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Temperature optimum for marsh resilience and carbon accumulation revealed in a whole-ecosystem warming experiment

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Abstract

Coastal marshes are globally important, carbon dense ecosystems simultaneously maintained and threatened by sea-level rise. Warming temperatures may increase wetland plant productivity and organic matter accumulation, but temperature-modulated feedbacks between productivity and decomposition make it difficult to assess how wetlands and their thick, organic-rich soils will respond to climate warming. Here, we actively increased aboveground plant-surface and belowground soil temperatures in two marsh plant communities, and found that a moderate amount of warming (1.7°C above ambient temperatures) consistently maximized root growth, marsh elevation gain, and belowground carbon accumulation. Marsh elevation loss observed at higher temperatures was associated with increased carbon mineralization and increased microtopographic heterogeneity, a potential early warning signal of marsh drowning. Maximized elevation and belowground carbon accumulation for moderate warming scenarios uniquely suggest linkages between metabolic theory of individuals and landscape-scale ecosystem resilience and function, but our work indicates nonpermanent benefits as global temperatures continue to rise.

KEYWORDS
carbon accumulation, ecosystem resilience, marsh elevation, vertical accretion, whole-ecosystem warming

1 | INTRODUCTION

Marshes are highly valuable ecosystems providing a range of ecosystem services from storm protection to carbon accumulation, but accelerating rates of sea-level rise threaten to drown them and eliminate these services (Jankowski et al., 2017; Kirwan & Megonigal, 2013; Mcleod et al., 2011; Shepard et al., 2011). Warming simultaneously accelerates sea-level rise and alters *in situ* process rates that regulate marsh elevation and vulnerability to drowning, namely production, decomposition, and vertical accretion. Vertical accretion maintains marsh elevation relative to sea level through autochthonous root production and the capture of allochthonous sediments

and organic matter (Kirwan & Megonigal, 2013; Morris et al., 2016). As increased damming and management practices decrease suspended sediment available for capture, temperature-sensitive biogenic controls to vertical accretion, such as production and decomposition, become increasingly important (Peteet et al., 2018; Temmerman et al., 2003). Aboveground and belowground production increase with temperature, which is expected to accelerate both vertical accretion and carbon inputs to the soil (Charles & Dukes, 2009; Coldren et al., 2016; Gedan & Bertness, 2009). Therefore, warming could increase vertical accretion rates and contribute to a negative carbon-climate feedback by increasing soil carbon storage (Kirschbaum, 1995; Najjar et al., 2000; Rogers et al., 2019). However,

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this conceptual framework largely neglects temperature-driven increases in decomposition, which can reduce marsh stability and potentially offset benefits from increased productivity (Kirschbaum, 1995; Kirwan & Blum, 2011; Kirwan et al., 2014).

Global climate models project mean global temperature increases of 2.6–5.0°C by the end of the 21st century (IPCC, 2021). Some studies have attempted to replicate these temperatures experimentally in salt marshes using aboveground heating lamps or passive heating systems (Charles & Dukes, 2009; Coldren et al., 2016; Gedan & Bertness, 2009; Zhong et al., 2019). While these designs have successfully simulated increased temperatures at the marsh surface, these methods fail to increase temperature at deep soil depths (~1 meter) that are expected to warm under future climate conditions (Phillips, 2020). Given the large, deep stores of organic material that have accumulated in marshes over time, these passive, surficial warming designs neglect to warm a significant portion of soil organic material that will experience warming in the future. Additionally, studies reliant on passive warming typically feature a single, low magnitude temperature treatment and therefore cannot account for nonlinear warming responses that may occur as the climate continues to warm. Therefore, experimental warming of just surface sediments and vegetation fails to accurately simulate whole-scale ecosystem warming, and its cascading impacts on marsh resilience and function.

To address uncertain marsh response and resilience to future temperatures, the Salt Marsh Accretion Response to Warming Experiment (SMARTX) actively warmed entire marsh ecosystems, from plant canopy to a soil depth of approximately 1.5 m, using heating lamps at the surface and subterranean cables to achieve four discrete temperature treatments (ambient, 1.7, 3.4, and 5.1°C above ambient temperatures) in two brackish marsh plant communities that are dominated by either C_3 or C_4 plant species (Figure S1) (Noyce et al., 2019). The C_3 site is dominated by the C_3 sedge *Schoenoplectus americanus* (93% of aboveground biomass) and is relatively wet due to lower elevation and more frequent tidal flooding while the C_4 site is dominated by *Spartina patens* and *Distichlis spicata* (76% of aboveground biomass) and is relatively elevated and dry (Jordan & Correll, 1991). We measured marsh surface elevation in response to whole-ecosystem warming at annual and seasonal timescales and found that while marsh resilience is optimized under moderate degrees of warming, further warming led to decreased rates of carbon accumulation, early signs of marsh collapse, and increased vulnerability to sea-level rise.

