Received: 5 December 2017 | Accepted: 6 July 2018
DOI: 10.1111/1365-2745.13049

RESEARCH ARTICLE

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

Warming accelerates mangrove expansion and surface elevation gain in a subtropical wetland

Glenn A. Coldren[1] | **J. Adam Langley**[1] | **Ilka C. Feller**[2] | **Samantha K. Chapman**[1]

[1]Department of Biology, Villanova University, Villanova, Pennsylvania

[2]Animal-Plant Interaction Lab, Smithsonian Environmental Research Center, Edgewater, Maryland

Correspondence
Glenn A. Coldren
Email: gcoldren@villanova.edu

Funding information
National Aeronautics and Space Administration, Grant/Award Number: NNX11AO94G and NNX12AF55G; National Science Foundation Division of Environmental Biology, Grant/Award Number: DEB1655659

Handling Editor: Brian Silliman

Abstract

1. Climatic warming can change how coastal wetland plants grow, thus altering their capacity to build land and keep pace with rising seas. As freeze events decline with climate change, mangroves expand their range to higher latitudes and displace salt marsh vegetation. Warmer air temperatures will likely alter above- and below-ground plant dynamics as this dramatic coastal wetland biome shift proceeds, which in turn may result in changes in ecosystem function such as sediment building.
2. We used a large scale in situ warming experiment in a subtropical wetland to increase both marsh and mangrove ecosystem air temperatures. We assessed how 2 years of continuous warming influenced above- and below-ground plant growth and surface elevation relative to sea level.
3. We found that chronic warming doubled plant height and accelerated the expansion of mangrove into salt marsh vegetation, as indicated by a sixfold greater increase in mangrove cover in warmed plots compared to ambient temperature plots and a corresponding loss in salt marsh cover. Surface elevation gain, a measure of soil-building capacity, increased due to warming over a 2-year period and these changes in surface elevation were driven by increased mangrove root production in warmed plots.
4. *Synthesis*. Our findings suggest that, in some coastal wetlands, warming can facilitate plant community changes from marsh to mangrove, with corresponding increases in growth that help coastal wetlands to keep pace with sea-level rise.

KEYWORDS
climate change, coastal wetland, mangrove, plant growth, range shift, salt marsh, surface elevation gain, warming

1 | INTRODUCTION

Mangroves are shifting their range poleward on at least five continents, mostly due to relief of temperature thresholds (Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014). This coastal biome shift usually entails mangroves, which are halotolerant, tropical, woody wetland plants, displacing the existing temperate herbaceous salt marsh plants. In some sites in Australia and New Zealand, increases in mangrove abundance are driven by nonclimatic processes such as sediment delivery and subsidence (Lovelock et al., 2007; Rogers, Saintilan, & Heijnis, 2005; Swales, Bentley, & Lovelock, 2015) as well as changes in rainfall patterns (Eslami-Andargoli, Dale, Sipe, & Chaseling, 2009). In some sites in Florida, USA, and Mexico, this expansion is thought to be due to sea-level rise (Krauss, From, Doyle, Doyle, & Barry, 2011; López-Medellín et al., 2011) and changes in freshwater inputs (Howard et al., 2017; Krauss et al., 2011). However, in other regions, like in China, the cause of expansion remains unknown (Durango et al., 2012). Along the Atlantic and Gulf coasts of the United States, mangrove expansion outside its range is most often attributed to a reduction in the severity and frequency of discrete freezing events (Cavanaugh et al., 2014; Osland, Day, Doyle, & Enwright, 2013). Where they are encroaching, mangroves can increase in abundance rapidly, with potential implications for biogeochemical processes and ecological interactions (Barreto, Morrissey, Wykoff, & Chapman, 2018; Cavanaugh et al., 2014; Doughty et al., 2016; Giri & Long, 2016; Osland et al., 2013). For example, at the Kennedy Space Center (KSC) in Florida, mangrove cover increased by 69% in only 7 years (2003–2010) (Doughty et al., 2016) and was accompanied by a 25% increase in above-ground wetland carbon (C) storage, although other studies show either no effect of mangrove expansion (McKee & Vervaeke, 2018; Perry & Mendelssohn, 2009) or effects constrained to specific locations (Comeaux, Allison, & Bianchi, 2012; Yando et al., 2016). While the impacts of this climate-driven range shift on wetland ecosystems are being studied, the effect of chronic warming on these dynamic ecosystems is relatively unknown (Saintilan & Rogers, 2015).

The dramatic plant-range shift that is occurring as mangroves encroach into marshes can alter ecosystem services of these habitats. Both salt marshes and mangrove forests improve water quality, maintain food webs, provide coastal protection through wave attenuation and surface elevation stability, and sequester C; however, the extent of these services varies with regard between habitat, species, and location (Barbier et al., 2011). Woody plant encroachment into other herb-dominated ecosystems alters a number of important below-ground processes such as root productivity, organic matter (OM) decomposition, and microbial carbon cycling (Jackson, Banner, Jobbágy, Pockman, & Wall, 2002; Knapp et al., 2008; Rundel, Dickie, & Richardson, 2014). Mangrove encroachment into salt marsh habitats can alter below-ground C storage, due to increased root production (Kelleway et al., 2016; Yando et al., 2016). However, effects are not consistent across locations and above- and below-ground biomass capacity of C storage can differ (Feher et al., 2017; McKee & Vervaeke, 2018; Perry & Mendelssohn, 2009; Yando et al., 2016). Both salt marshes and mangroves can exhibit high levels of root production and sediment trapping, processes that can maintain biome position with respect to sea levels (Langley, McKee, Cahoon, Cherry, & Megonigal, 2009; McKee, Cahoon, & Feller, 2007). As mangroves expand into salt marsh habitat, their relative contribution to sediment accretion will likely have strong implications for habitat persistence and dominance. In Louisiana, USA, salt marsh and mangrove habitats have shown equivalent accretion rates, suggesting that mangrove encroachment will not alter surface elevation of salt marshes (McKee & Vervaeke, 2018; Perry & Mendelssohn, 2009). However, in Texas, USA, mangroves had a 4-cm greater elevation gain than salt marshes in one site (Comeaux et al., 2012). These studies have considered how these ecosystem services of salt marsh change with mangrove expansion as a result of reduced freeze frequency but have not investigated how the coupling of chronic warming may further alter these interactions.

It remains unknown how chronic warming will impact marsh conversion into mangrove forest and subsequent soil-building processes, which play a key role in determining the long-term stability of these ecosystems. Recent predictions suggest that the sediment accretion of many salt marshes will not keep pace with sea-level rise, resulting in potential losses of salt marsh habitat of over 60% (Crosby et al., 2016). Mangrove wetlands too are threatened by rising sea levels and lack of sediment (Lovelock et al., 2015). However, other effects of global change may also influence coastal wetlands ability to keep pace with sea level. Elevated carbon dioxide and temperatures may accelerate salt marsh growth and subsequently enhance elevation gains (Charles & Dukes, 2009; Cherry, McKee, & Grace, 2009; Coldren et al., 2016; Kirwan, Guntenspergen, & Morris, 2009). Elevated temperature may also increase wetland OM decomposition rates which have the potential to counter the positive effects of accelerated growth on elevation change (Kirwan & Blum, 2011).

Canopy height, above-ground biomass, and productivity in coastal wetlands are likely to increase with increases in minimum and mean annual temperatures (Feher et al., 2017). In situ warming studies performed in temperate salt marshes found that warming increases salt marsh standing biomass (Charles & Dukes, 2009; Gedan & Bertness, 2010). We might expect that warming in wetland soils could speed up OM decomposition, but microbial responses to altered temperatures in low-oxygen wetland soils are poorly characterized (Gill, Giasson, Yu, & Finzi, 2017). Warming experiments in the tropics are extremely rare even though tropical organisms can exhibit more sensitivity to warming than temperate counterparts given the relative stability of tropical temperatures over evolutionary time (Cavaleri, Reed, Smith, & Wood, 2015). In a small-scale warming study targeted at assessing the response of mangrove seedlings and salt marsh plants to warming in a temperate-tropical transition area, we recently found that chronic warming enhanced salt marsh biomass but had little effect on associated mangrove seedlings (Coldren et al., 2016). However, as mangrove seedlings have small root systems, we would not expect mangroves at an early life stage to mediate effects of warming on soil elevation gain. Larger mangroves, which may have the capacity to alter surface elevation to keep pace with sea-level rise, have not been subjected to in situ experimental warming despite their likelihood to be heavily impacted by climatic warming (Ward, Friess, Day, & MacKenzie, 2016).

