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Response of salt-marsh carbon accumulation to climate change

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About half of annual marine carbon burial takes place in shallow water ecosystems where geomorphic and ecological stability is driven by interactions between the flow of water, vegetation growth and sediment transport[1]. Although the sensitivity of terrestrial and deep marine carbon pools to climate change has been studied for decades, there is little understanding of how coastal carbon accumulation rates will change and potentially feed back on climate[2,3]. Here we develop a numerical model of salt marsh evolution, informed by recent measurements of productivity and decomposition, and demonstrate that competition between mineral sediment deposition and organic-matter accumulation determines the net impact of climate change on carbon accumulation in intertidal wetlands. We find that the direct impact of warming on soil carbon accumulation rates is more subtle than the impact of warming-driven sea level rise, although the impact of warming increases with increasing rates of sea level rise. Our simulations suggest that the net impact of climate change will be to increase carbon burial rates in the first half of the twenty-first century, but that carbon–climate feedbacks are likely to diminish over time.

Salt marshes, mangroves and seagrass meadows are among the most valuable ecosystems in the world, yet vulnerable to climate change and direct anthropogenic disturbance[2,4,5]. Understanding how coastal ecosystems and their carbon pools react to climate change and sea level rise is difficult because landscape-forming processes and biological processes work on similar timescales and are thoroughly intertwined. For example, vegetation growth depends on physical conditions such as sea level rise and inundation duration, but can also mediate physical conditions because plants influence their elevation by accreting peat and trapping mineral sediment[6]. Rates of carbon accumulation are therefore dependent on ecosystem engineering processes, and in some cases, determine whether a marsh survives sea level rise.

Recent work suggests that some individual aspects of global change may increase the resiliency of coastal wetlands facing sea level rise and their ability to sequester carbon. For example, increased CO_2, warmer temperatures, and moderate increases in rates of sea level rise all tend to increase rates of plant productivity, marsh accretion, and presumably the ability of marshes to survive sea level rise[7–13]. However, accelerated sea level rise also leads to more mineral sediment deposition, which influences the elevation of coastal wetlands in ways that might limit their ability to sequester carbon[12,14]. Increases in decay rates may accompany increased CO_2 and warmer temperatures[15,16]. Finally, the accumulation rate of labile organic matter tends to equilibrate through time because decay rates are proportional to the size of the active carbon pool[12]. Here we model these ecogeomorphic feedbacks to explore how one of the most complex carbon sinks responds to interactive components of global change including temperature warming and sea level rise.

Our numerical model couples two previous models that separately simulated the influence of vegetation on the deposition of mineral sediment[17] and the interactions between inundation, root zone processes and carbon accumulation[12]. In our model, inundation stimulates plant growth up to a threshold water depth, as observed in long-term records of salt marsh biomass and field experiments[7,12,13]. Increased temperatures tend to increase rates of productivity and decay in the model according to sensitivities determined from a latitudinal gradient and field experimentation[10,16]. Organic matter produced by root growth is distributed throughout the soil profile when productivity exceeds decay, and changes in soil volume (that is, marsh elevation) affect both mineral and organic components of accretion. Whereas previous modelling efforts focused on the influence of mineral sedimentation on marsh evolution, we deliberately chose parameter values (sediment grain size, suspended sediment concentrations) that allowed us to explore the evolution of organic-matter-rich marshes dominated by root-zone processes (Table 1). In the discussion below, we refer to organic-matter accumulation and carbon accumulation interchangeably, given that the two are intrinsically linked[18].

We first performed model experiments that explored how competition between enhanced productivity and decay associated with warmer temperatures determine carbon accumulation rates. We took a hypothetical marsh dominated by the macrophyte *Spartina alterniflora* in equilibrium with a slow, constant rate of sea level rise (1 mm yr^{-1}), and subjected it to an instantaneous 4 °C increase in temperature. After the temperature change, we found that rates of organic-matter decomposition exceeded rates of root production, leading to a slight decrease in organic-matter accumulation (Fig. 1a). Concurrently, warming enhanced aboveground productivity and its ability to trap mineral sediment, leading to a small increase in vertical accretion rate and marsh elevation relative to sea level (Fig. 1b). When temperature was perturbed under a higher rate of sea level rise (3 mm yr^{-1}), ambient plant productivity was relatively high, so that warming led to an increase in productivity that was greater than the increase in decay rate. Thus, rates of carbon accumulation and vertical accretion both increased after the step change in temperature (Fig. 1c, d). Accretion rates were momentarily higher than the rate of sea level rise, so the marsh platform built up elevation relative to sea level, and reduced inundation led to progressive reduction of plant productivity and vertical accretion. Consistent with a variety of numerical models of salt marsh evolution[6], vertical accretion rates decreased until they approached a new equilibrium with the rate of sea level rise. Our results predict that the new equilibrium condition (under a moderate rate of sea level rise and warmer temperature) will be characterized by a higher elevation of the platform relative to sea level, a small increase in the rate

Table 1 | Parameter values used in model simulations

Parameter	Value
Sediment concentration, *C*	1 mg l^{-1}
Particle diameter	0.03 mm
Maximum biomass, *B*	2,500 g m^{-2}
Fast decay, k_l	2 yr^{-1}
Slow decay, k_r	0.001 yr^{-1}
Spring tidal range	1.4 m

Parameters not listed have values identical to those in refs 12 and 16.

