1   Temperature optimum for marsh resilience and carbon accumulation revealed in a whole

2   ecosystem warming experiment

3   Alexander J. Smith*[1], Genevieve L. Noyce[2], J. Patrick Megonigal[2], Glenn R. Guntenspergen[3],

4   Matthew L. Kirwan[1]

5   *Corresponding Author, ORCID iD: 0000-0002-9966-8726

6   1 Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, 23062,

7   Virginia, USA

8   2 Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, 21037,

9   Maryland, USA

10   3 U.S. Geological Survey, Eastern Ecological Science Center, 12100 Beech Forest Road, Laurel,

11   MD 20708-4035

12   **Abstract:** Coastal marshes are globally important, carbon dense ecosystems simultaneously

13   maintained and threatened by sea-level rise. Warming temperatures may increase wetland plant

14   productivity and organic matter accumulation, but temperature-modulated feedbacks between

15   productivity and decomposition make it difficult to assess how wetlands and their thick, organic

16   rich soils will respond to climate warming. Here, we actively increased aboveground plant-

17   surface and below-ground soil temperatures in two marsh plant communities, and found that a

18   moderate amount of warming (1.7°C above ambient temperatures) consistently maximized root

19   growth, marsh elevation gain, and below-ground carbon accumulation. Marsh elevation loss

20   observed at higher temperatures was associated with increased carbon mineralization and

21   increased microtopographic heterogeneity, a potential early warning signal of marsh drowning.

22   Maximized elevation and below-ground carbon accumulation for moderate warming scenarios

23   uniquely suggest linkages between metabolic theory of individuals and landscape-scale

24 ecosystem resilience and function, but our work indicates nonpermanent benefits as global

25 temperatures continue to rise.

26 **Keywords:** Whole-ecosystem warming, ecosystem resilience, vertical accretion, marsh

27 elevation, carbon accumulation

28

Introduction

29

30   Marshes are highly valuable ecosystems providing a range of ecosystem services from

31   storm protection to carbon accumulation, but accelerating rates of sea-level rise threaten to

32   drown them and eliminate these services (Mcleod et al., 2011; Shepard et al., 2011; Kirwan and

33   Megonigal, 2013; Jankowski et al., 2017). Warming simultaneously accelerates sea-level rise

34   and alters *in situ* process rates that regulate marsh elevation and vulnerability to drowning,

35   namely production, decomposition, and vertical accretion. Vertical accretion maintains marsh

36   elevation relative to sea level through autochthonous root production and the capture of

37   allochthonous sediments and organic matter (Kirwan and Megonigal, 2013; Morris et al., 2016).

38   As increased damming and management practices decrease suspended sediment available for

39   capture, temperature sensitive biogenic controls to vertical accretion, such as production and

40   decomposition, become increasingly important (Temmerman et al., 2003; Peteet et al., 2018).

41   Above- and belowground production increase with temperature, which is expected to accelerate

42   both vertical accretion and carbon inputs to the soil (Gedan and Bertness, 2009; Charles and

43   Dukes, 2009; Coldren et al., 2016). Therefore, warming could increase vertical accretion rates

44   and contribute to a negative carbon-climate feedback by increasing soil carbon storage

45   (Kirschbaum, 1995; Najjar et al., 2000; Rogers et al., 2019). However, this conceptual

46   framework largely neglects temperature driven increases in decomposition, which can reduce

47   marsh stability and potentially offset benefits from increased productivity (Kirschbaum, 1995;

48   Kirwan and Blum, 2011; Kirwan et al., 2014).

49   Global climate models project mean global temperature increases of 2.6-5.0 °C by the

50   end of the 21st century (IPCC, 2021). Some studies have attempted to replicate these

51   temperatures experimentally in salt marshes using aboveground heating lamps or passive heating

52   systems (Gedan and Bertness, 2009; Charles and Dukes, 2009; Coldren et al., 2016, Zhong et al.,

53   2019). While these designs have successfully simulated increased temperatures at the marsh

54   surface, these methods fail to increase temperature at deep soil depths (~1 meter) that are

55   expected to warm under future climate conditions (Phillips, 2020). Given the large, deep stores

56   of organic material that have accumulated in marshes over time, these passive, surficial warming

57   designs neglect to warm a significant portion of soil organic material that will experience

58   warming in the future. Additionally, studies reliant on passive warming typically feature a single,

59   low magnitude temperature treatment and therefore cannot account for non-linear warming

60   responses that may occur as the climate continues to warm. Therefore, experimental warming of

61   just surface sediments and vegetation fails to accurately simulate whole-scale ecosystem

62   warming, and its cascading impacts on marsh resilience and function.

63   To address uncertain marsh response and resilience to future temperatures, the Salt Marsh

64   Accretion Response to Warming Experiment (SMARTX) actively warmed entire marsh

65   ecosystems, from plant canopy to a soil depth of approximately 1.5 m, using heating lamps at the

66   surface and subterranean cables to achieve four discrete temperature treatments (ambient, 1.7,

67   3.4, and 5.1 °C above ambient temperatures) in two brackish marsh plant communities that are

68   dominated by either C_3 or C_4 plant species (SI Fig. 1) (Noyce et al., 2019). The C_3 site is

69   dominated by the C_3 sedge *Schoenoplectus americanus* (93% of aboveground biomass) and is

70   relatively wet due to lower elevation and more frequent tidal flooding while the C_4 site is

71   dominated by *Spartina patens* and *Distichlis spicata* (76% of aboveground biomass) and is

72   relatively elevated and dry (Jordan and Correll, 1991). We measured marsh surface elevation in

73   response to whole-ecosystem warming at annual and seasonal time scales and found that while

74   marsh resilience is optimized under moderate degrees of warming, further warming led to

75 decreased rates of carbon accumulation, early signs of marsh collapse, and increased

76 vulnerability to sea-level rise.