We hypothesized that experimental warming will alter mangrove and salt marsh growth and that changes in growth will alter surface elevation. To test this hypothesis, we deployed a large-scale (14.6 m^2 plots) warming experiment in a subtropical coastal wetland at the transition latitudes of salt marsh and mangroves at the KSC inside the Merritt Island National Refuge, Florida, USA. Over a 2-year experiment, we measured plant above-ground growth and root biomass to assess plant responses to warming. We also assessed changes in surface elevation and linked those to changes in root biomass. Using this experiment, we tested the predictions that warmer temperatures will increase salt marsh and mangrove (a) above-ground growth, (b) below-ground growth, and (c) surface elevation gain.

2 | MATERIALS AND METHODS

2.1 | Study site description

We performed this experiment at the KSC within the Merritt Island National Wildlife Refuge (MINWR) on Merritt Island, Florida, USA. This ecosystem is part of the Indian River Lagoon (IRL), which spans 260 km of the east coast of Florida and represents an important subtropical transition zone between temperate and tropical species, such as salt marsh and mangroves. Because of its position at the ecotone of these two wetland biomes (marshes and mangroves), KSC is an ideal location to test the effects of chronically elevated temperatures on wetland plant growth and maintenance of surface elevation. The MINWR area is undergoing rapid encroachment of tropical species into areas historically dominated by subtropical species as a result of shifts in climatic patterns. The reduction in the frequency of severe freeze events since a series of freeze events in 1982, 1983, 1985, and 1989 has resulted in significant shifts from salt marsh- to mangrove-dominated areas (Lonard & Judd, 1991; Osland et al., 2017; Provancha, Schmalzer, & Hall, 1986). At KSC, coastal wetlands and sand dunes help protect NASA's $5.6 billion of low-lying infrastructure against rising seas (Doughty et al., 2016; Doughty, Cavanaugh, Hall, Feller, & Chapman, 2017). Recently, Hurricane Matthew highlighted this area's vulnerability to storm surge, a threat that is compounded by ongoing sea-level rise and increased frequency of strong storms (Nicholls & Cazenave, 2010; Nicholls, Hoozemans, & Marchand, 1999).

Sea levels at the KSC are projected to rise by 13–20 cm by 2050 (the middle 67% of modelled values using seven Global Circulation Models and three emissions scenarios; Rosenzweig et al., 2014). Downscaled climate projections predict 1.5–2.6°C (summer–winter) of warming at KSC by 2050 (Rosenzweig et al., 2014). Due to the availability of such precise projections, we targeted our warming experiment to meet these levels of warming.

Our salt marsh and mangrove experimental ecotone was located in the Mosquito Control Impoundment C20-C (28.4889°N, 80.5778°W), which is open to natural tidal flow, and experiences microtidal tides similar to those found in the surrounding IRL, between 0.1 and 0.7 m (Smith, 1987). This site has hydric sandy soils with an average organic layer of 10 cm. Mean monthly air temperatures at this site range from 10°C in winter and 33.3°C in summer. The heaviest rainfall occurs in the late summer (June–September), with a mean annual precipitation of 137 cm and soil pore water salinity that ranges from 30.0 to 50.8 ppt. The dominant salt marsh plant species, located in the middle to high intertidal zone, at this site was *Distichlis spicata*, mixed with low densities of *Juncus roemerianus*, *Salicornia virginica*, and *Batis maritima*. Other associated salt marsh grasses, *Spartina alterniflora* and *Spartina patens*, and succulents including *Sesuvium portulacastrum*, also occur, but these plants are not found within the experimental plots. The dominant mangrove species in the experimental plots was *Laguncularia racemosa*; however, *Avicennia germinans* does occur in the local vicinity. *Laguncularia* is found throughout the tropical and subtropical regions, occupying similar geographic limits as *Rhizophora mangle* and is predicated to have similar expansion potential under warming conditions (Cavanaugh et al., 2014). Within the KSC and our site, *L. racemosa* was found consistently interacting with *D. spicata* along an invasion front.

2.2 | Experimental design

The warming experiment was initiated in August 2014 and continued for 22 months. To provide a chronic warming treatment, we deployed large-passive warming chambers on plots where juvenile mangroves had established in the marsh (Figure 1). Six plots were located along a front of mangrove expansion. A minimum 2 m buffer zone between plots was established to minimize root interaction between plots as trees were *c.* 2 m in height at experiment initiation. The study was only performed for 22 months in part to minimize

FIGURE 1 Location of the study site, which occurs at the intersection of the mangrove-dominant and marsh-dominant zones on the East Coast of Florida

root interaction between plots as the trees grow in size. Open-top passive warming chambers (2.4 m × 6.1 m × 2.4 m height) were built to cover three of six plots. Disturbance to the plots during installation was minimized with the use of temporary platforms when working inside plots.

Each plot was positioned so that it incorporated a mangrove-dominated area (“mangrove zone”) and a salt marsh-dominated area ("salt marsh zone") (Figure 1, Supporting Information Figure S1). Salt marsh zones of plots were primarily composed of *D. spicata*. Adult and juvenile mangroves did not occur in the salt marsh zone and seedlings occurred rarely accounting for less than 1% of vegetation cover. Mangrove zones contained large juvenile (~2 m height) *L. racemosa* mangrove trees. These two vegetation zones allow for direct comparison between warming effects on salt marsh versus mangrove vegetation.

Thus, the experimental design encompassed two treatments, temperature (warmed and control), and vegetation type (mangrove- and salt marsh-dominated “zones”). We designed the experiment using a split-plot design. The whole plot treatment was temperature with vegetation zone as subplots within each whole plot treatment (Supporting Information Figure S1). The whole plot treatments were replicated three times for a total of six plots with two zones each (2 temperatures × 2 vegetation zones × 3 replicates). A split-plot design was chosen as it allowed both mangroves and salt marsh to occur inside each plot, which allowed for the measurements of change in plot cover and dominance between the two vegetation types.

In line with the downscaled projections for KSC in 2050 (Rosenzweig et al., 2014), the passive warming chambers we constructed generated average air temperatures 1.8°C higher than adjacent control plots. The chambers consisted of reinforced PVC and SUNTUF clear corrugated polycarbonate panels (Parlam Americas, PA, USA; Figure 1) that allow 90% full light transmission. The warming chambers enclosed wetland vegetation on all sides in a 2.4 × 6.1 × 2.4 m rectangle. To minimize effects of shading, precipitation, and gas exchange, the tops of the chambers were left uncovered (modified from Charles & Dukes, 2009; Coldren et al., 2016). This resulted in an average 95% PAR transmission into the experimental chambers. Each chamber had a 5-cm gap between the base of the frame and the soil surface to allow natural tidal flow between plots. Control treatment (nonwarmed) plots were marked with PVC stakes and contained the same vegetation composition as warmed plots.

We recorded air and soil temperatures at 30-min intervals to assess relative warming throughout the experiment using HOBO pendant data loggers (Onset Computer Corporation, Bourne, MA, USA). Shielded sensors were attached to PVC poles at 20 cm above the sediment surface to record air temperature. Soil temperature sensors were buried at 10 cm below the sediment surface to record soil temperature. No freezes were recorded during the experiment by the temperature loggers, and a NASA weather station within 0.2 km of the experimental site confirmed that no freezes occurred during the study. Over the entire study, the air temperature in the passive warming treatment was 1.8°C warmer on average; however, the difference between control and warmed ranged from +0.04 to +15.6°C. Soil temperatures, relative humidity, and soil pore water salinity were unaffected by the passive warming treatment (Supporting Information Table S1).