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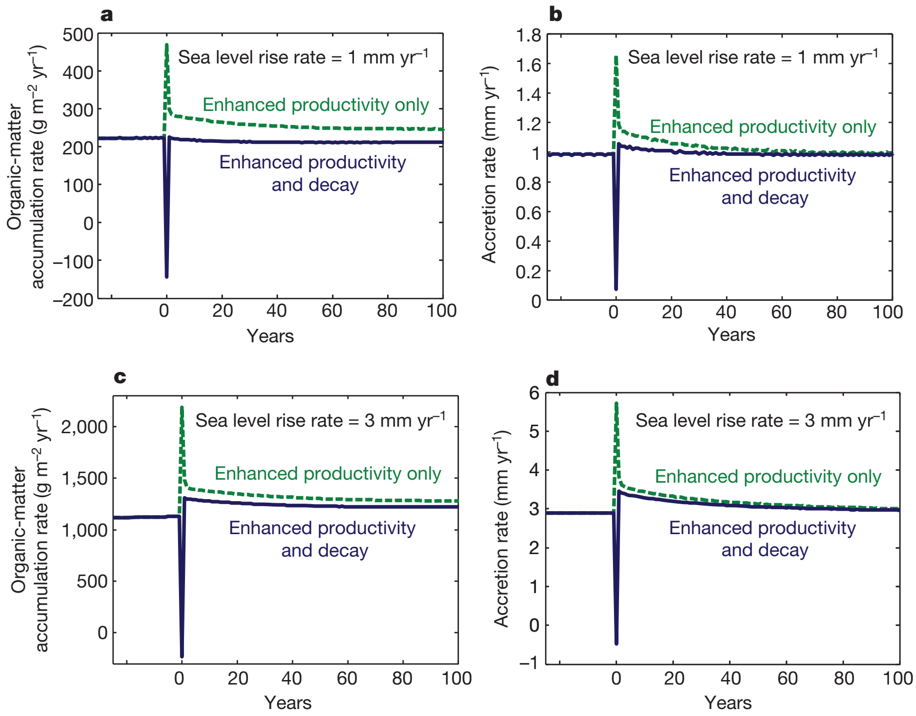

Figure 1 | Response of organic-matter accumulation and vertical accretion rates to an instantaneous 4 °C change in temperature at year 0. **a**, **b**, 1 mm yr^{-1} rate of sea level rise. **c**, **d**, 3 mm yr^{-1} rate of sea level rise. The solid line denotes the model with temperature influence on productivity and decay, and the dashed line denotes the model with no effect of temperature on decay. The sharply negative accretion and organic accumulation rates at year 0 should be considered a model artefact arising from enhanced decay that takes place immediately, whereas enhanced productivity takes one year to reach the soil profile in the model. Enhanced productivity and decay have no long-term effect on accretion rate (**b**, **d**), but have moderate impacts on organic-matter accumulation (**a**, **c**).

of plant productivity and organic-matter accretion, but no change in vertical accretion rate.

This simple experiment provides two important insights into carbon dynamics in salt marshes. First, it illustrates that if plant productivity drives changes in wetland elevation, then the results of short-term experiments are likely to overestimate the long-term effect of climate change on carbon burial and vertical accretion. Field and laboratory experiments, for example, demonstrate that increased CO_2 leads to an increase in productivity and marsh accretion[8,9]. Our model results are consistent with these observations because enhanced productivity via warming also leads to an increase in marsh accretion rate. The response was most pronounced when the effect of temperature on decomposition was not modelled (dashed line in Fig. 1b, d), analogous to increased-CO_2 experiments that do not warm soil temperatures[8]. However, our experiments indicate that the enhanced vertical accretion rate quickly returns to the rate of sea level rise because the progressive building of wetland elevations ultimately limits plant productivity. At the same time, losses of labile soil carbon increase in proportion to the size of the growing carbon pool. Together, decreasing rates of plant productivity and increasing rates of decay cause carbon burial rates to decline after their initial increase (Fig. 1d).