2 | RESULTS AND DISCUSSION

2.1 | Moderate warming optimizes marsh resilience and carbon accumulation

We measured marsh surface elevation response across warming gradients in C_3 and C_4 plant communities over a 4-year period (June 2016 to February 2020). Marsh surface elevation was regressed against time for each individual surface elevation table (SET) pin (Lynch et al., 2015), resulting in derived rates of elevation gain and loss, but more generally marsh surface elevation increased through time in the C_3 community and decreased through time in the C_4 community (Figure 1a and b). Despite these contrasting elevation trends, both communities responded similarly to warming treatments, where elevation gain was optimized at 1.7°C above current ambient conditions (Figure 1c). This optimal temperature treatment increased elevation gain by approximately 2.1 mm y^{-1} and 2.5 mm y^{-1} in the C_3 and C_4 communities, respectively (Table S1), but elevation gain was still less than the 3.8 mm yr^{-1} mean sea-level rise trend for the past 50 years in this region (NOAA Sea Level Trends, 2021). Warming beyond the temperature optimum reduced this positive effect and resulted in a 0.8 mm y^{-1} and 0.9 mm y^{-1} loss of elevation at the +5.1°C treatment (Figure 1c), a rate equivalent to or less than ambient rates of elevation gain. Root production was also optimized at +1.7°C in our experiment driven by optimum allocation of growth to belowground biomass in response to nitrogen limitation; above 1.7°C increased nitrogen mineralization reduces plant nitrogen demand and root productivity (Noyce et al., 2019). Therefore, belowground organic matter production drives the long-term elevation response to warming, with a consistent temperature optimum for root productivity and elevation change in both plant communities (Figure 1c).

Carbon accumulation rates were also maximized at moderate warming treatments. Carbon accumulation rates were calculated as the product of elevation change in each experimental plot (ranging from 2.5 to −0.9 mm yr^{-1}) and the average carbon density of all C_3 (104.8 kg C m^{-3}) and all C_4 plots (238.8 kg C m^{-3}). These estimates assume that elevation change is driven predominately by organic matter accumulation at our sites, as evidenced by high soil organic matter content (~90%), limited allochthonous input of mineral sediment (Morris et al., 2016; Rietl et al., 2021), and accretion rates that are tightly controlled by root zone processes (Langley et al., 2009; Rietl et al., 2021). The C_3 community carbon accumulation rate was maximized at +1.7°C (262 g C m^{-2} y^{-1}) and minimized at the control and +5.1°C treatments (25 and −71 g C m^{-2} y^{-1}, respectively). The C_4 carbon accumulation rate was also maximized at +1.7°C (24 g C m^{-2} y^{-1}), but with a net loss of carbon storage in the control and +5.1°C treatments (−249 and −296 g C m^{-2} y^{-1}, respectively) (Figure S2). Our finding that the more flood-tolerant C_3 community responses to warming are more positive than less-flood-tolerant C_4 responses offer empirical support to numerical modeling that suggests the positive impacts of temperature on marsh carbon accumulation are maximized at high sea-level rise rates (Couto et al., 2014; Kirwan & Mudd, 2012), but also highlights that warming-induced gains in one part of the system (C_3) may be offset by losses elsewhere (C_4).