77 **Results and Discussion**

78 *Moderate warming optimizes marsh resilience and carbon accumulation*

79   We measured marsh surface elevation response across warming gradients in C_3 and C_4

80 plant communities over a 4-year period (June 2016 to February 2020). Marsh surface elevation

81 was regressed against time for each individual surface elevation table (SET) pin (Lynch et al.,

82 2015), resulting in derived rates of elevation gain and loss, but more generally marsh surface

83 elevation increased through time in the C_3 community and decreased through time in the C_4

84 community (Fig. 1a, 1b). Despite these contrasting elevation trends, both communities responded

85 similarly to warming treatments, where elevation gain was optimized at 1.7 °C above current

86 ambient conditions (Fig. 1c). This optimal temperature treatment increased elevation gain by

87 approximately 2.1 mm y^{-1} and 2.5 mm y^{-1} in the C_3 and C_4 communities, respectively (SI Table

88 1), but elevation gain was still less than the 3.8 mm yr^{-1} mean sea-level rise trend for the past 50

89 years in this region (NOAA Sea Level Trends, 2021). Warming beyond the temperature

90 optimum reduced this positive effect and resulted in a 0.8 mm y^{-1} and 0.9 mm y^{-1} loss of

91 elevation at the +5.1 °C treatment (Fig. 1c), a rate equivalent to or less than ambient rates of

92 elevation gain. Root production was also optimized at +1.7 °C in our experiment driven by

93 optimum allocation of growth to belowground biomass in response to nitrogen limitation; above

94 1.7 °C increased nitrogen mineralization reduces plant nitrogen demand and root productivity

95 (Noyce et al., 2019). Therefore, belowground organic matter production drives the long-term

96 elevation response to warming, with a consistent temperature optimum for root productivity and

97 elevation change in both plant communities (Fig. 1c).

98   Carbon accumulation rates were also maximized at moderate warming treatments.

99   Carbon accumulation rates were calculated as the product of elevation change in each

100   experimental plot (ranging from 2.5 to -0.9 mm yr^{-1}) and the average carbon density of all C$_3$

101   (104.8 kg C m^{-3}) and all C$_4$ plots (238.8 kg C m^{-3}). These estimates assume that elevation change

102   is driven predominately by organic matter accumulation at our sites, as evidenced by high soil

103   organic matter content (~90%), limited allochthonous input of mineral sediment (Morris et al.,

104   2016; Rietl et al., 2021), and accretion rates that are tightly controlled by root zone processes

105   (Langley et al., 2009; Rietl et al., 2021). The C$_3$ community carbon accumulation rate was

106   maximized at +1.7 °C (262 g C m^{-2} y^{-1}) and minimized at the control and +5.1 °C treatments (25

107   and -71 g C m^{-2} y^{-1} respectively). The C$_4$ carbon accumulation rate was also maximized at +1.7

108   °C (24 g C m^{-2} y^{-1}), but with a net loss of carbon storage in the control and +5.1 °C treatments (-

109   249 and -296 g C m^{-2} y^{-1} respectively) (SI Fig. 2). Our finding that the more flood-tolerant C$_3$

110   community responses to warming are more positive than less-flood tolerant C$_4$ responses offer

111   empirical support to numerical modeling that suggests the positive impacts of temperature on

112   marsh carbon accumulation are maximized at high sea-level rise rates (Couto et al., 2014), but

113   also highlights that warming-induced gains in one part of the system (C$_3$) may be offset by losses

114   elsewhere (C$_4$).

115   Warming responses have traditionally been interpreted in the context of an optimal

116   temperature for metabolism, where rates of productivity increase up to a point of typical summer

117   temperatures and then decline with further warming (Long et al., 1975; Giurgevich and Dunn,

118   1979; Seneca and Blum, 1984; O'Sullivan et al., 2017). The photosynthetic optimum of

119   *Spartina*, a common C$_4$ salt marsh genus, is approximately 2.2 to 7.2 °C above the mean high

120   temperature during summer days at our study site (~28°C) (Giurgevich and Dunn, 1979; Kirwan

121   et al., 2009). This, and decreased net primary production observed during elevated regional

122   summer temperatures (Noyce et al., 2019), indicates that moderate amounts of warming in the

123   region are likely elevating temperatures closer to or above this metabolic optimum. Although

124   some studies have indicated that marsh grasses can acclimate leaf respiration and photosynthetic

125   capacity to increasing temperatures (Wang et al., 2020; Sturchio et al., 2021), the warmest

126   treatment likely exceeds the metabolic temperature optimum during warm summer days leading

127   to a reduction in marsh elevation, analogous to the hump-shaped relationships between

128   temperature and productivity proposed for *S. alterniflora* more globally (Rogers et al., 2006;

129   Więski and Pennings, 2014; Liu et al., 2016; Liu et al., 2020). Our observations of consistent

130   treatment optima, where root production, elevation change, and carbon accumulation rates in two

131   disparate plant communities were maximized at +1.7 °C, suggest that the qualitative patterns are

132   applicable beyond our particular study area, but that the exact temperature optimum may vary

133   around +1.7 °C (Fig. 1c). Moreover, because autochthonous, plant-mediated mechanisms drive

134   these consistent optima, this suggests that metabolic temperature optima for individual plants or

135   communities can cascade up to whole-marsh elevation change dynamics, thereby uniquely

136   linking metabolic theory to ecosystem resilience and function.

