a cause other than the hurricanes. Sediment deposition did not vary during the hurricane years (Figure 3F). Physical attributes did not vary consistently across sites as a function of salinity or landscape position (Appendix S2: Figures S11, S13, and S15).

In the post-hurricane years, there were no substantive trends in biological attributes that differed from pre-hurricane years (Appendix S2: Table S4, Figures S5–S10). Four out of 60 (7%) of plant biomass responses, 3 out of 60 (5%) of crab burrow density responses, and 4 out of 60 (7%) of snail density responses increased from the pre-hurricane period; one snail response decreased (Appendix S2: Table S4). All changes in snail abundance, even when significant, were small (Appendix S2: Figures S9 and S10). Percent wrack disturbance and sediment elevation also lacked strong trends in the post-hurricane years (Appendix S2: Figures S13–S16). Three out of 30 (10%) wrack disturbance responses increased from the pre-hurricane period (Appendix S2: Figure S14). Sediment elevation did not vary in the post-hurricane years (Appendix S2: Figure S16). These proportions of significant tests are what would be expected by chance if there was no real effect. In contrast to the other physical variables, percent slumping increased in 10 out of 30 cases (33%) relative to the pre-hurricane period (Appendix S2: Table S4, Figure S12).

DISCUSSION

Although hurricanes can cause extreme damage to some coastal systems such as coral reefs, dunes, and coastal forests (Ayala & Matyas, 2016; Claudino-Sales et al., 2008; Gardner et al., 2005; Lugo, 2008), our large-scale study complements a growing body of evidence that coastal marshes can be relatively resistant to hurricanes (Castagno et al., 2021; Elsey-Quirk, 2016; Mo et al., 2020). This finding is especially relevant if hurricanes are weaker or not direct landfalls—as in our study—in which case the biota and physical marsh attributes may not exhibit long-term effects from short-lived, pulse disturbances. In coastal Georgia, we observed brief, striking changes in water salinity and depth associated with hurricanes, but these effects did not translate to changes in the biological or physical attributes of coastal marshes. Increases in salinity in oligohaline sites were greater than the declines in salinity in normally salty areas. Thus, the push of salt water up the estuary due to the hurricanes' storm surge was stronger in this system than freshening due to excessive rainfall. Other studies showed that these two hurricanes also affected other aspects of the system, particularly increased dissolved organic carbon and dissolved organic matter concentrations in the estuary and enhanced rates of biodegradation that lasted for at least a month (Medeiros, 2022). However, our observed changes in water salinity and depth were short-lived. This finding is consistent with a review of hurricane effects that found that the strongest effects (typically on water column variables) were also the shortest in duration (Walker et al., 2021). These changes in water conditions function as positive controls, signaling that hurricane effects are detectable in our system, albeit with ephemeral influence.

In contrast, in our study, the biological and physical attributes of marshes were only weakly affected by the hurricanes. The exception to this pattern may have been creekbank slumping. Increased slumping during a period of high water is consistent with previous studies that indicate that soil creep at creekbanks is greatest during periods of high water, which can destabilize the soil (Mariotti et al., 2019). However, a rise in creekbank