2.3 | Above-ground plant growth

We measured mangrove and salt marsh growth in summer and winter of each year. For mangrove growth assessments, we measured mangrove height, canopy volume and area, leaf abundance (number of leaves per a 50 cm branch), leaf surface area (for a subset of 10 leaves per tree), leaf mass (for a subset of 10 leaves per tree), branch length (for a subset of 10 branches), branch density, and leaf scar abundance (on a subset of 10 branches). For salt marsh vegetation assessments, we measured canopy height, percent cover, and shoot density. Salt marsh height was determined from averaging the height of the four tallest stems of the dominant salt marsh, *D. spicata* from the subsampled plots. Percent cover of salt marsh was estimated visually for both vegetation zones. Shoot density of salt marsh was measured for all observed salt marsh species (primarily *D. spicata* with *J. roemerianus*, *S. virginica*, and *B. maritima*) in two 10 × 10 cm randomly subsampled areas within each zone of the plot (two per salt marsh zone and two per mangrove zone; total four per plot). These same subsampled areas were collected for salt marsh biomass in each sampling period. Within each 10 × 10 cm subsampled area, all live above-ground salt marsh was collected (clipped and gathered) and sorted by species. All biomass was dried at 70°C until a constant mass was achieved. The above-described plant growth measurements have been used in many coastal wetland studies and provide a comprehensive picture of growth of these wetland plants (Morris, 2007).

2.4 | Plant cover and dominance

We also assessed above-ground plant changes using percent cover and dominance to establish changes in plant composition across the mangrove-salt marsh interface established in each plot (Supporting Information Figure S1). Percent cover by species group (salt marsh, mangrove, and bare ground) was estimated across the whole plot treatment. Change in percent cover by species group was determined from the difference in percent cover from experiment initiation and after 22 months. To determine species expansion and contraction across the zones, we also used a metric that we termed “percent dominance.” To assess changes in species expansion and retraction at this interface, we assessed percent dominance as a change in relative cover along the horizontal extent of the chambers (similar to Yando, Osland, & Hester, 2018). This was measured as an average of the maximum and minimum horizontal extent (m) of dominance by salt marsh, mangroves, and bare areas across the chamber (Supporting Information Figure S2). Dominance by species group was assigned based on the species group with the greater proportion of cover in any given area within the plot. From this, percent dominance was calculated as the proportion of the average horizontal extent across the 6.6 m length of the chamber. At the time of initiation, each chamber was established with *c*. 35% dominance by mangroves (average 2.3 m horizontal extent across the chamber), with the remainder of the plot dominated by salt marsh and bare ground. However, bare ground accounted for less than 5% of the horizontal extent of plots. Change in percent dominance by species group (salt marsh, mangrove, and bare ground) was determined from the differences between horizontal extents established at experiment initiation and measurements after 22 months. This approach provides a measurement of change in dominance due to mangrove expansion and/or retraction and a corresponding decrease and/or increase in salt marsh.

2.5 | Below-ground plant mass

In October 2014 and again in March 2016, we took soil cores (60 cm depth, 6.2 cm diameter) to obtain total below-ground plant mass in warming and control plots across the two vegetation zones. We term this variable "belowground plant mass" in the text because we include both roots and rhizomes in this measurement. We only sampled below-ground plant mass two times over the course of the experiment in order to avoid excess coring in plots where soil elevation tables were deployed (see below). Soil cores were taken in all plots (6 plots × 2 vegetation zones) to a depth of 60 cm using a stainless steel gouge auger (AMS sampling, American Falls, ID) and sectioned into 0–20 cm, 20–40 cm, and 40–60 cm segments. The majority of the roots and rhizomes (>80%) were in the top 20 cm, so we report below-ground plant mass from 0 to 20 cm. After washing through a 2 mm sieve, roots and rhizomes were sorted into fine (<2 mm) and coarse (>2 mm) diameter categories, oven dried, and weighed. Live versus dead and mangrove versus grass roots were distinguished visually. Below-ground plant mass bulk density was determined using wet and dry tissue masses and volume via water displacement. Because any change in mass (live or dead) could contribute to soil elevation change, we report the total below-ground plant mass by zone here. Using the two sampling dates, we estimated net below-ground plant mass change over time. Roots could have died and decomposed during this time period, so we report these data as "net change in mass."

2.6 | Surface elevation change

To determine how warming and vegetation type affect soil building, changes in surface elevation were assessed using shallow rod surface elevation tables (shallow RSETs) positioned across the salt marsh- and mangrove-dominated zones of each plot. RSETs are a technique developed for wetland ecosystems to provide precise assessments of sediment surface elevation changes (Cahoon, Lynch, Hensel, et al., 2002; Cahoon, Lynch, Perez, et al., 2002; McKee, 2011). We chose to only use shallow RSETs to evaluate the changes within the rooting depth of salt marsh and mangrove zones, as this technique is designed to measure elevation changes over the soil profile, integrating below-ground plant growth and other geomorphic processes. The shallow RSETs, however, will not provide insight to subsidence processes that may occur below the root zone (Cahoon, Lynch, Hensel, et al., 2002). In each plot, we installed a shallow RSET with four aluminium legs to a benchmark depth of 2 m to encompass the plant-rooting zone (McKee, 2011). We determined that the plant-rooting depth in the plots at KSC was a maximum of 1 m through sediment cores at experimental initiation. Our shallow RSETs were designed to be placed at the transition between salt marsh and mangrove zones within the plots and thus allow paired measurements of each zone. This design (Supporting Information Figure S1) provided a total of eight distinct positions from the shallow RSET with four in the mangrove and four in the salt marsh portions of each plot.

The shallow RSETs were measured at 0, 12, and 22 months. RSETs measure the relative elevation change over time in up to eight distinct positions around a permanently anchored RSET, encompassing approximately a 1.5 m^2 area (McKee, 2011). In each position, a portable levelling device (hereafter "RSET arm") was horizontally extended from the RSET. From the RSET arm, nine-pin readings were made by lowering the pins to the sediment surface. The difference in the length of the pin remaining above the RSET arm is measured to the nearest millimetre. A shallow RSET measured in eight positions yields a total of 72 observations in a single-sampling period. The stable benchmark of the RSET allows for repeat measurements at precise locations over time. The change in the height of pins over time reflects changes in the elevation of the sediment surface. In our study, the elevation change was averaged across the four positions per vegetation zone in each temperature treatment plot to provide the sediment elevation at each sampling period. Sediment elevation change was change from experiment initiation to 22 months. This design allowed for accurate assessment of how surface elevation changes within salt marsh and mangrove zones under warmed and control temperature conditions.

Sediment deposition can also impact surface elevation through "vertical accretion." In order to account separately for sediment dynamics and thus determine the impact of root dynamics on surface elevation, two feldspar horizon markers were established in each vegetation zone (salt marsh and mangrove) within each plot to assess vertical accretion (four per plot). Markers were established and measured in conjunction with RSETs. For each a marker, ~2 cm deep feldspar layer was laid on the wetland surface in 25 × 25 cm plots. However, the plots experienced no measurable deposition, as none of the horizon markers were buried through the course of our experiment. Therefore, we report no vertical accretion occurred. See Supporting Information Figure S1 for an illustration of SET and marker horizon design in plots.

2.7 | Statistical analysis

Mangrove growth data were analysed using a one-way analysis of variance (ANOVA) with warming treatments (two levels: warmed and control). The mangrove growth response variables were change in height (cm), canopy volume (m^3), canopy area (cm^2), leaf abundance, leaf surface area (cm^2), leaf mass (g), branch length (cm), branch density, and leaf scar abundance. Canopy area was based on the area of an ellipse, using maximum and minimum canopy widths. Canopy volume was based on the volume of an ellipsoid using the maximum and minimum canopy widths and maximum canopy height. A one-way ANOVA was used as the adult mangroves were constrained to the mangrove-dominated zones as per the split-plot design. Therefore, a direct comparison of mangrove growth in both vegetation zones was not possible. To meet the assumptions of normality and homogeneity of variances, all mangrove variables were log transformed except leaf mass, which was square root transformed.

Surface elevation change, salt marsh growth, above-ground biomass, and change in below-ground plant mass were analysed using split-plot ANOVA with temperature treatments (two levels: warmed and control) as whole plot and vegetation zone (two levels: salt marsh and mangrove) as subplot factor within the whole plot. Salt marsh growth and biomass response variables were plant height (cm), percent cover, density (per m^2), and above-ground biomass (g/m^2) at 22 months. To meet assumptions of normality and homogeneity of variances, salt marsh height, density, and biomasses were log transformed. Surface elevation and salt marsh percent cover were not transformed.