137   *Interactions between productivity and decomposition drive seasonal elevation trends*

138   From March 2019 to February 2020, we measured marsh elevation every two months to

139   quantify the potential influence of temperature over seasonal timescales (Fig. 2a). Surprisingly,

140   we found seasonal variations in relative marsh elevation that ranged from 8.75 to 13.25 mm,

141   approximately 10 times greater than the long-term accretion rates observed in this study (Fig. 2a,

142   2b). Seasonal variation was maximized in the +1.7 °C treatment in both the C_3 and C_4

143   community, closely following patterns in annual elevation gain and root productivity (Fig. 2b).

144   Marsh elevations were consistently maximized in the early spring (March to May) prior to

145   increased sedge and grass productivity and were minimized in the fall (August to December).

146   While multiple factors are known to influence seasonal marsh elevation change, we

147   attribute it largely to seasonal changes in organic matter accumulation, expressed as the

148   temperature-modulated balance between decomposition and production. Previous work links

149   seasonal elevation change to declines in water level associated with evapotranspiration and

150   drought during warm periods (Friedrichs and Perry, 2001; Cahoon et al., 2011; Bashan et al.,

151   2013), but we found that water level fluctuations were only loosely correlated with fluctuations

152   in seasonal elevation patterns (p=0.10) and could not explain variation between treatments

153   (p=0.54). Previous work in mineral-rich systems suggests that seasonal elevation change can be

154   driven by changes in plant growth and its effect on sediment trapping (Palinkas and Engelhardt,

155   2019; Noyce and Megonigal, 2021), but at our site, seasonal elevation change is inversely

156   correlated with productivity (Fig. 2a). Instead, seasonal elevation patterns correspond to organic

157   matter decomposition inferred from methane emissions measured at our study site. In particular,

158   methane emissions correlate closely with temperature (Darby and Turner, 2008) and inversely

159   with marsh elevation (p=0.01), signifying increased organic matter preservation in the winter and

160   increased decomposition in the summer. Warming is known to increase both organic matter

161   productivity (Connor and Chmura, 2000; Crosby et al., 2016) and decomposition (Najjar et al.,

162   2000; Kirwan et al., 2014; Mueller et al., 2016; Hanson et al., 2020) separately, but the observed

163   summer elevation loss uniquely indicates that the balance between these processes is largely

164   negative, with higher rates of decomposition dominating productivity and reducing organic

165   matter storage. Though counterintuitive, the loss of elevation during the most productive portions

166   of the growing season could be explained by soil priming effects, where root growth delivers

167   oxygen and organic carbon to anaerobic soils and enhances decomposition (Dakos et al., 2012;

168   Mueller et al., 2020; Rietl et al., 2021). The amplitude of seasonal marsh elevation variability

169   (Fig. 2b) mirrors interannual trends in marsh elevation under manipulated warming treatments

170   (Fig. 1c). Therefore, at both the seasonal and annual timescales, marsh resilience and carbon

171   storage are decreased at high temperatures (Fig. 1c, Fig. 2a).

172   *Increasing heterogeneity in microtopography: evidence for decreasing resilience*

173   Ecosystems often respond to stressors with increased spatial variability, such as increased

174   autocorrelation and variance, which can signal an approaching critical threshold and imminent

175   state change (Kéfi et al., 2007; Veraart et al., 2012; Kéfi et al., 2014; Van Belzen et al., 2017),

176   but few spatial indicators have been tested as early indicators of state change in coastal wetlands

177   (Moffett et al., 2015; Martinez, 2021). Over the duration of this three year study, we observed an

178   increase in the number of elevation measurements that were greater than 20 mm different than

179   adjacent pin measurements in the C_3 community as the marsh degraded. These observations

180   inspired us to examine the effect of temperature and plant community on spatial variability using

181   three metrics of microtopography heterogeneity (tortuosity, random roughness, and number of

182   holes, with holes defined as differences in elevation between adjacent SET pin measurements

183   greater than 20 mm) that may predict proximity to state change. Microtopographic heterogeneity

184   decreased through time in the C_4 community, and increased through time in the C_3 community

185   (Fig. 3). This pattern could be expected given that the high elevation C_4 marsh is higher in the

186   tidal frame than the C_3 marsh and is therefore farther from an extinction threshold (Rietl et al.,

187   2021). Additionally, we found that heterogeneity increased sharply in the warmest treatments in

188   the C_3 community, as evidenced by a tripling in the number of holes formed in the +5.1 °C

189   treatment (Fig. 3a) and a sharp increase in tortuosity and random roughness in the +5.1 °C

190   treatment (Fig. 3b), suggesting a threshold response to warming at high temperatures. Previous

191   work examines heterogeneity at landscape scales, including the development and/or recovery of

192   unvegetated ponds in salt marshes (Temmerman et al., 2003; Ganju et al., 2017). However, our

193   finding that microtopographic heterogeneity is increasing faster in a drowning, low elevation

194   marsh suggests that early signs of ecosystem transition are visible at far smaller spatial scales

195   that precede landscape transitions. Integrating vertical and lateral metrics of marsh vulnerability

196   is critical to understanding the fate of marshes (Van Belzen et al., 2017; Ganju et al., 2017), and

197   we find that the warmest temperature treatments amplify both vertical (i.e. elevation change) and

198   spatial (i.e. microtopographic heterogeneity) metrics of marsh vulnerability.