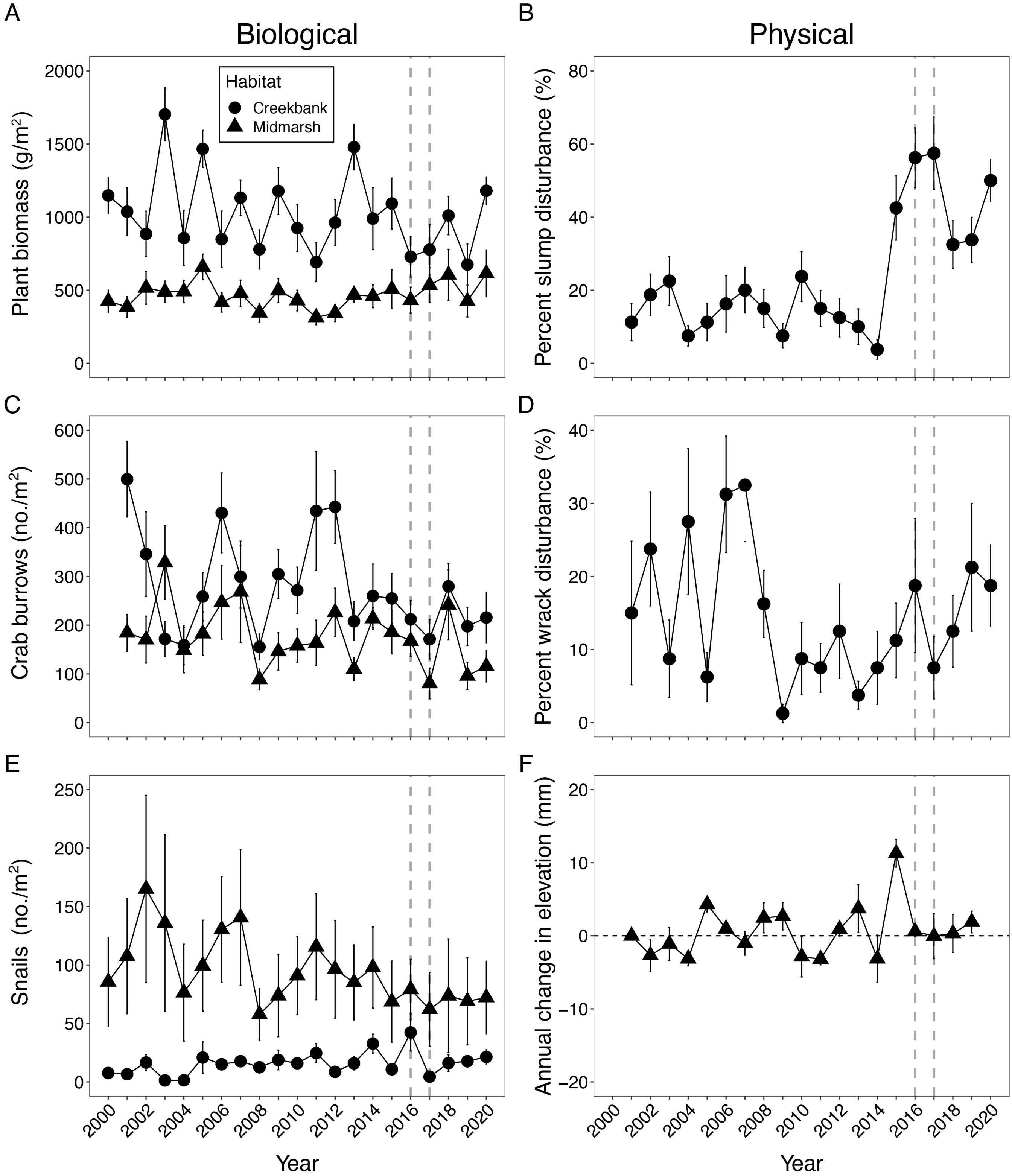

FIGURE 3 Mean ± SE values for the biological attributes of (A) plant biomass density, (C) crab burrow density, and (E) snail density and physical attributes of (B) percent slump disturbance, (D) percent wrack disturbance, and (F) annual change in sediment elevation compared with the previous year as measured by surface elevation tables. Data points for (A–E) are averaged over all 10 coastal marsh sites (Georgia Coastal Ecosystems [GCE] 1–10) monitored from 2000 or 2001 through 2020; data points for (F) are averaged across the seven sites for which we have complete records (GCE 1–6, 10) from 2001 to 2019, with 2001 set to 0 (see *Methods* for details). Vertical dashed lines indicate the two hurricane years. Horizontal dashed line in panel (F) marks the value of no change in elevation.

slumping began at many sites before Hurricane Matthew in 2016 (Figure 3B, Appendix S2: Figure S11). Thus, creekbank slumping may have been initiated by a different ecological driver, although hurricanes could have contributed to the process after initiation. Furthermore, attributing the slumping to pre-hurricane conditions is consistent with the finding that long-term marsh erosion is dictated by average wave conditions, while violent storms and hurricanes contribute less than 1% to long-term salt marsh erosion rates (Leonardi et al., 2016). Creekbank slumping remained high in the post-hurricane years (Figure 3B, Appendix S2: Figure S11), likely because it can take several years for a plot to slide from the creekbank into the creek.