Percent change in cover and dominance were both calculated as the difference in salt marsh, mangroves, and bare ground at experiment initiation (0 month) and termination (22 months). As change in percent cover and dominance were measured across the whole plot, each group (salt marsh, mangrove, bare ground) was analysed as separate one-way ANOVAs with warming treatments (two levels: warmed and control). Both percent cover and dominance met the assumptions of normality and homogeneity of variances and did not need to be transformed. All statistical analyses were performed using sas version 9.3 (SAS Institute Inc., 2011).

3 | RESULTS

3.1 | Mangrove response

Final mangrove height was double in warmed plots compared to control plots (Warming $F_{1,5} = 7.95$, $p < 0.0479$; Figure 2a and Table 1). Mangrove canopy volume increase was nearly double in warming plots compared to control plots (Volume warming $F_{1,5} = 8.30$, $p < 0.0450$; Supporting Information Figure S3, Table 1) corresponding with the increases in mangrove cover in warming plots

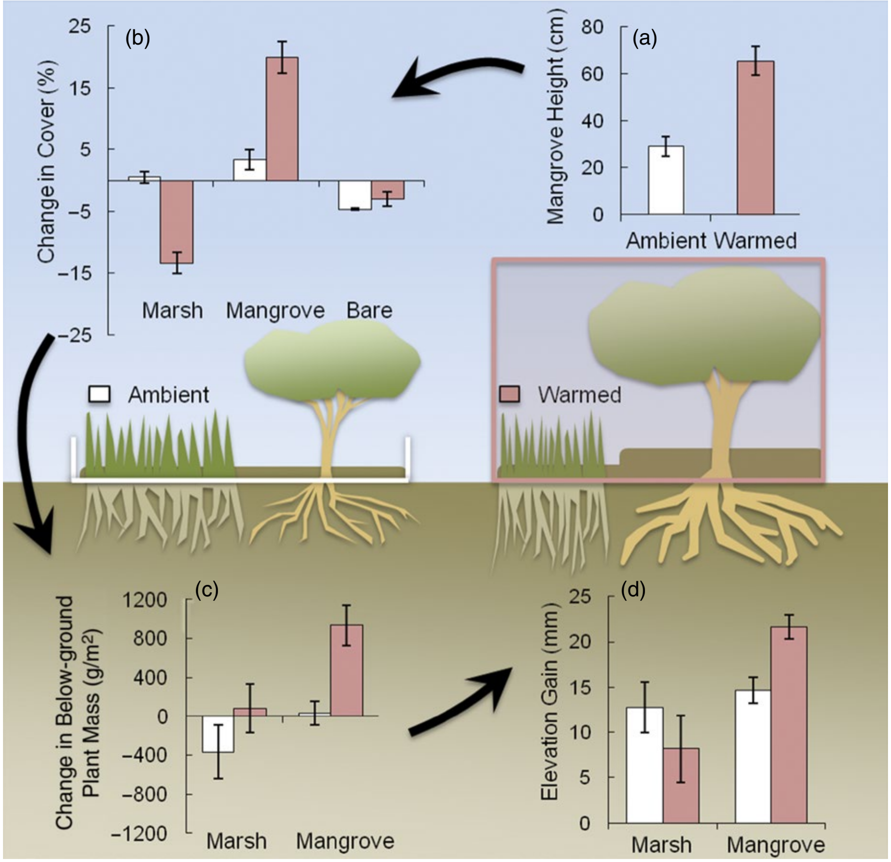

FIGURE 2 Response of mangroves and salt marshes to warming conditions: (a) mangrove height (cm), where chronic warming accelerates vertical growth, (b) percent change in cover, where areal expansions of mangrove shade out salt marsh plants, (c) change in below-ground plant mass (g/m^2), where increased root productivity and areal coverage of individual mangroves result in greater below-ground growth, and (d) change in elevation (mm), which is largely determined by the changes in below-ground biomass. Warming treatments included ambient (control) and warming chamber. Data are $M \pm SE$

(Figure 2b). Canopy area had a marginally significant effect, with increased area under warming conditions (Table 1). The changes in canopy volume in warmed plots corresponded with a 400% greater increase in percentage of plot dominated by mangroves than control plots (Supporting Information Figure S4 and Table S2). Leaf abundance and leaf surface area were also positively impacted by chronic warming (Abundance warming $F_{1,5} = 8.95$, $p < 0.0402$; Surface area warming $F_{1,5} = 16.04$, $p < 0.0161$; Supporting Information Figure S5 and Table 1). However, leaf mass, branch length, branch density, and leaf scar abundance were unaffected by warming (Table 1).

3.2 | Salt marsh response

Chronic warming positively affected salt marsh percent cover and shoot density and had a marginally significant positive effect on height (Cover warming $F_{1,11} = 26.74$, $p < 0.0009$, Shoot density warming $F_{1,11} = 32.29$, $p < 0.0005$, Height warming $F_{1,11} = 5.06$, $p < 0.0546$; Table 2). The effect of chronic warming on salt marsh biomass was not significant; however, a trend towards warming increasing biomass existed (Supporting Information Figure S6 and Table 2). Although not statistically significant, a consistent trend of salt marsh in the mangrove-dominated zones having a reduced response to warming compared to salt marsh in the salt marsh-dominated zone existed (Table 2).

3.3 | Changes in plant cover and dominance

Chronic warming altered relative plant cover and dominance. Percent mangrove covered significantly increased, with a corresponding decrease in salt marsh cover (Mangrove $F_{1,5} = 25.00$, $p < 0.0075$, Marsh $F_{1,5} = 10.00$, $p < 0.0341$; Figure 2b and Table 3). Percent change in bare area did not significantly changed with warming conditions ($F_{1,5} = 3.27$, $p = 0.1448$; Figure 2b and Table 3). Percent dominance followed similar patterns as percent cover. Percent mangrove dominance significantly increased by 25% in warmed plots with an average 1.62 m increase in linear extent (Supporting Information Figure S4 and Table S2). Salt marsh dominance showed a corresponding decrease of 26%, with an average 1.74 m loss in warmed chambers compared to control plots (Supporting Information Figure S4 and Table S2). Change in percent dominance of bare areas between warmed and control plots was not significantly different (Supporting Information Figure S4 and Table S2).

TABLE 1 Mangrove (*Laguncularia racemosa*) growth analysed using individual one-way ANOVAs with warming treatments (warmed and control)

	df	MS	*F*	*p*
Height (cm)	1,5	2008.18	7.95	**0.0479**
Canopy volume (m^3)	1,5	65.45	8.30	**0.0450**
Canopy area (cm^2)	1,5	0.17	7.66	0.0504
Leaf abundance	1,5	797.98	8.95	**0.0402**
Per leaf surface area (cm^2)	1,5	927.5267	16.04	**0.0161**
Leaf mass (g)	1,5	0.00	4.82	0.0932
Branch length (cm)	1,5	14.23	0.62	0.4743
Branch density	1,5	2.59	1.62	0.2723
Leaf scar abundance	1,5	0.12	0.0001	0.9777

Note. Significant differences are bolded ($p < 0.05$).
df : degrees of freedom; MS: mean squares; *F*: *F*-statistic; *p*: *p*-value.

TABLE 2 Salt marsh (*Distichlis spicata*) growth analysed using a split-plot ANOVA with warming treatments (warmed and control) as whole plot and vegetation type (salt marsh and mangrove) as subplot within warming treatments

	df	MS	*F*	*p*
Salt marsh above-ground biomass (g)				
Warming treatment	1,11	360.36	3.64	0.0927
Vegetation zone	1,11	166.95	1.69	0.2300
Vegetation × Warming	1,11	273.80	2.77	0.1347
Percent cover				
Warming treatment	1,11	3,008.33	26.74	**0.0009**
Vegetation zone	1,11	33.33	0.30	0.6011
Vegetation × Warming	1,11	8.33	0.07	0.7924
Height (cm)				
Warming treatment	1,11	1,240.33	5.06	**0.0546**
Vegetation zone	1,11	75.00	0.31	0.5952
Vegetation × Warming	1,11	280.33	1.14	0.3160
Shoot density (per m^2)				
Warming treatment	1,11	1,200.00	32.29	**0.0005**
Vegetation zone	1,11	12.00	0.32	0.5855
Vegetation × Warming	1,11	40.33	1.09	0.3280

Note. Significant differences are bolded ($p < 0.05$).
df: degrees of freedom; MS: mean squares; *F*: *F*-statistic; *p*: *p*-value.