199   *Implications for coastal marsh survival*

200   Coastal carbon pools are simultaneously threatened and maintained by sea-level rise

201   (Najjar et al., 2000; Rogers et al., 2019), and the limits of soil organic matter accumulation help

202   determine the resilience of the microtidal, sediment-deficient marshes most vulnerable to sea-

203   level rise (Mudd et al., 2010; Kirwan et al., 2016; Kearney and Turner, 2016). Temperature

204   warming is well known to increase rates of both soil organic matter production (Kirwan et al.,

205   2009; Gedan and Bertness, 2010) and decomposition (Kirschbaum, 1995; Kirwan and Blum,

206   2011; Kirwan et al., 2014) which are opposing processes that affect elevation gain in opposite

207   directions. However, the balance between these processes, and their impact on marsh resilience,

208   has been difficult to isolate and quantify (Fig. 4). Previous experiments that rely solely on

209   passive warming generally find positive increases in productivity and elevation change (Gedan

210   and Bertness, 2009; Charles and Dukes, 2009; Kirwan et al., 2009; Baldwin et al., 2014; Coldren

211   et al., 2016, Coldren et al., 2019), but the warming these experiments achieve is relatively

212   modest aboveground and negligible below the soil surface, limiting the ability to influence

213   decomposition. In contrast, our whole-ecosystem soil warming experiment reveals a prominent

214   link between productivity and decomposition expressed over seasonal timescales (i.e. Fig. 2) that

215   leads to a consistent temperature optimum of +1.7 °C for marsh resilience and carbon

216   accumulation in two disparate plant communities. Our observation of a distinct temperature

217   optimum helps rectify observations of elevation loss in response to warming at low latitudes

218   (Coldren et al., 2019) with the more general positive responses observed in mid and high-latitude

219   warming experiments (Gedan and Bertness, 2009; Charles and Dukes, 2009; Baldwin et al.,

220   2014), thereby indicating a latitudinal increase in resilience (Fig. 4). However, our observations

221   also suggest that positive responses will likely diminish through time with further warming, as

222   marshes approach and surpass their temperature optima (Fig. 1; Fig. 4). Temperature increases of

223   2 °C have been identified as tipping points for mass coral bleaching and mortality, increased

224   mortality and reproductive failure for intertidal barnacles and mussels, and the expansion of

225   tropical mangroves into temperate wetlands (Hoegh-Guldberg et al., 2007; Helmuth et al., 2010;

226   Cavanaugh et al., 2019). Here, we quantify a distinct and consistent temperature optimum (+1.7

227   °C) for U.S. mid-Atlantic marsh resilience and soil carbon accumulation. Our work uniquely

228   connects metabolic theory to ecosystem resilience to identify a potential temperature optimum

229   for coastal wetland resilience and therefore contributes to the growing body of evidence that

230   continued warming will negatively impact many coastal and marine ecosystems.

Materials and Methods

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 and Correll, 1991). Soils at the site are organic-rich (>80%) to a depth of approximately 5 m (Jordan and Correll, 1991; Rietl et al., 2021). Soil bulk densities range from 0.079 to 0.180 g cm^3 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

254   long-term mean sea-level rise trend for the past 50 years in this region is 3.8 mm yr^{-1} (NOAA

255   Sea Level Trends, 2021)

256   Six replicate transects within the Kirkpatrick Marsh, three in each of the dominant plant

257   communities, were established in 2016. A heating gradient consisting of an ambient temperature

258   plot and heated plots raised to +1.7, +3.4, and +5.1 °C above ambient temperatures was

259   established along each transect. Transects were designed to have similar plant community

260   compositions along the entire transect. All plots are 2 by 2 meters with a 0.2 m buffer between

261   plots to mitigate an edge effect. Heating was achieved aboveground using infrared heaters while

262   vertical resistance cables heated soils down to 1.5 m, a depth not reached using passive warming

263   techniques. Temperatures were maintained using an integrated microprocessor based feedback

264   control to create a fixed temperature differential from the ambient temperature for each plot.

265   Ambient temperature plots have dummy equipment to emulate site disturbance without

266   manipulating temperature. Temperature variation is assessed via thermocouples embedded in

267   acrylic plates in the plant canopy and in the surface soils. Heating began in June of 2016 and is

268   applied year-round.

269   *Elevation Trends*

270   Soil surface elevations were tracked using surface elevation tables (SETs). SETs were

271   installed in each plot to measure soil surface elevation. Elevation benchmarks were installed

272   outside of the experimental plot in June 2016 by driving a series of stainless-steel rods through

273   the entire soil profile to "refusal" (approximately 12.5 meters, but ranging from 6 to 13.5 meters)

274   and then permanently anchored (Lynch et al., 2015). SET benchmark vertical stability over time

275   was assessed by periodically surveying them relative to each other with a Trimble S5 Total

276   Station and no significant differences in elevation were found. Elevation measurements were

277   collected from approximately 60 "pins" that are 4.5 mm apart and measure the distance from a

278   parallel bar attached to the anchored benchmark to the ground surface, and recorded to the

279   nearest millimeter. This resulted in high-precision measurements of soil surface elevations

280   relative to the base of the benchmark. Measurements were taken every June, August, and January

281   since warming began on June 1, 2016. In addition to this, measurements were taken more

282   frequently (every two months from March 2019 to February 2020) to examine inter-annual

283   variability in marsh elevation.