Warming responses have traditionally been interpreted in the context of an optimal temperature for metabolism, where rates of productivity increase up to a point of typical summer temperatures and then decline with further warming (Giurgevich & Dunn, 1979; Long et al., 1975; O'Sullivan et al., 2017; Seneca & Blum, 1984). The photosynthetic optimum of *Spartina*, a common C_4 salt marsh genus,
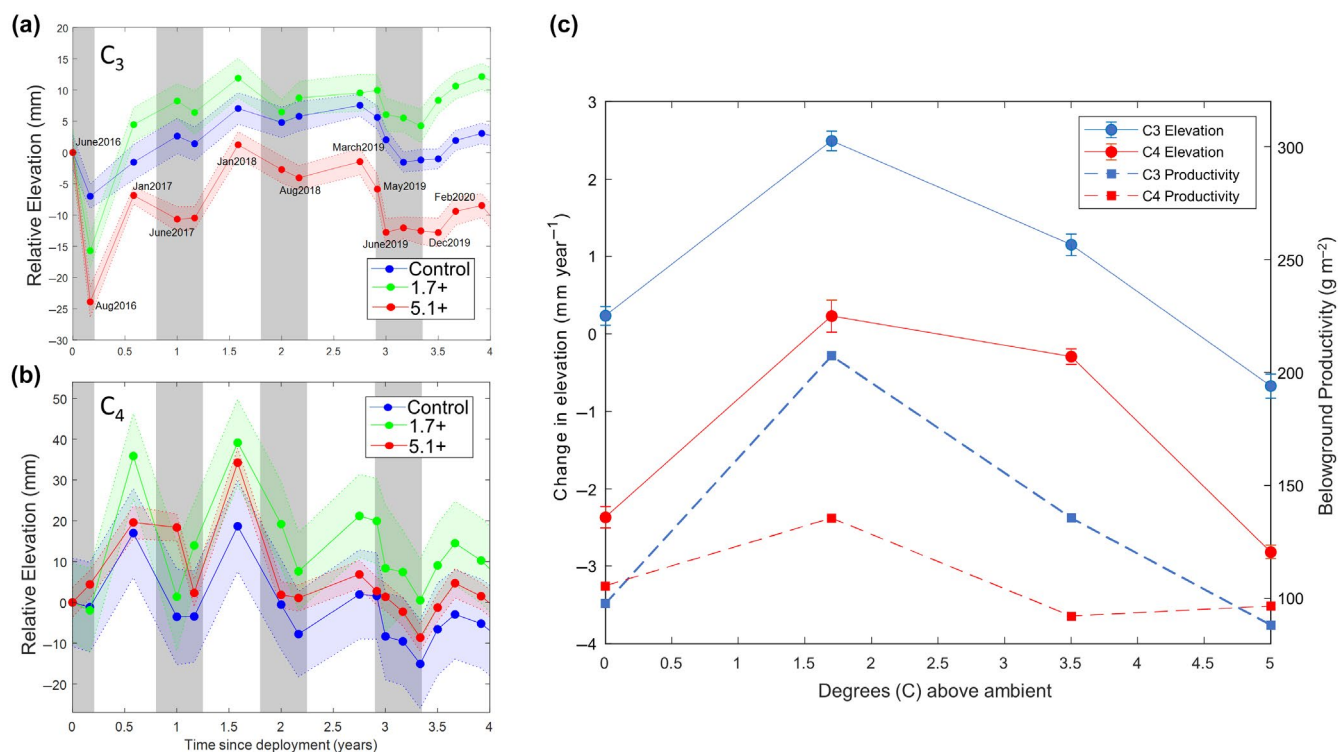
FIGURE 1 Elevation trends through time in response to warming in the C_3 (a) and C_4 (b) plant communities. Shaded regions correspond to the standard error in elevation associated with each treatment. Gray areas represent the approximate growing season (April–September). For clarity, the +3.4°C treatment is not shown, but tracks with similar seasonal trends as the displayed treatments (Figure S3). Relative elevation measurements were averaged across plots and replications ($n = 3$). (c) Average elevation change rate (mm y^{-1}) of triplicate replications in the C_3 and C_4 community averaged through time under the four temperature treatments. Regression analyses were applied to individual pins and then averaged between plots and treatments ($n = \sim120$). Belowground productivity data are from Noyce et al. (2019), updated with an additional 2 years of data to encompass 2018–2020
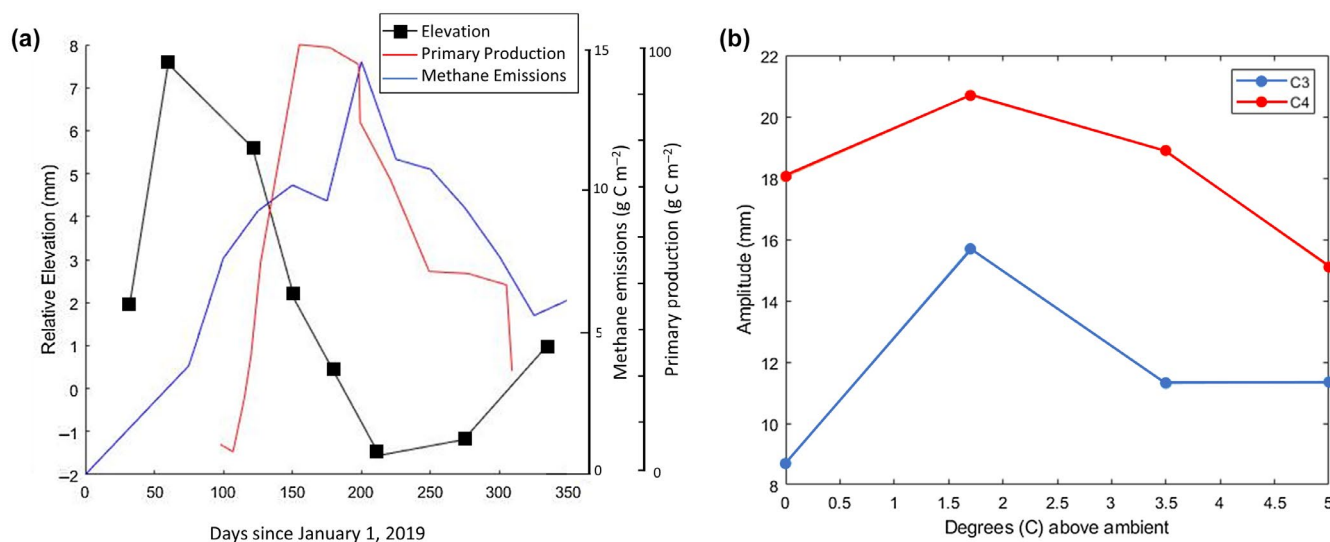