TABLE 3 Percent change in cover of salt marsh, mangroves, and bare areas were analysed using individual one-way ANOVAs with warming treatments (warmed and control)

Percent change in cover	*df*	MS	*F*	*p*
Mangrove	1,5	416.67	25.00	**0.0075**
Salt Marsh	1,5	416.67	10.00	**0.0341**
Bare Ground	1,5	20.17	3.27	0.1448

Note. Significant differences are bolded ($p < 0.05$).
df: degrees of freedom; MS: mean squares; *F*: *F*-statistic; *p*: *p* value.

3.4 | Below-ground response

Warming increased below-ground plant mass, consistent with the changes in the above-ground wetland plant growth, (Warming $F_{1,11} = 9.33$, $p < 0.0157$, Vegetation zone $F_{1,11} = 8.00$, $p < 0.0222$; Figure 2c and Table 4). Vegetation also influenced below-ground plant mass and both mangrove and marsh plots gained roots over the

TABLE 4 Effect on below-ground plant mass (g) analysed using a split-plot ANOVA with warming treatments (warmed and control) as whole plot and vegetation type (salt marsh and mangrove) as subplots within warming treatments

Change in the below-ground plant mass change (g)	*df*	MS	*F*	*p*
Warming treatment	1,11	360.36	9.33	**0.0157**
Vegetation zone	1,11	166.95	8.00	**0.0222**
Vegetation × Warming	1,11	273.80	1.02	0.3422

Note. Significant differences are bolded ($p < 0.05$).
df: degrees of freedom; MS: mean squares; *F*: *F*-statistic; *p*: *p*-value.

TABLE 5 Effect on sediment elevation change (mm) analysed using a split-plot ANOVA with warming treatments (warmed and control) as whole plot and vegetation type (salt marsh and mangrove) as subplot within warming treatments

Change in sediment elevation (mm)	*df*	MS	*F*	*p*
Warming treatment	1,11	175.81	9.28	**0.0159**
Vegetation zone	1,11	4.33	0.23	0.6454
Vegetation × Warming	1,11	101.37	5.35	**0.0495**

Note. Significant differences are bolded ($p < 0.05$).
df: degrees of freedom; MS: mean squares; *F*: *F*-statistic; *p*: *p*-value.

time of the experiment (Vegetation zone $F_{1,11} = 8.00$, $p < 0.0222$; Figure 2c and Table 4), but there was no interaction between warming and vegetation. As is evident in Figure 2c, warming had a much larger influence on below-ground plant mass in mangrove plots than in marsh plots. Specifically, warmed mangrove plots gained about 1 kg/m^2 of roots during the 22-month experiment, more than mangrove control plots and salt marsh regardless of treatment.

3.5 | Sediment elevation response and correlation with root mass

Under ambient conditions, salt marsh and mangroves had similar amounts of elevation gain over the study period. This was reflected with similar annual rates of accretion in the control plots across vegetation types (control salt marsh: 6.98 mm/year; control mangrove: 6.56 mm/year). However, there was a significant interaction between warming and vegetation so that chronic warming caused mangroves to have significantly enhanced elevation gain compared to mangrove areas in ambient temperatures and salt marsh regardless of temperature. Annual accretion rate in mangroves under warming was 12.24 mm/year; a threefold increase over the accretion rate of salt marshes under warming (4.46 mm/year). Salt marsh elevation gain was reduced in warmed plots compared to ambient plots (Warming $F_{1,11} = 9.28$, $p < 0.0159$, Vegetation × Warming $F_{1,11} = 5.35$, $p < 0.0495$; Figure 2d, Supporting Information Figure S7 and Table 5). Surface elevation gain related positively to measured change in below-ground plant mass, particularly in warming plots ($R^2 = 0.565$; Figure 3). Converting measured plant mass to plant volume using tissue bulk density yielded elevation estimates that closely match the magnitude of treatment effects on measured elevation (Figure 3).

4 | DISCUSSION

With climate change, annual average temperatures have increased, while the frequency of freeze events has declined, releasing mangroves from previous freeze-limited distributions (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). As a result, mangroves are rapidly moving poleward, invading salt marsh habitat, and altering ecotonal wetland dynamics (Saintilan & Rogers, 2015). Displacement of salt marsh by mangroves is of growing concern and while the community and ecosystem impacts of this dramatic range shift are being assessed as a result of reduced freeze frequency (Doughty et al., 2017; Guo et al., 2017; Perry & Mendelssohn, 2009), few studies have examined how ongoing chronic warming will affect plant species interactions and ecosystem resilience of coastal wetlands. Our overall hypothesis was supported in that warming temperatures altered mangrove and salt marsh growth which affected surface elevation. Using this large-scale in situ warming experiment, we showed that warming influences plant growth and enhances dominance of mangroves over salt marsh habitat. Mangrove dominance was associated with prolific root growth under warming, corresponding with increases in surface elevation. Chronic warming accelerated the conversion of salt marsh into mangrove habitat, altering the trajectory of habitat dominance in these critical ecosystems.

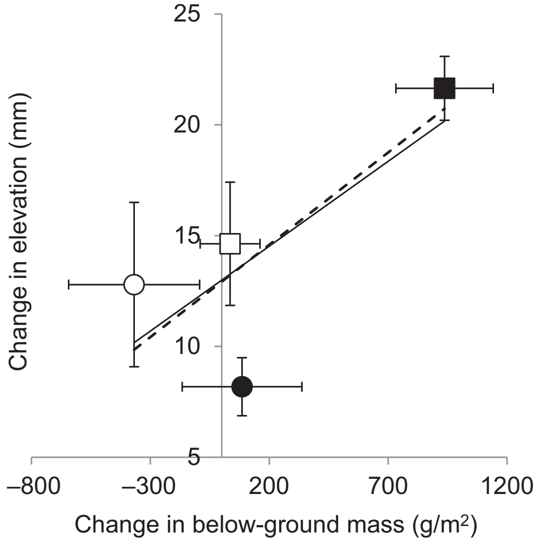

FIGURE 3 Relationship between below-ground plant mass over the course of the study and measured elevation change for marsh (circle) and mangrove plots (square) under control (open) or warmed conditions (filled). The solid line represents the field data (Elevation change = 0.0077 [mass] + 12.992, $R^2 = 0.565$). The dashed line represents treatment effects on elevation change that we would predict based on the bulk density of below-ground plant mass (0.12 g/cm^3) and changes in below-ground plant mass (slope = 0.0083 mm [g m^{-2}]$^{-1}$)

In agreement with our first prediction, we found that chronic warming increased both mangrove and marsh plant growth above-ground. Mangroves responded strongly to warming according to most of the growth parameters measured, including a doubling of height and canopy volume, which contributed to an increase in mangrove dominance. This is consistent with predictions by Feher et al. (2017) where increases in the minimum temperature were associated with increased canopy height of coastal wetland species. However, we previously found that mangrove seedlings had minimal response to chronic warming, this study shows that once mangroves are established, their growth rate is enhanced in warmed conditions, which may help drive salt marsh habitat conversion to mangrove habitat (Coldren et al., 2016). Increased mangrove growth provides evidence that even tropical wetland species can respond strongly to chronic warming, similar to that observed in temperate wetland species (Charles & Dukes, 2009; Gedan & Bertness, 2010). In contrast to mangroves, salt marsh plants had varied responses to warming. In salt marsh-dominated zones, salt marsh showed positive gains in cover and density under warming, which is consistent with other warming studies that showed increased above-ground growth of wetland species (Charles & Dukes, 2009; Coldren et al., 2016; Gray & Mogg, 2001). However, we found a trend that the salt marsh plant, *D. spicata*, did not respond to warming when growing *under* mangroves, potentially pointing to competitive interactions between marshes and mangroves. Mangrove cover increased in all plots, with warmed chambers having a greater increase compared to control plots. Salt marsh cover changed very little in control plots but decreased in warmed plots, corresponding with the increase in mangrove cover. The percentage of the plot dominated by salt marsh declined across all temperature treatments; however, this decline was greater in warmed plots. Lack of differences in bare ground cover and dominance also support our claim that changes in relative mangrove and salt marsh are a result of the latter overtaking the former.