Hurricanes did not substantially affect soil surface elevation (Figure 3F). Storms can have multiple, often opposing influences on wetland sediment elevations through sediment deposition, erosion, compaction, or root decomposition or growth (Cahoon, 2006). The influence of these processes may depend on storm characteristics and local wetland conditions. Our marsh sites were located along channels with limited fetch and were not exposed to sizable wave action. In other locations with greater fetch, such as the outer coast, increased wave action associated with hurricanes can cause considerable sediment erosion (Gharagozlou et al., 2020) or deposition (Zang et al., 2018).

Surprisingly, we did not see appreciable changes in wrack at the study sites. High winds and water depths from hurricanes can transport large quantities of wrack out of the marsh and into surrounding uplands (Smith et al., 2020). Although we did observe large accumulations of wrack at the upland-marsh border after these storms, the permanent plots were not in areas known to accumulate wrack, such as near creek bends or at the highest tidal elevations (Fischer et al., 2000). Thus, the storms may have moved wrack past the permanent plots to higher elevations. A remote sensing approach that considers the entire area would complement our measurements of how wrack distribution was affected by hurricanes.

The relatively minor impact of hurricanes on coastal marshes observed here could be because neither hurricane passed directly over the study area. A direct hit, especially by a stronger (Category 4 or 5) hurricane, might have more dramatic effects. However, even stronger hurricanes can have short-lived influences in coastal systems. For example, in 2017, water quality in Texas estuaries after Category 4 Hurricane Harvey returned to baseline levels within days to a few months (Walker et al., 2021). In 1989, the impacts of Category 4 Hurricane Hugo that directly hit South Carolina had limited effects on salt marsh creek geomorphology (Gardner et al., 1991), and fish and shrimp populations recovered quickly—within two months (Knott & Martore, 1991). Given the short generation times of marsh invertebrates and clonal growth of many plants, the life histories of dominant marsh species allow for rapid recovery.

Intertidal marsh organisms are generally adapted to deal with high short-term variability in physical factors. The effects of hurricanes can be similar to the range of natural variation to which these organisms are exposed during tidal or diurnal cycles. For example, short-term flooding associated with a hurricane likely affects salt marshes minimally, because it is similar to an extended high tide and the ecosystems are adapted to regular high tides. In fact, the submergence of vegetation likely protects it from damage caused by high winds (Armitage et al., 2020). Moderate changes in salinity—similar to those caused by hurricanes—commonly occur in estuaries; thus, estuarine organisms often have adaptations that help them tolerate such variation (Li & Pennings, 2018; Torres et al., 2011). For example, a four-year field experiment within the GCE-LTER domain examining salinity intrusion into an oligohaline tidal marsh found that plant communities were strongly affected by permanent salinity increases, but relatively tolerant of extended (2-month) salinity pulses (Li et al., 2022). Additionally, marsh plants in Georgia undergo natural senescence of aboveground biomass in the fall (O'Connell et al., 2020), which is when hurricanes typically strike the southeastern United States, so plants are less likely to be affected at this time of year.

Our study's strength lies in its holistic approach. By examining a 20-year dataset, we put the hurricane years in historical context. By examining multiple sites spanning 100,000 ha and using two water column variables and a suite of biological and physical marsh variables, our approach assessed the evidence for many possible hurricane impacts. Hurricanes can have site-dependent and storm-dependent effects, but our study highlights the overall resistance of Georgia coastal marshes to weaker storms that do not directly hit the coastline that are typical for this area. Combined with other studies, our findings suggest that coastal marshes can be resistant to hurricane effects, especially if the hurricanes are of lower strength or do not pass directly overhead. Coastal marshes protect inland areas, potentially serving as frontline ecosystems that can absorb some of the brunt of a hurricane's force as it comes ashore (Costanza et al., 2008; Shepard et al., 2011), while remaining largely intact in structure and function.

AUTHOR CONTRIBUTIONS

Steven C. Pennings conceptualized the study. Rachel S. Smith analyzed the data. James E. Byers drafted the manuscript. All the authors contributed to interpreting the results and editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data analyzed are publicly available in two locations, at NSF-sponsored Environmental Data Initiative (EDI): https://portal.edirepository.org/nis/home.jsp and the Georgia Coastal Ecosystems Long-Term Ecological Research (LTER) website: https://gce-lter.marsci.uga.edu/public/data/data.htm. EDI and the LTER website both serve as the final repositories for these data and all data included in the paper are archived in both locations. Citations and direct links to the specific datasets used are cited in full in Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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