284   To determine long term trends, marsh surface elevation was regressed against time for

285   each individual SET pin resulting in approximately 60 estimates of linear elevation trends for

286   each plot. Pin linear regressions across replicate plots (~180 linear regressions per treatment)

287   were then averaged together to estimate the average long-term change in elevation at the

288   treatment level. Treatments were compared using paired t-tests. To examine the effect of an

289   installation effect (the loss of elevation driven by compaction and disturbance during the

290   installation of a SET), we similarly analyzed elevation trends omitting the August 2016

291   measurement and found general trends to be unaffected and statistically insignificant differences

292   in long-term rates of elevation change. In addition to long term and annual elevation trends, we

293   used SET data to calculate two metrics of microheterogeneity (random roughness ($\sqrt{\frac{\sum(x_i - x_\mu)}{n-1}}$)

294   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

295   surface breakup (Moser et al., 2007; Karstens et al., 2016). As an additional metric of

296   microheterogeneity, we quantified the number of holes, defined as locations with an elevation

297   difference between that exceeded 20 mm. Spatial dependence between pins was calculated using

298   a gamma autocorrelation metric as well as the number of pins away from one pin where pin

299   height becomes independent (similar to van Belzen et al. (2017); SI Table 2). Low levels of

300   autocorrelation within plots indicate a lack of dependence between pins within plots, especially

301   beyond pins more than 27 mm from one another, and negligible dependence between plots.

302   Annual above- and belowground productivity was measured as described in Noyce et al.

303   (2019). Aboveground productivity was determined by tracking the height and width of 653 stems

304   from Apr to Nov 2019 and converting to biomass using allometric equations. For belowground

305   productivity, root ingrowth cores were installed in November 2018 and removed a year later,

306   after which the dry weight of fine roots in the core was determined. Methane emissions were

307   measured as described in Noyce and Megonigal (2021) using static chambers and a Los Gatos

308   Research Ultraportable Greenhouse Gas Analyzer. Water level was derived from one water level

309   sensor (AquaTROLL 200) located in each plant community, which was then corrected to water

310   level above marsh surface (m) using three averaged RTK elevation measurements from each

311   plot. To examine the effect of productivity, decomposition, and water level on seasonal elevation

312   trends, an ANOVA and multiple paired t-tests were applied.

313

323 firm, or product names is for descriptive purposes only and does not imply endorsement by the

324 US Government. This is contribution no. XXXX of the Virginia Institute of Marine Science.

325 **Contributions**

326 JPM, GLN, GRG, and MLK conceived of and designed this study. AJS analyzed data, created

327 figures, and wrote the manuscript. GLN and GRG provided data supplementing the manuscript.

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

329 **Data Availability**

330 Elevation data that support the findings of this study is available on Smithsonian figshare:

331 https://doi.org/10.25573/serc.19213938.v1

332

333 References:

334 1. Baldwin, A. H., Jensen, K., & Schönfeldt, M. (2014). Warming increases plant biomass and

335   reduces diversity across continents, latitudes, and species migration scenarios in experimental

336   wetland communities. *Global change biology*, *20*(3), 835-850.

337 2. Bashan, Y., Moreno, M., Salazar, B. G., & Alvarez, L. (2013). Restoration and recovery of

338   hurricane-damaged mangroves using the knickpoint retreat effect and tides as dredging

339   tools. *Journal of environmental management*, *116*, 196-203.

340 3. Cahoon, D. R., Perez, B. C., Segura, B. D., & Lynch, J. C. (2011). Elevation trends and

341   shrink–swell response of wetland soils to flooding and drying. *Estuarine, Coastal and Shelf

342   Science*, *91*(4), 463-474.

343 4. Cavanaugh, K. C., Dangremond, E. M., Doughty, C. L., Williams, A. P., Parker, J. D.,

344   Hayes, M. A., ... & Feller, I. C. (2019). Climate-driven regime shifts in a mangrove–salt

345   marsh ecotone over the past 250 years. *Proceedings of the National Academy of

346   Sciences*, *116*(43), 21602-21608.

347 5. Charles, H., and J. S. Dukes. 2009. Effects of warming and altered precipitation on plant and

348   nutrient dynamics of a New England salt marsh. *Ecological Applications* **19**:1758–1773.

349 6. Coldren, G. A., Barreto, C. R., Wykoff, D. D., Morrissey, E. M., Langley, J. A., Feller, I. C.,

350   & Chapman, S. K. (2016). Chronic warming stimulates growth of marsh grasses more than

351   mangroves in a coastal wetland ecotone. *Ecology*, *97*(11), 3167-3175.

352 7. Coldren, G. A., Langley, J. A., Feller, I. C., & Chapman, S. K. (2019). Warming accelerates

353   mangrove expansion and surface elevation gain in a subtropical wetland. *Journal of Ecology*,

354   107(1), 79-90.

355   8. Connor, R., & Chmura, G. L. (2000). Dynamics of above-and belowground organic matter in

356   a high latitude macrotidal saltmarsh. *Marine Ecology Progress Series*, *204*, 101-110.