Taken together, enhanced mangrove growth and cover and decline of salt marsh cover in response to warming shows that conversion of salt marsh to mangroves was accelerated in chronically warmed plots. However, expansion and retraction of mangrove coverage have occurred multiple times in the last century, corresponding with minimum annual threshold events (Osland et al., 2017). Our results indicated that temperature between freezing events may also impact the rates of expansion between minimum temperature threshold events. Future studies should consider if the amount of expansion under increased temperatures carry through freeze events, such as by providing propagules sources for rapid recolonization, thus altering community trajectories. As mangroves expand, they have strong effects on plant community structure and in intertidal wetlands outcompete salt marsh (Guo et al., 2017). Across salt marsh–mangrove interfaces, Yando et al. (2018) showed that the horizontal expansion of mangrove roots is positively associated with increases in relative height, which subsequently altered the extent of associated salt marsh cover. Our results also suggest that mangroves are likely to shade out marsh grasses, reducing available light for grasses and potentially suppressing their ability to respond to warming (Stevens, Fox, & Montague, 2006). This competition is likely to be maintained and potentially enhanced due to chronic warming as mangroves expand poleward, invading salt marsh habitat.

Our second prediction was that warming would also increase mangrove and marsh plot below-ground plant mass and this prediction was only partially supported. Because we could not sufficiently determine the difference between mangrove and marsh below-ground plant matter, we can only report whether mangrove-dominated and marsh-dominated plots respond differently to warming. Thus, we are assuming the majority of the below-ground plant matter is coming from the plants contained in the warming or control plots. Warming strongly increased below-ground plant mass only in the mangrove zones, likely due to an increase in available photosynthate for allocation below-ground (Michelsen, Rinnan, & Jonasson, 2012; Rinnan, Michelsen, & Jonasson, 2008). Warmed mangrove plots gained about 1 kg/m^2 of roots during the experiment, more than mangrove control plots and salt marsh regardless of treatment, none of which showed a significant change in below-ground mass over 22 months. However, below-ground plant matter gain measured was a balance between root growth and root decomposition. With no significant changes in below-ground plant mass between salt marsh in control and warmed plots, we suggest that warming-induced increases in salt marsh above-ground growth were not sufficient to increase allocation to roots. This lack of a warming effect on below-ground dynamics was somewhat surprising, given that studies of *Spartina anglica* showing increased below-ground biomass under elevated temperatures (Gray & Mogg, 2001), but this study was done in a laboratory setting. Wetlands at KSC can be nutrient limited (data not published), and thus, root growth is likely advantageous for increasing growth. If mangroves continue to increase in abundance, chronic warming induced increases in below-ground plant mass will likely support further above-ground growth due to increased nutrient acquisition. However, coastal wetland nutrient availability will depend on site-specific factors such as local tides, proximity to development, and soil fertility, texture, and OM.

We obtained support for our third prediction in our finding that the highest surface elevation gain occurred in warmed mangrove plots. Coastal wetland below-ground plant matter is not only important for nutrient provisioning but also is critical to allowing surface elevation increases necessary to keep pace with sea-level rise (McKee, 2011; McKee et al., 2007), particularly in areas with low sedimentation but high plant biomass (Krauss et al., 2014), such as at KSC. Warming and vegetation both boosted surface elevation gain such that warmed mangrove plots gained more elevation than any other plots. Surface elevation gain related positively to measured change in below-ground plant mass, particularly in warming plots, potentially highlighting the importance of biotic processes in regulating elevation change in this system. In order to examine this idea further, we converted plant mass to plant volume using bulk density estimates, and we found that these conversions yielded elevation estimates that closely matched the magnitude of treatment effects in measured surface elevation. This agreement between below-ground plant dynamics and elevation change, along with the lack of measurable surface sediment deposition supports the prominent role of endogenous OM in regulating elevation gain at this site. We suggests that in these sandy soils, root inputs may be critical to elevation increases to keep pace with sea-level rise (McKee, 2011; Nicholls & Cazenave, 2010). Increased gains in surface elevation under chronic warming highlights the importance of multiple factors of climate change on ecosystem processes. Under reduced freeze scenarios, salt marsh and mangrove showed equivalent sediment accretion rates (McKee & Vervaeke, 2018; Perry & Mendelssohn, 2009); however, these do not account for increased temperatures altering biomass production during the remainder of year.

Many coastal wetlands rely primarily on sediment inputs to drive surface elevation gain (Swales et al., 2015). In Indo-Pacific mangroves, researchers have found that sediment supply and resultant accretion are essential for mangroves to maintain surface elevation and prevent submergence (Lovelock et al., 2015). The KSC wetlands we studied have low sediment inputs, indicated by a lack of measurable deposition of sediment on the feldspar marker horizons we deployed during the study period. Similarly, in Caribbean atoll mangroves, OM deposition drives surface elevation (McKee et al., 2007). The surface elevation increases, we report here, exceed many of the published rates, possibly owing to the pioneer status of the mangroves as they encroach into the marsh. However, our surface elevation increases (up to 12 mm/year) are similar to those observed by (Krauss et al., 2017) across mangrove restoration sites, where we would expect mangrove organic inputs to be similarly high as young trees are rapidly growing. However, in areas of greater tidal regimes, these results may differ from our microtidal area in the KSC and the IRL. Our experimental findings advance our knowledge of the role biotic influences can play in driving warming-induced changes in surface elevation in certain systems, especially where sediments are low and sandy soils are likely more resistant to compaction.

Our study showed significant warming effects on *L. racemosa* and *D. spicata*, which were the dominant species in the wetlands at KSC; however, wetland species composition can be quite variable. Among mangroves, *A. germinans* and *R. mangle* are predominant throughout Florida wetlands, with the former likely to have the widest poleward expansion among mangroves due its higher cold tolerance. Studies of *A. germinans* invasion into salt marshes have shown mixed responses under reduced freezes (Comeaux et al., 2012; Yando et al., 2016) and warming conditions (Coldren et al., 2016). However, *L. racemosa* is considered to have expansion potential up to 31° latitude, similar to *R. mangle*; providing an important baseline comparison to future *R. mangle* studies under these conditions (Cavanaugh et al., 2014). Differences among mangrove species and life stages (i.e., seedlings, juveniles, adults) will likely have important impacts on plant interactions under warming conditions (Coldren et al., 2016) as observed under freezing conditions (Coldren & Proffitt, 2017). As mangroves expand poleward, they will also encounter a variety of salt marsh species, including *Spartina* species in the lower intertidal zones (Osland et al., 2013). At higher latitudes, *D. spicata* showed a greater response to warming compared to co-occurring *S. patens* and *S. alterniflora* (Charles & Dukes, 2009). This is consistent with *D. spicata* responses at the KSC site (lower latitudes) as observed in this study and in small-scale warming chambers in Coldren et al., (2016). Future studies are needed to further understand chronic warming effects on the range of potential wetland species and their interactions.

We found that chronic warming stimulates mangrove growth and accelerates mangrove expansion into salt marshes. We predict that chronic warming will act additively and perhaps synergistically with declining freeze events, which were previously shown to facilitate the poleward expansion of mangroves (Cavanaugh et al., 2014; Osland et al., 2013). In the short term, mangrove expansion and increased growth at KSC under warming conditions may provide more resistance to storms (Doughty et al., 2017), and surface elevation responses may enhance the sustainability of these ecotonal coastal wetlands as they face accelerating sea-level rise in a warmer future.

ACKNOWLEDGEMENTS

Funding for this work was provided by grants from the National Aeronautics and Space Administration (NASA) Climate and Biological Response Program (NNX11AO94G, NNX12AF55G) and from the National Science Foundation Division of Environmental Biology (DEB1655659). This work was conducted as part of NASA's Climate Adaptation Science Investigators (CASI) Workgroup. We would like to thank Chelsea Barreto, Cheryl Doughty, Drew Freed, Brendan Kelly, Tara Malanga, Heather Tran, and Richard Mulroy for support in field collections and laboratory processing. We also acknowledge Carlton Hall from Integrated Mission Support Services and the KSC Ecological Program and Lynne Phillips, the NASA Kennedy Space Center Environmental Planning Branch for continued support. Jim Lyon from the United States Fish and Wildlife Service provided assistance with permitting.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; G.A.C. constructed the experiment. G.A.C., S.K.C., and, J.A.L. collected and analysed the data; G.A.C., S.K.C., and, J.A.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.7b150n7 (Coldren, Langley, Feller, & Chapman, 2018).