FIGURE 2 (a) Seasonal patterns in marsh elevation, productivity, and decomposition. Relative elevation (black), primary production (red) and methane emissions (blue) from March 2019 to February 2020. Primary production is measured as changes in total green biomass relative to total green biomass during peak productivity. Methane emissions are measured monthly using static chambers and act as a proxy for organic matter decomposition. Relative elevation is the average elevation of the C_3 community only at ambient temperatures. (b) Average amplitude (mm) of the seasonal variability between the highest and lowest average elevations over the year-long intensive sampling period

is approximately 2.2–7.2°C above the mean high temperature during summer days at our study site (~28°C) (Giurgevich & Dunn, 1979; Kirwan et al., 2009). This, and decreased net primary production observed during elevated regional summer temperatures (Noyce et al., 2019), indicates that moderate amounts of warming in the region are likely elevating temperatures closer to or above this metabolic optimum. Although some studies have indicated that marsh grasses can acclimate leaf respiration and photosynthetic capacity to increasing temperatures (Sturchio et al., 2021; Wang et al., 2020), the warmest treatment likely exceeds the metabolic temperature optimum during warm summer days leading to a reduction in marsh elevation, analogous to the hump-shaped relationships between temperature and productivity proposed for *S. alterniflora* more globally (Liu et al., 2016, 2020; Rogers et al., 2006; Więski & Pennings, 2014). Our observations of consistent treatment optima, where root production, elevation change, and carbon accumulation rates in two disparate plant communities were maximized at +1.7°C, suggest that the qualitative patterns are applicable beyond our particular study area, but that the exact temperature optimum may vary around +1.7°C (Figure 1c). Moreover, because autochthonous, plant-mediated mechanisms drive these consistent optima, this suggests that metabolic temperature optima for individual plants or communities can cascade up to whole-marsh elevation change dynamics, thereby uniquely linking metabolic theory to ecosystem resilience and function.

2.2 | Interactions between productivity and decomposition drive seasonal elevation trends

From March 2019 to February 2020, we measured marsh elevation every 2 months to quantify the potential influence of temperature over seasonal timescales (Figure 2a). Surprisingly, we found seasonal variations in relative marsh elevation that ranged from 8.75 to 13.25 mm, approximately 10 times greater than the long-term accretion rates observed in this study (Figure 2a and b). Seasonal variation was maximized in the +1.7°C treatment in both the C_3 and C_4 community, closely following patterns in annual elevation gain and root productivity (Figure 2b). Marsh elevations were consistently maximized in the early spring (March–May) prior to increased sedge and grass productivity and were minimized in the fall (August–December).

While multiple factors are known to influence seasonal marsh elevation change, we attribute it largely to seasonal changes in organic matter accumulation, expressed as the temperature-modulated balance between decomposition and production. Previous work links seasonal elevation change to declines in water level associated with evapotranspiration and drought during warm periods (Bashan et al., 2013; Cahoon et al., 2011; Friedrichs & Perry, 2001), but we found that water level fluctuations were only loosely correlated with fluctuations in seasonal elevation patterns ($p = .10$) and could not explain variation between treatments ($p = .54$). Previous work in mineral-rich systems suggests that seasonal elevation change can be driven by changes in plant growth and its effect on sediment