357   9. Couto, T., Martins, I., Duarte, B., Caçador, I., & Marques, J. C. (2014). Modelling the effects

358   of global temperature increase on the growth of salt marsh plants. *Applied Ecology and*

359   *Environmental Research*, *12*(3), 753-764.

360   10. Crosby, S. C., Sax, D. F., Palmer, M. E., Booth, H. S., Deegan, L. A., Bertness, M. D., &

361   Leslie, H. M. (2016). Salt marsh persistence is threatened by predicted sea-level

362   rise. *Estuarine, Coastal and Shelf Science*, *181*, 93-99.

363   11. Dakos, V., Van Nes, E. H., d'Odorico, P., & Scheffer, M. (2012). Robustness of variance and

364   autocorrelation as indicators of critical slowing down. *Ecology*, *93*(2), 264-271.

365   12. Darby, F. A., & Turner, R. E. (2008). Below-and aboveground Spartina alterniflora

366   production in a Louisiana salt marsh. *Estuaries and Coasts*, *31*(1), 223-231.

367   13. Flury, S., & Gessner, M. O. (2011). Experimentally simulated global warming and nitrogen

368   enrichment effects on microbial litter decomposers in a marsh. *Applied and Environmental*

369   *Microbiology*, 77(3), 803-809.

370   14. Friedrichs, C. T., & Perry, J. E. (2001). Tidal salt marsh morphodynamics: a

371   synthesis. *Journal of Coastal Research*, 7-37.

372   15. Ganju, N. K., Defne, Z., Kirwan, M. L., Fagherazzi, S., D'Alpaos, A., & Carniello, L.

373   (2017). Spatially integrative metrics reveal hidden vulnerability of microtidal salt

374   marshes. *Nature communications*, *8*(1), 1-7.

375   16. Gedan, K. B., & Bertness, M. D. (2009). Experimental warming causes rapid loss of plant

376   diversity in New England salt marshes. *Ecology Letters*, *12*(8), 842-848.

377 17. Gedan, K. B., & Bertness, M. D. (2010). How will warming affect the salt marsh foundation

378   species Spartina patens and its ecological role?. *Oecologia*, 164(2), 479-487.

379 18. Giurgevich, J. R., & Dunn, E. L. (1979). Seasonal patterns of CO 2 and water vapor

380   exchange of the tall and short height forms of Spartina alterniflora Loisel in a Georgia salt

381   marsh. *Oecologia*, *43*(2), 139-156.

382 19. Gray, A. J., & Mogg, R. J. (2001). Climate impacts on pioneer saltmarsh plants. *Climate*

383   *Research*, *18*(1-2), 105-112.

384 20. Hanson, P. J., Griffiths, N. A., Iversen, C. M., Norby, R. J., Sebestyen, S. D., Phillips, J. R.,

385   ... & Ricciuto, D. M. (2020). Rapid net carbon loss from a whole-ecosystem warmed

386   Peatland. *AGU Advances*, *1*(3), e2020AV000163.

387 21. Helmuth, B., Broitman, B. R., Yamane, L., Gilman, S. E., Mach, K., Mislan, K. A. S., &

388   Denny, M. W. (2010). Organismal climatology: analyzing environmental variability at scales

389   relevant to physiological stress. *Journal of Experimental Biology*, 213(6), 995-1003.

390 22. Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E.,

391   ... & Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean

392   acidification. *science*, *318*(5857), 1737-1742.

393 23. IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working

394   Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change

395   [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y.

396   Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K.

397   Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University

398   Press. In Press.

399   24. Jankowski, K. L., Törnqvist, T. E., & Fernandes, A. M. (2017). Vulnerability of Louisiana's

400   coastal wetlands to present-day rates of relative sea-level rise. *Nature Communications*, *8*(1),

401   1-7.

402   25. Jordan, T. E., & Correll, D. L. (1991). Continuous automated sampling of tidal exchanges of

403   nutrients by brackish marshes. *Estuarine, Coastal and Shelf Science*, 32(6), 527-545.

404   26. Karstens, S., Jurasinski, G., Glatzel, S., & Buczko, U. (2016). Dynamics of surface elevation

405   and microtopography in different zones of a coastal Phragmites wetland. Ecological

406   Engineering, 94, 152-163.

407   27. Kearney, M. S., & Turner, R. E. (2016). Microtidal marshes: Can these widespread and

408   fragile marshes survive increasing climate–sea level variability and human action?. *Journal*

409   *of Coastal Research*, *32*(3), 686-699.

410   28. Kefi, S., Guttal, V., Brock, W. A., Carpenter, S. R., Ellison, A. M., Livina, V. N., ... &

411   Dakos, V. (2014). Early warning signals of ecological transitions: methods for spatial

412   patterns. *PloS one*, *9*(3), e92097.

413   29. Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & De

414   Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in

415   Mediterranean arid ecosystems. *Nature*, *449*(7159), 213-217.

416   30. Kirschbaum, M. U. (1995). The temperature dependence of soil organic matter

417   decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and*

418   *biochemistry*, 27(6), 753-760.

419   31. Kirwan, M. L., & Blum, L. K. (2011). Enhanced decomposition offsets enhanced

420   productivity and soil carbon accumulation in coastal wetlands responding to climate change.

421   *Biogeosciences*, 8(4), 987-993.

422   32. Kirwan, M. L., & Megonigal, J. P. (2013). Tidal wetland stability in the face of human

423   impacts and sea-level rise. *Nature*, *504*(7478), 53-60.