ORCID

Glenn A. Coldren http://orcid.org/0000-0002-9745-6121
J. Adam Langley http://orcid.org/0000-0001-5164-4760
Ilka C. Feller http://orcid.org/0000-0002-6391-1608
Samantha K. Chapman http://orcid.org/0000-0002-5825-2329

REFERENCES

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Barreto, C. R., Morrissey, E. M., Wykoff, D. D., & Chapman, S. K. (2018). Co-occuring mangroves and salt marshes differ in microbial community composition. *Wetlands*, *38*, 497. https://doi.org/10.1007/s13157-018-0994-9

Cahoon, D. R., Lynch, J. C., Hensel, P., Boumans, R., Perez, B. C., Segura, B., & Day, J. W. (2002). High-precision measurements of wetland sediment elevation: I. Recent improvements to the sedimentation-erosion table. *Journal of Sedimentary Research*, *72*(5), 730–733. https://doi.org/10.1306/020702720730

Cahoon, D. R., Lynch, J. C., Perez, B. C., Segura, B., Holland, R. D., Stelly, C., … Hensel, P. (2002). High-precision measurements of wetland sediment elevation. II The rod surface elevation table. *Journal of Sedimentary Research*, *72*(5), 734–739. https://doi.org/10.1306/020702720734

Cavaleri, M. A., Reed, S. C., Smith, W. K., & Wood, T. E. (2015). Urgent need for warming experiments in tropical forests. *Global Change Biology*, *21*(6), 2111–2121. https://doi.org/10.1111/gcb.12860

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(2), 723–727. https://doi.org/10.1073/pnas.1315800111

Charles, H., & Dukes, J. S. (2009). Effects of warming and altered precipitation on plant and nutrient dynamics of a New England salt marsh. *Ecological Applications: A Publication of the Ecological Society of America*, *19*(7), 1758–1773. https://doi.org/10.1890/08-0172.1

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Cherry, J. A., McKee, K. L., & Grace, J. B. (2009). Elevated CO_2 enhances biological contributions to elevation change in coastal wetlands by offsetting stressors associated with sea-level rise. *Journal of Ecology*, *97*(1), 67–77. https://doi.org/10.1111/j.1365-2745.2008.01449.x

Coldren, G. A., Barreto, C. R., Wykoff, D. D., Morrissey, E. M., Langley, J. A., Feller, I. C., & Chapman, S. K. (2016). Chronic warming stimulates growth of marsh grasses more than mangroves in a coastal wetland ecotone. *Ecology*, *97*(11), 3167–3175. https://doi.org/10.1002/ecy.1539

Coldren, G. A., Langley, J. A., Feller, I. C., & Chapman, S. K. (2018). Data from: Warming accelerates mangrove expansion and surface elevation gain in a subtropical wetland. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.7b150n7

Coldren, G. A., & Proffitt, C. E. (2017). Mangrove seedling freeze tolerance depends on salt marsh presence, species, salinity, and age. *Hydrobiologia*, *803*(1), 159–171. https://doi.org/10.1007/s10750-017-3175-6

Comeaux, R. S., Allison, M. A., & Bianchi, T. S. (2012). Mangrove expansion in the Gulf of Mexico with climate change: Implications for wetland health and resistance to rising sea levels. *Estuarine, Coastal and Shelf Science*, *96*, 81–95. https://doi.org/10.1016/j.ecss.2011.10.003

Crosby, S. C., Sax, D. F., Palmer, M. E., Booth, H. S., Deegan, L. A., Bertness, M. D., & Leslie, H. M. (2016). Salt marsh persistence is threatened by predicted sea-level rise. *Estuarine, Coastal and Shelf Science*, *181*, 93–99. https://doi.org/10.1016/j.ecss.2016.08.018

Doughty, C. L., Cavanaugh, K. C., Hall, C. R., Feller, I. C., & Chapman, S. K. (2017). Impacts of mangrove encroachment and mosquito impoundment management on coastal protection services. *Hydrobiologia*, *803*(1), 105–120. https://doi.org/10.1007/s10750-017-3225-0

Doughty, C. L., Langley, J. A., Walker, W. S., Feller, I. C., Schaub, R., & Chapman, S. K. (2016). Mangrove range expansion rapidly increases coastal wetland carbons storage. *Estuaries and Coasts*, *39*(2), 385–396. https://doi.org/10.1007/s12237-015-9993-8

Durango, J., Satyanarayana, B., Zhang, J., Wang, J., Chen, M., Fanghong, X. … Dahdouh-Guebas, F. (2012). Vegetation structure at Zhanjiang Mangrove National Nature Reserve (ZMNNR), P.R. China: Comparison between original and non-original trees using ground-truth, remote sensing and GIS techniques.

Eslami-Andargoli, L., Dale, P., Sipe, N., & Chaseling, J. (2009). Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. *Estuarine, Coastal and Shelf Science*, *85*(2), 292–298. https://doi.org/10.1016/j.ecss.2009.08.011

Feher, L. C., Osland, M. J., Griffith, K. T., Grace, J. B., Howard, R. J., Stagg, C. L., … Rogers, K. (2017). Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands. *Ecosphere*, *8*(10), e01956. https://doi.org/10.1002/ecs2.1956

Gedan, K. B., & Bertness, M. D. (2010). How will warming affect the salt marsh foundation species *Spartina patens* and its ecological role? *Oecologia*, *164*(2), 479–487. https://doi.org/10.1007/s00442-010-1661-x

Gill, A. L., Giasson, M.-A., Yu, R., & Finzi, A. C. (2017). Deep peat warming increases surface methane and carbon dioxide emissions in a black spruce-dominated ombrotrophic bog. *Global Change Biology*, *23*(12), 5398–5411. https://doi.org/10.1111/gcb.13806

Giri, C., & Long, J. (2016). Is the geographic range of mangrove forests in the conterminous United States really expanding? *Sensors*, *16*(12), E2010. https://doi.org/10.3390/s16122010

Gray, A. J., & Mogg, R. J. (2001). Climate impacts on pioneer saltmarsh plants. *Climate Research*, *18*(1–2), 105–112. https://doi.org/10.3354/cr018105

Guo, H., Weaver, C., Charles, S. P., Whitt, A., Dastidar, S., D'Odorico, P., … Pennings, S. C. (2017). Coastal regime shifts: Rapid responses of coastal wetlands to changes in mangrove cover. *Ecology*, *98*(3), 762–772. https://doi.org/10.1002/ecy.1698

Howard, R. J., Day, R. H., Krauss, K. W., From, A. S., Allain, L., & Cormier, N. (2017). Hydrologic restoration in a dynamic subtropical mangrove-to-marsh ecotone. *Restoration Ecology*, *25*(3), 471–482. https://doi.org/10.1111/rec.12452

Jackson, R. B., Banner, J. L., Jobbágy, E. G., Pockman, W. T., & Wall, D. H. (2002). Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, *418*(6898), 623–626. https://doi.org/10.1038/nature00910

Kelleway, J. J., Saintilan, N., Macreadie, P. I., Skilbeck, C. G., Zawadzki, A., & Ralph, P. J. (2016). Seventy years of continuous encroachment substantially increases 'blue carbon' capacity as mangroves replace intertidal salt marshes. *Global Change Biology*, *22*(3), 1097–1109. https://doi.org/10.1111/gcb.13158

Kirwan, M. L., & Blum, L. K. (2011). Enhanced decomposition offsets enhanced productivity and soil carbon accumulation in coastal wetlands responding to climate change. *Biogeosciences*, *8*(4), 987–993. https://doi.org/10.5194/bg-8-987-2011

Kirwan, M. L., Guntenspergen, G. R., & Morris, J. T. (2009). Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Global Change Biology*, *15*(8), 1982–1989. https://doi.org/10.1111/j.1365-2486.2008.01834.x

Knapp, A. K., Briggs, J. M., Collins, S. L., Archer, S. R., Bret-Harte, M. S., Ewers, B. E., … Cleary, M. B. (2008). Shrub encroachment in North American grasslands: Shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, *14*(3), 615–623. https://doi.org/10.1111/j.1365-2486.2007.01512.x