trapping (Noyce & Megonigal, 2021; Palinkas & Engelhardt, 2019), but at our site, seasonal elevation change is inversely correlated with productivity (Figure 2a). Instead, seasonal elevation patterns correspond to organic matter decomposition inferred from methane emissions measured at our study site. In particular, methane emissions correlate closely with temperature (Darby & Turner, 2008) and inversely with marsh elevation ($p = .01$), signifying increased organic matter preservation in the winter and increased decomposition in the summer. Warming is known to increase both organic matter productivity (Connor & Chmura, 2000; Crosby et al., 2016) and decomposition (Hanson et al., 2020; Kirwan & Mudd, 2012; Kirwan et al., 2014; Mueller et al., 2016; Najjar et al., 2000) separately, but the observed summer elevation loss uniquely indicates that the balance between these processes is largely negative, with higher rates of decomposition dominating productivity and reducing organic matter storage. Though counterintuitive, the loss of elevation during the most productive portions of the growing season could be explained by soil priming effects, where root growth delivers oxygen and organic carbon to anaerobic soils and enhances decomposition (Dakos et al., 2012; Mueller et al., 2020; Rietl et al., 2021). The amplitude of seasonal marsh elevation variability (Figure 2b) mirrors interannual trends in marsh elevation under manipulated warming treatments (Figure 1c). Therefore, at both the seasonal and annual timescales, marsh resilience and carbon storage are decreased at high temperatures (Figure 1c, Figure 2a).

2.3 | Increasing heterogeneity in microtopography: evidence for decreasing resilience

Ecosystems often respond to stressors with increased spatial variability, such as increased autocorrelation and variance, which can signal an approaching critical threshold and imminent state change (Kéfi et al., 2007; Kéfi et al., 2014; Van Belzen et al., 2017; Veraart et al., 2012). However, few spatial indicators have been tested as early indicators of state change in coastal wetlands (Martinez, 2021; Moffett et al., 2015). Over the duration of this 3-year study, we observed an increase in the number of elevation measurements that were greater than 20 mm different than adjacent pin measurements in the C_3 community as the marsh degraded. These observations inspired us to examine the effect of temperature and plant community on spatial variability using three metrics of microtopography heterogeneity (tortuosity, random roughness, and number of holes, with holes defined as differences in elevation between adjacent SET pin measurements greater than 20 mm) that may predict proximity to state change. Microtopographic heterogeneity decreased through time in the C_4 community, and increased through time in the C_3 community (Figure 3). This pattern could be expected given that the high elevation C_4 marsh is higher in the tidal frame than the C_3 marsh and is therefore farther from an extinction threshold (Rietl et al., 2021). Additionally, we found that heterogeneity increased sharply in the warmest treatments in the C_3 community, as evidenced by a tripling in the number of holes formed in the +5.1°C
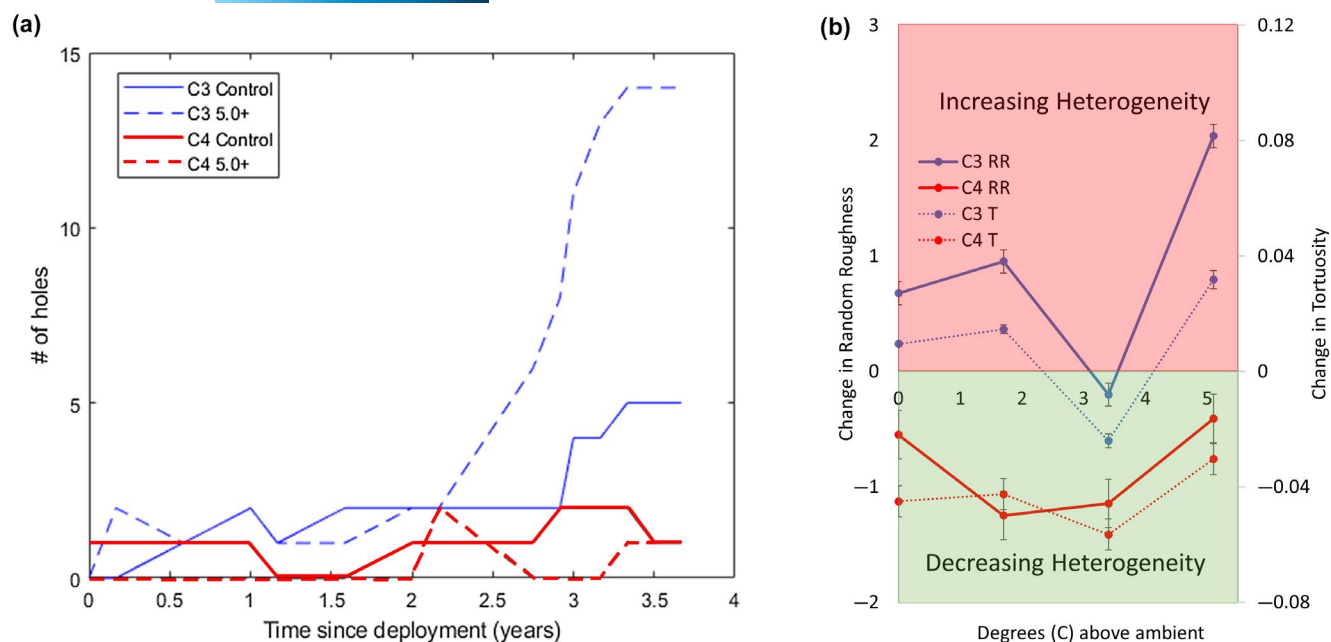
FIGURE 3 (a) Changes in heterogeneity across temperature treatments and plant community as represented by the number of holes in a given year. Holes were defined as locations with a difference in adjacent elevation measurements of greater than 20 mm. Adjacent pins were approximately 4.5 mm apart. (b) The average change in random roughness (RR) and tortuosity (T) over the duration of this experiment. Positive values indicate an increase in heterogeneity, which we associate with a decrease in marsh resilience, while negative values indicate a decrease in heterogeneity, where the marsh surface becomes less variable