424   33. Kirwan, M. L., & Mudd, S. M. (2012). Response of salt-marsh carbon accumulation to

425   climate change. *Nature*, *489*(7417), 550-553.

426   34. Kirwan, M. L., Guntenspergen, G. R., & Langley, J. A. (2014). Temperature sensitivity of

427   organic-matter decay in tidal marshes. *Biogeosciences*, *11*(17), 4801-4808.

428   35. Kirwan, M. L., Guntenspergen, G. R., & Morris, J. T. (2009). Latitudinal trends in Spartina

429   alterniflora productivity and the response of coastal marshes to global change. *Global*

430   *Change Biology*, *15*(8), 1982-1989.

431   36. Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R., & Fagherazzi, S.

432   (2016). Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change*, *6*(3),

433   253-260.

434   37. Langley, J. A., McKee, K. L., Cahoon, D. R., Cherry, J. A., & Megonigal, J. P. (2009).

435   Elevated CO2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings*

436   *of the National Academy of Sciences*, *106*(15), 6182-6186.

437   38. Lewis, D. B., Brown, J. A., & Jimenez, K. L. (2014). Effects of flooding and warming on soil

438   organic matter mineralization in Avicennia germinans mangrove forests and Juncus

439   roemerianus salt marshes. *Estuarine, Coastal and Shelf Science*, *139*, 11-19.

440   39. Liu, W., Chen, X., Strong, D. R., Pennings, S. C., Kirwan, M. L., Chen, X., & Zhang, Y.

441   (2020). Climate and geographic adaptation drive latitudinal clines in biomass of a widespread

442   saltmarsh plant in its native and introduced ranges. *Limnology and Oceanography*, *65*(6),

443   1399-1409.

444   40. Liu, W., Maung-Douglass, K., Strong, D. R., Pennings, S. C., & Zhang, Y. (2016).

445   Geographical variation in vegetative growth and sexual reproduction of the invasive Spartina

446   alterniflora in China. *Journal of Ecology*, *104*(1), 173-181.

447   41. Long, S. P., Incoll, L. D., & Woolhouse, H. W. (1975). C 4 photosynthesis in plants from

448   cool temperate regions, with particular reference to Spartina townsendii. *Nature*, 257(5527),

449   622-624.

450   42. Lynch, J. C., Hensel, P., & Cahoon, D. R. (2015). The surface elevation table and marker

451   horizon technique: A protocol for monitoring wetland elevation dynamics (No.

452   NPS/NCBN/NRR—2015/1078). National Park Service.

453   43. Martinez, M. (2021). *State Changes in Coastal Wetlands: Anticipating Transitions and*

454   *Evaluating the Role of Ghost Forests in Regional Greenhouse Gas Emissions* (Doctoral

455   dissertation, North Carolina State University).

456   44. Mcleod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., ... & Silliman,

457   B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of

458   vegetated coastal habitats in sequestering CO2. *Frontiers in Ecology and the*

459   *Environment*, *9*(10), 552-560.

460   45. Moffett, K. B., Nardin, W., Silvestri, S., Wang, C., & Temmerman, S. (2015). Multiple stable

461   states and catastrophic shifts in coastal wetlands: Progress, challenges, and opportunities in

462   validating theory using remote sensing and other methods. *Remote Sensing*, *7*(8), 10184-

463   10226.

464   46. Morris, J. T., Barber, D. C., Callaway, J. C., Chambers, R., Hagen, S. C., Hopkinson, C. S.,

465   ... & Wigand, C. (2016). Contributions of organic and inorganic matter to sediment volume

466   and accretion in tidal wetlands at steady state. *Earth's future*, *4*(4), 110-121.

467   47. Moser, K., Ahn, C., & Noe, G. (2007). Characterization of microtopography and its influence

468   on vegetation patterns in created wetlands. *Wetlands*, 27(4), 1081-1097.

469   48. Mudd, S. M., D'Alpaos, A., & Morris, J. T. (2010). How does vegetation affect

470   sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on

471   biologically mediated sedimentation. *Journal of Geophysical Research: Earth Surface*,

472   115(F3).

473   49. Mueller, P., Jensen, K., & Megonigal, J. P. (2016). Plants mediate soil organic matter

474   decomposition in response to sea level rise. *Global Change Biology*, *22*(1), 404-414.

475   50. Mueller, P., Mozdzer, T. J., Langley, J. A., Aoki, L. R., Noyce, G. L., & Megonigal, J. P.

476   (2020). Plant species determine tidal wetland methane response to sea level rise. *Nature

477   communications*, 11(1), 1-9.

478   51. Najjar, R. G., Walker, H. A., Anderson, P. J., Barron, E. J., Bord, R. J., Gibson, J. R., ... &

479   Swanson, R. S. (2000). The potential impacts of climate change on the mid-Atlantic coastal

480   region. *Climate Research*, 14(3), 219-233.

481   52. NOAA. Sea Level Trends. Available at:

482   https://tidesandcurrents.noaa.gov/sltrends/sltrends.html. (Accessed: Nov 2021)

483   53. Noyce, G. L., & Megonigal, J. P. (2021). Biogeochemical and plant trait mechanisms drive

484   enhanced methane emissions in response to whole-ecosystem warming. *Biogeosciences*,

485   18(8), 2449-2463.