Krauss, K. W., Cormier, N., Osland, M. J., Kirwan, M. L., Stagg, C. L., Nestlerode, J. A., … Almario, A. E. (2017). Created mangrove wetlands store belowground carbon and surface elevation change enables them to adjust to sea-level rise. *Scientific Reports*, *7*(1), 1030. https://doi.org/10.1038/s41598-017-01224-2

Krauss, K. W., From, A. S., Doyle, T. W., Doyle, T. J., & Barry, M. J. (2011). Sea-level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. *Journal of Coastal Conservation*, *15*(4), 629–638. https://doi.org/10.1007/s11852-011-0153-4

Krauss, K. W., McKee, K. L., Lovelock, C. E., Cahoon, D. R., Saintilan, N., Reef, R., & Chen, L. (2014). How mangrove forests adjust to rising sea level. *New Phytologist*, *202*(1), 19–34. https://doi.org/10.1111/nph.12605

Langley, J. A., McKee, K. L., Cahoon, D. R., Cherry, J. A., & Megonigal, J. P. (2009). Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(15), 6182–6186. https://doi.org/10.1073/pnas.0807695106

Lonard, R. I., & Judd, F. W. (1991). Comparison of the effects of the severe freezes of 1983 and 1989 on native woody plants in the lower Rio Grande Valley. Texas. *The Southwestern Naturalist*, *36*(2), 213–217. https://doi.org/10.2307/3671923

López-Medellín, X., Ezcurra, E., González-Abraham, C., Hak, J., Santiago, L. S., & Sickman, J. O. (2011). Oceanographic anomalies and sea-level rise drive mangroves inland in the Pacific coast of Mexico. *Journal of Vegetation Science*, *22*(1), 143–151. https://doi.org/10.1111/j.1654-1103.2010.01232.x

Lovelock, C. E., Cahoon, D. R., Friess, D. A., Guntenspergen, G. R., Krauss, K. W., Reef, R., … Triet, T. (2015). The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature*, *526*(7574), 559–563. https://doi.org/10.1038/nature15538

Lovelock, C. E., Feller, I. C., Ellis, J., Schwarz, A. M., Hancock, N., Nichols, P., & Sorrell, B. (2007). Mangrove growth in New Zealand estuaries: The role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, *153*(3), 633–641. https://doi.org/10.1007/s00442-007-0750-y

McKee, K. L. (2011). Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science*, *91*(4), 475–483. https://doi.org/10.1016/j.ecss.2010.05.001

McKee, K. L., Cahoon, D. R., & Feller, I. C. (2007). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, *16*(5), 545–556. https://doi.org/10.1111/j.1466-8238.2007.00317.x

McKee, K. L., & Vervaeke, W. C. (2018). Will fluctuations in salt marsh–mangrove dominance alter vulnerability of a subtropical wetland to sea-level rise? *Global Change Biology*, *24*(3), 1224–1238. https://doi.org/10.1111/gcb.13945

Michelsen, A., Rinnan, R., & Jonasson, S. (2012). Two decades of experimental manipulations of heaths and forest understory in the subarctic. *AMBIO*, *41*(3), 218–230. https://doi.org/10.1007/s13280-012-0303-4

Morris, J. T. (2007). Estimating net primary production of salt marsh macrophytes. In T. J. Fahey & A. K. Knapp (Eds.), *Principles and standards for measuring primary production* (pp. 106–119). New York, NY: Oxford University Press.

Nicholls, R. J., & Cazenave, A. (2010). Sea-level rise and its impact on coastal zones. *Science*, *328*(5985), 1517–1520. https://doi.org/10.1126/science.1185782

Nicholls, R. J., Hoozemans, F. M. J., & Marchand, M. (1999). Increasing flood risk and wetland losses due to global sea-level rise: Regional and global analyses. *Global Environmental Change*, *9*, S69–S87. https://doi.org/10.1016/S0959-3780(99)00019-9

Osland, M. J., Day, R. H., Doyle, T. W., & Enwright, N. (2013). Winter climate change and coastal wetland foundation species: Salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology*, *19*(5), 1482–1494. https://doi.org/10.1111/gcb.12126

Osland, M. J., Day, R. H., Hall, C. T., Brumfield, M. D., Dugas, J. L., & Jones, W. R. (2017). Mangrove expansion and contraction at a poleward range limit: Climate extremes and land-ocean temperature gradients. *Ecology*, *98*(1), 125–137. https://doi.org/10.1002/ecy.1625

Perry, C. L., & Mendelssohn, I. A. (2009). Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. *Wetlands*, *29*(1), 396–406. https://doi.org/10.1672/08-100.1

Provancha, M. J., Schmalzer, P. A., & Hall, C. R. (1986). Effects of the December 1983 and January 1985 freezing air temperatures on select aquatic poikilotherms and plant species of Merritt Island, Florida. *Florida Scientist*, *49*(4), 199–212.

Rinnan, R., Michelsen, A., & Jonasson, S. (2008). Effects of litter addition and warming on soil carbon, nutrient pools and microbial communities in a subarctic heath ecosystem. *Applied Soil Ecology*, *39*(3), 271–281. https://doi.org/10.1016/j.apsoil.2007.12.014

Rogers, K., Saintilan, N., & Heijnis, H. (2005). Mangrove encroachment of salt marsh in Western Port Bay, Victoria: The role of sedimentation, subsidence, and sea level rise. *Estuaries*, *28*(4), 551–559. https://doi.org/10.1007/BF02696066

Rosenzweig, C., Elliott, J., Deryng, D., Ruane, A. C., Müller, C., Arneth, A., … Jones, J. W. (2014). Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(9), 3268–3273. https://doi.org/10.1073/pnas.1222463110

Rundel, P. W., Dickie, I. A., & Richardson, D. M. (2014). Tree invasions into treeless areas: Mechanisms and ecosystem processes. *Biological Invasions*, *16*(3), 663–675. https://doi.org/10.1007/s10530-013-0614-9

Saintilan, N., & Rogers, K. (2015). Woody plant encroachment of grasslands: A comparison of terrestrial and wetland settings. *New Phytologist*, *205*(3), 1062–1070. https://doi.org/10.1111/nph.13147

Saintilan, N., Wilson, N. C., Rogers, K., Rajkaran, A., & Krauss, K. W. (2014). Mangrove expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*, *20*(1), 147–157. https://doi.org/10.1111/gcb.12341

SAS Institute Inc. (2011). *SAS/STAT® 9.3 user's guide*. Cary, NC: SAS Institute Inc.

Smith, N. P. (1987). An introduction to the tides of Florida's Indian River Lagoon. I. Water Levels. *Florida Scientist*, *50*(1), 49–61.

Stevens, P. W., Fox, S. L., & Montague, C. L. (2006). The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, *14*(5), 435–444. https://doi.org/10.1007/s11273-006-0006-3

Swales, A., Bentley, S. J., & Lovelock, C. E. (2015). Mangrove-forest evolution in a sediment-rich estuarine system: Opportunists or agents of geomorphic change? *Earth Surface Processes and Landforms*, *40*(12), 1672–1687. https://doi.org/10.1002/esp.3759

Ward, R. D., Friess, D. A., Day, R. H., & MacKenzie, R. A. (2016). Impacts of climate change on mangrove ecosystems: A region by region overview. *Ecosystem Health and Sustainability*, *2*(4), e01211. https://doi.org/10.1002/ehs2.1211

Yando, E. S., Osland, M. J., & Hester, M. W. (2018). Microspatial ecotone dynamics at a shifting range limit: Plant–soil variation across salt marsh–mangrove interfaces. *Oecologia*, *187*(1), 319–331. https://doi.org/10.1007/s00442-018-4098-2

Yando, E. S., Osland, M. J., Willis, J. M., Day, R. H., Krauss, K. W., & Hester, M. W. (2016). Salt marsh-mangrove ecotones: Using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. *Journal of Ecology*, *104*(4), 1020–1031. https://doi.org/10.1111/1365-2745.12571

SUPPORTING INFORMATION

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

How to cite this article: Coldren GA, Langley JA, Feller IC, Chapman SK. Warming accelerates mangrove expansion and surface elevation gain in a subtropical wetland. *J Ecol*. 2018;00:1–12. https://doi.org/10.1111/1365-2745.13049