treatment (Figure 3a) and a sharp increase in tortuosity and random roughness in the +5.1°C treatment (Figure 3b), suggesting a threshold response to warming at high temperatures. Previous work examines heterogeneity at landscape scales, including the development and/or recovery of unvegetated ponds in salt marshes (Ganju et al., 2017; Temmerman et al., 2003). However, our finding that microtopographic heterogeneity is increasing faster in a drowning, low elevation marsh suggests that early signs of ecosystem transition are visible at far smaller spatial scales that precede landscape transitions. Integrating vertical and lateral metrics of marsh vulnerability is critical to understanding the fate of marshes (Ganju et al., 2017; Van Belzen et al., 2017), and we find that the warmest temperature treatments amplify both vertical (i.e. elevation change) and spatial (i.e. microtopographic heterogeneity) metrics of marsh vulnerability.

2.4 | Implications for coastal marsh survival

Coastal carbon pools are simultaneously threatened and maintained by sea-level rise (Najjar et al., 2000; Rogers et al., 2019), and the limits of soil organic matter accumulation help determine the resilience of the microtidal, sediment-deficient marshes most vulnerable to sea-level rise (Kearney & Turner, 2016; Kirwan et al., 2016; Mudd et al., 2010). Temperature warming is well known to increase rates of both soil organic matter production (Gedan & Bertness, 2010; Kirwan et al., 2009) and decomposition (Kirschbaum, 1995; Kirwan & Blum, 2011; Kirwan et al., 2014) which are opposing processes that affect elevation gain in opposite directions. However, the balance between