486   54. Noyce, G. L., Kirwan, M. L., Rich, R. L., & Megonigal, J. P. (2019). Asynchronous nitrogen

487   supply and demand produce nonlinear plant allocation responses to warming and elevated

488   CO2. *Proceedings of the National Academy of Sciences*, *116*(43), 21623-21628.

489   55. O'Sullivan, O. S., Heskel, M. A., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K.,

490   Penillard, A., ... & Atkin, O. K. (2017). Thermal limits of leaf metabolism across

491   biomes. *Global Change Biology*, *23*(1), 209-223.

492   56. Palinkas, C. M., & Engelhardt, K. A. (2019). Influence of inundation and suspended-

493   sediment concentrations on spatiotemporal sedimentation patterns in a tidal freshwater

494   marsh. *Wetlands*, *39*(3), 507-520.

495   57. Peteet, D. M., Nichols, J., Kenna, T., Chang, C., Browne, J., Reza, M., ... & Stern-Protz, S.

496   (2018). Sediment starvation destroys New York City marshes' resistance to sea level

497   rise. *Proceedings of the National Academy of Sciences*, *115*(41), 10281-10286.

498   58. Phillips, C. L. (2020). How Much Will Soil Warm?. *Journal of Geophysical Research:*

499   *Biogeosciences*, *125*(7), e2020JG005668.

500   59. Rietl, A. J., Megonigal, J. P., Herbert, E. R., & Kirwan, M. L. (2021). Vegetation Type and

501   Decomposition Priming Mediate Brackish Marsh Carbon Accumulation Under Interacting

502   Facets of Global Change. *Geophysical Research Letters*, *48*(8), e2020GL092051.

503   60. Rogers, K., Kelleway, J. J., Saintilan, N., Megonigal, J. P., Adams, J. B., Holmquist, J. R., ...

504   & Woodroffe, C. D. (2019). Wetland carbon storage controlled by millennial-scale variation

505   in relative sea-level rise. *Nature*, 567(7746), 91-9

506   61. Rogers, K., Wilton, K. M., & Saintilan, N. (2006). Vegetation change and surface elevation

507   dynamics in estuarine wetlands of southeast Australia. *Estuarine, Coastal and Shelf*

508   *Science*, *66*(3-4), 559-569.

509   62. Sallenger, A. H., Doran, K. S., & Howd, P. A. (2012). Hotspot of accelerated sea-level rise

510   on the Atlantic coast of North America. Nature Climate Change, 2(12), 884-888.

511   63. Seneca, E. D., & Blum, U. (1984). Response to photoperiod and temperature by Spartina

512   alterniflora (Poaceae) from North Carolina and Spartina foliosa from California. *American*

513   *journal of botany*, *71*(1), 91-99.

514   64. Shepard, C. C., Crain, C. M., & Beck, M. W. (2011). The protective role of coastal marshes:

515   a systematic review and meta-analysis. *PloS one*, *6*(11), e27374.

516   65. Sturchio, M. A., Chieppa, J., Chapman, S. K., Canas, G., & Aspinwall, M. J. (2021).

517   Temperature acclimation of leaf respiration differs between marsh and mangrove vegetation

518   in a coastal wetland ecotone. *Global Change Biology*.

519   66. Temmerman, S., Govers, G., Meire, P., & Wartel, S. (2003). Modelling long-term tidal

520   marsh growth under changing tidal conditions and suspended sediment concentrations,

521   Scheldt estuary, Belgium. *Marine Geology*, *193*(1-2), 151-169.

522   67. Van Belzen, J., Van De Koppel, J., Kirwan, M. L., Van Der Wal, D., Herman, P. M., Dakos,

523   V., ... & Bouma, T. J. (2017). Vegetation recovery in tidal marshes reveals critical slowing

524   down under increased inundation. *Nature Communications*, *8*(1), 1-7.

525   68. Veraart, A. J., Faassen, E. J., Dakos, V., van Nes, E. H., Lürling, M., & Scheffer, M. (2012).

526   Recovery rates reflect distance to a tipping point in a living system. *Nature*, *481*(7381), 357-

527   359.

528   69. Wang, H., Atkin, O. K., Keenan, T. F., Smith, N. G., Wright, I. J., Bloomfield, K. J., ... &

529   Prentice, I. C. (2020). Acclimation of leaf respiration consistent with optimal photosynthetic

530   capacity. *Global Change Biology*, *26*(4), 2573-2583.

531   70. Więski, K., & Pennings, S. (2014). Latitudinal variation in resistance and tolerance to

532   herbivory of a salt marsh shrub. *Ecography*, *37*(8), 763-769.

533   71. Zhong, Q., Wang, K., Nie, M., Zhang, G., Zhang, W., Zhu, Y., ... & Gao, Y. (2019).

534   Responses of wetland soil carbon and nutrient pools and microbial activities after 7 years of

535   experimental warming in the Yangtze Estuary. *Ecological Engineering*, *136*, 68-78.

536
537

Figure Legends

Fig. 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 to September). For clarity, the +3.4 °C treatment is not shown, but tracks with similar seasonal trends as the displayed treatments (SI Fig. 3). 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=~120). Belowground productivity data is from Noyce et al. (2019), updated with an additional two years of data to encompass 2018-2020.

Fig. 2. (a) Seasonal patterns in marsh elevation, productivity, and decomposition. Relative elevation (black), primary production (red) and methane emissions (blue) from March 2019 to Feb 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.

Fig. 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.

Fig. 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). 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.