these processes, and their impact on marsh resilience, has been difficult to isolate and quantify (Figure 4). Previous experiments that rely solely on passive warming generally find positive increases in productivity and elevation change (Baldwin et al., 2014; Charles & Dukes, 2009; Coldren et al., 2016, 2019; Gedan & Bertness, 2009; Kirwan et al., 2009), but the warming these experiments achieve is relatively modest aboveground and negligible below the soil surface, limiting the ability to influence decomposition. In contrast, our whole-ecosystem soil warming experiment reveals a prominent link between productivity and decomposition expressed over seasonal timescales (i.e. Figure 2) that leads to a consistent temperature optimum of +1.7°C for marsh resilience and carbon accumulation in two disparate plant communities. Our observation of a distinct temperature optimum helps rectify observations of elevation loss in response to warming at low latitudes (Coldren et al., 2019) with the more general positive responses observed in mid- and high-latitude warming experiments (Baldwin et al., 2014; Charles & Dukes, 2009; Gedan & Bertness, 2009), thereby indicating a latitudinal increase in resilience (Figure 4). However, our observations also suggest that positive responses will likely diminish through time with further warming, as marshes approach and surpass their temperature optima (Figures 1 and 4). Temperature increases of 2°C have been identified as tipping points for mass coral bleaching and mortality, increased mortality and reproductive failure for intertidal barnacles and mussels, and the expansion of tropical mangroves into temperate wetlands (Cavanaugh et al., 2019; Helmuth et al., 2010; Hoegh-Guldberg et al., 2007). Here, we quantify a distinct and consistent temperature optimum (+1.7°C) for U.S. mid-Atlantic marsh resilience
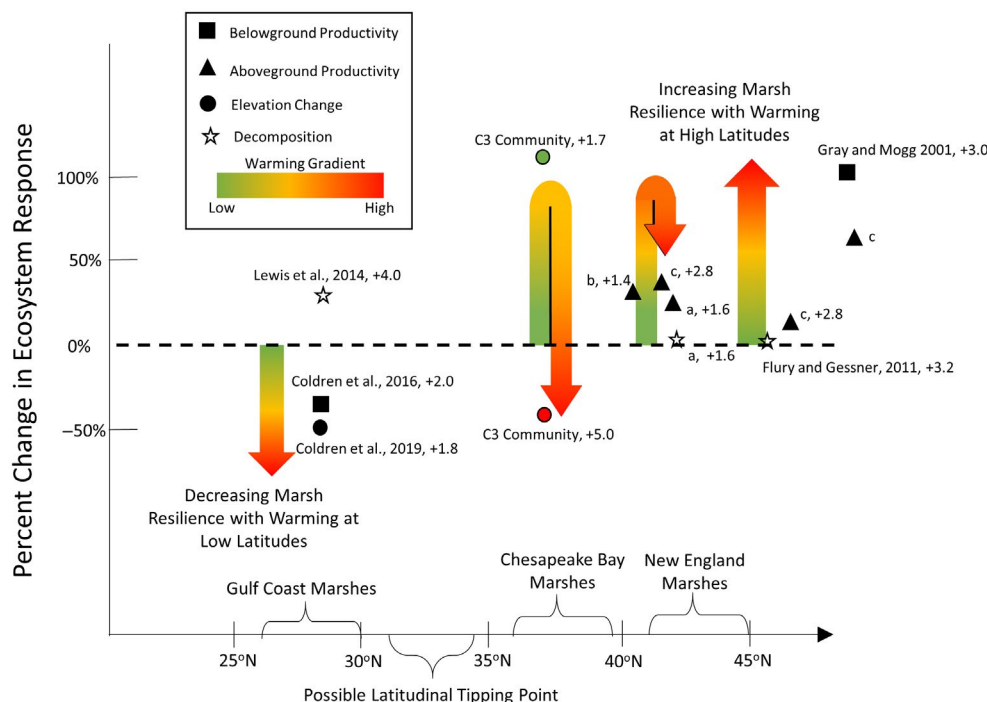
FIGURE 4 Meta-analysis and conceptual diagram showing that the effect of warming on ecosystem response will vary with latitude in the United States. Colors of the arrows represent degree of warming where green represents slight increases above ambient temperatures and red represents extreme warming. In low-latitude marshes, ambient temperatures are above metabolic optima so that warming will lead to decreased marsh resilience. In high-latitude marshes, warming increases marsh resilience. The possible latitudinal tipping point represents a range of potential latitudes along the North American Atlantic seaboard below which any degree of warming is expected to decrease resilience. Squares, triangles, circles, and stars in the figure represent percent changes in belowground productivity, aboveground productivity, elevation change, and decomposition measured in prior warming experiments, where the numbers to the right of the citation indicate the magnitude of warming treatment (°C). Symbols a, b, and c represent data from Charles and Dukes (2009), Gedan and Bertness (2009), and Baldwin et al. (2014) and data from Flury and Gessner (2011), Gray and Mogg (2001), and Lewis et al. (2015) are denoted in the figure. The red and green points near the middle of the figure represent the results of our warming experiment in the C3 community, where elevation gain is enhanced +1.7°C and reduced at +5.1°C, demonstrating a switch from positive to negative effects on marsh resilience

and soil carbon accumulation. Our work uniquely connects metabolic theory to ecosystem resilience to identify a potential temperature optimum for coastal wetland resilience and therefore contributes to the growing body of evidence that continued warming will negatively impact many coastal and marine ecosystems.

3 | MATERIALS AND METHODS

3.1 | Site description and experimental design

The Salt Marsh Accretion Response to Temperature Experiment (SMARTX) was conducted in the Kirkpatrick Marsh, part of the Smithsonian's Global Change Research Wetland (GCReW) (Noyce et al., 2019). Kirkpatrick Marsh is a 22-ha brackish high marsh located in the United States on a microtidal subestuary of the Chesapeake Bay (38°53′ N, 76°33′ W). The site is characterized by C_4 plant communities, dominated by *Spartina patens* and *Distichlis spicata*, and C_3 plant communities, dominated by the C_3 sedge *Schoenoplectus americanus*. The marsh platform is 40–60 cm above daily mean low

water level and is inundated during approximately 28% of high tides. The average elevation of C_4 communities at this site range on average between 0.234 and 0.255 m while the average elevation of the C_3 marsh dominated by *Schoenoplectus americanus* is 0.214 m (Jordan & Correll, 1991). Soils at the site are organic rich (>80%) to a depth of approximately 5 m (Jordan & Correll, 1991; Rietl et al., 2021). Soil bulk densities range from 0.079 to 0.180 g cm³ in the upper 60 cm of soil indicating that the soil profile reflects historic uniform organic matter deposition. While there are abiotic and biotic differences between C_3 and C_4 plant communities (e.g., elevation, inundation frequency, organic matter content, vegetation composition, and shoot density), experimental transects were established in portions of the marsh with distinct C_3 and C_4 communities so that variance within sites is relatively low. The high organic matter content of the marsh soils allows us to assume that changes in marsh elevation are analogous to changes in the soil carbon stock due to a lack of mineral sedimentation and allochthonous carbon influx (Morris et al., 2016). The Kirkpatrick Marsh is within a regional hotspot of late 20th century sea-level rise, driven by geologic conditions along the mid-Atlantic seaboard of the United States (Sallenger

et al., 2012), and the long-term mean sea-level rise trend for the past 50 years in this region is 3.8 mm yr^{-1} (NOAA Sea Level Trends, 2021).

Six replicate transects within the Kirkpatrick Marsh, three in each of the dominant plant communities, were established in 2016. A heating gradient consisting of an ambient temperature plot and heated plots raised to +1.7, +3.4, and +5.1°C above ambient temperatures was established along each transect. Transects were designed to have similar plant community compositions along the entire transect. All plots are 2 by 2 meters with a 0.2 m buffer between plots to mitigate an edge effect. Heating was achieved aboveground using infrared heaters while vertical resistance cables heated soils down to 1.5 m, a depth not reached using passive warming techniques. Temperatures were maintained using an integrated microprocessor-based feedback control to create a fixed temperature differential from the ambient temperature for each plot. Ambient temperature plots have dummy equipment to emulate site disturbance without manipulating temperature. Temperature variation is assessed via thermocouples embedded in acrylic plates in the plant canopy and in the surface soils. Heating began in June of 2016 and is applied year-round.

3.2 | Elevation trends

Soil surface elevations were tracked using surface elevation tables (SETs). SETs were installed in each plot to measure soil surface elevation. Elevation benchmarks were installed outside of the experimental plot in June 2016 by driving a series of stainless-steel rods through the entire soil profile to "refusal" (approximately 12.5 meters, but ranging from 6 to 13.5 meters) and then permanently anchored (Lynch et al., 2015). SET benchmark vertical stability over time was assessed by periodically surveying them relative to each other with a Trimble S5 Total Station and no significant differences in elevation were found. Elevation measurements were collected from approximately 60 "pins" that are 4.5 mm apart and measure the distance from a parallel bar attached to the anchored benchmark to the ground surface, and recorded to the nearest millimeter. This resulted in high-precision measurements of soil surface elevations relative to the base of the benchmark. Measurements were taken every June, August, and January since warming began on June 1, 2016. In addition to this, measurements were taken more frequently (every 2 months from March 2019 to February 2020) to examine inter-annual variability in marsh elevation.

To determine long-term trends, marsh surface elevation was regressed against time for each individual SET pin resulting in approximately 60 estimates of linear elevation trends for each plot. Pin linear regressions across replicate plots (~180 linear regressions per treatment) were then averaged together to estimate the average long-term change in elevation at the treatment level. Treatments were compared using paired t-tests. To examine the effect of an installation effect (the loss of elevation driven by compaction and disturbance during the installation of a SET), we similarly analyzed elevation trends omitting the August 2016 measurement and found general trends to be unaffected and statistically insignificant differences in long-term rates of elevation change. In addition to long-term and annual elevation trends, we used SET data to calculate two metrics of microheterogeneity (random roughness ($\sqrt{\frac{\sum (x_i - x_\mu)}{n-1}}$) and tortuosity (($\sum \sqrt{((x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2)})/l$)), in an effort to quantify marsh surface breakup (Karstens et al., 2016; Moser et al., 2007). As an additional metric of microheterogeneity, we quantified the number of holes, defined as locations with an elevation difference between that exceeded 20 mm. Spatial dependence between pins was calculated using a gamma autocorrelation metric as well as the number of pins away from one pin where pin height becomes independent (similar to van Belzen et al. (2017); Table S2). Low levels of autocorrelation within plots indicate a lack of dependence between pins within plots, especially beyond pins more than 27 mm from one another, and negligible dependence between plots.

Annual aboveground and belowground productivity was measured as described in Noyce et al. (2019). Aboveground productivity was determined by tracking the height and width of 653 stems from April to November 2019 and converting to biomass using allometric equations. For belowground productivity, root ingrowth cores were installed in November 2018 and removed a year later, after which the dry weight of fine roots in the core was determined. Methane emissions were measured as described in Noyce and Megonigal (2021) using static chambers and a Los Gatos Research Ultraportable Greenhouse Gas Analyzer. Water level was derived from one water level sensor (AquaTROLL 200) located in each plant community, which was then corrected to water level above marsh surface (m) using three averaged RTK elevation measurements from each plot. To examine the effect of productivity, decomposition, and water level on seasonal elevation trends, an ANOVA and multiple paired t-tests were applied.

AUTHOR CONTRIBUTION

JPM, GLN, GRG, and MLK conceived of and designed this study. AJS analyzed the data, created the figures, and wrote the manuscript. GLN and GRG provided data supplementing the manuscript. All

coauthors contributed to the interpretation of the results and the editing of the manuscript.

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