A second implication of our results is that the rate of sea level rise, and its influence on ambient plant productivity, determines the net response of organic accumulation rates to climate change. Warming leads to reductions in organic matter accumulation at low rates of sea level rise (Fig. 1a), while warming leads to increases in organic-matter

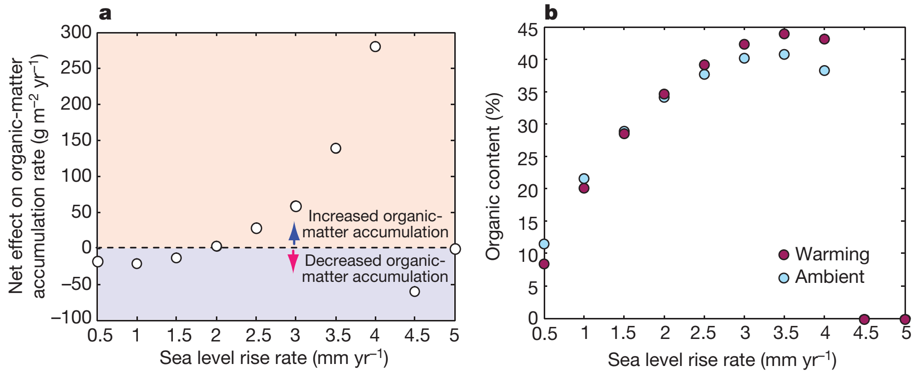

Figure 2 | Impact of warming under constant sea-level-rise rates. **a**, Net impact of warming on organic-matter accumulation rate defined as the deviation from ambient accumulation rate 100 years after the step change in temperature modelled in Fig. 1. The net influence of warming is negative at low rates of sea level rise, but positive at high rates of sea level rise. For experiments with different decay coefficients see the Supplementary Information. **b**, Impact of warming on the fraction of organic material deposited at the soil surface. Warming leads to an increase in mineral content at low rates of sea level rise, but an increase in organic content at high rates of sea level rise. In general, warming temperatures and accelerating sea-level-rise rates lead to more organic-enriched soils until the marsh submerges (4.5 mm yr^{-1} in this experiment).

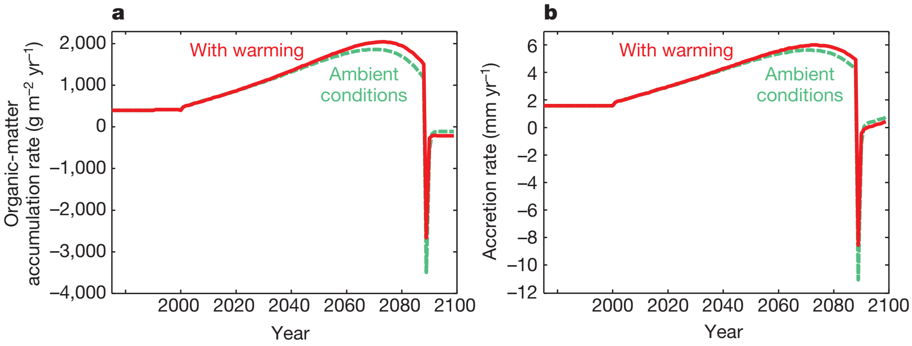

Figure 3 | Impact of warming under accelerating sea-level-rise rates. **a**, Response of organic-matter accumulation rate to temperature-driven changes in productivity, decay and sea-level-rise rates over the next century. **b**, Response of accretion rate to the same warming and sea-level-rise scenario. For most of the twenty-first century, plant productivity and organic-matter accumulation rates increase with progressive inundation of the marsh surface. The abrupt decline in organic-matter accumulation and marsh accretion near 2085 is due to plant mortality as plants cross an inundation threshold. At this point, carbon ceases to be deposited into marsh sediment, even as existing carbon near the soil surface continues to decay. For alternative climate scenarios and the impacts of varying suspended sediment concentrations, see the Supplementary Information.

accumulation at high rates of sea level rise (Fig. 1c). Although the net impact of warming declines through time in either case, discernible differences in carbon accumulation persist for centuries. Figure 2 summarizes the impact of warmer temperature on long-term (100-year) carbon accumulation rates over a variety of sea-level-rise rates. Vertical accretion rates equilibrate to the rate of sea level rise within 100 years, so the response of carbon accumulation rates to warming is driven by competition between organic-matter production and mineral sediment trapping efficiency. More productive plants in a warmer climate can have a positive influence on either process. At low rates of sea level rise, the marsh starts high in the tidal frame with little productivity. Enhanced productivity associated with warming leads to more inorganic trapping at the expense of organic accumulation (Fig. 2a), and marsh soils become more mineral-rich (Fig. 2b). At high rates of sea level rise, the marsh starts low in the tidal frame with high plant productivity and high organic-matter accumulation rates. Enhanced productivity leads to an increase in organic accumulation at the expense of inorganic sediment trapping (Fig. 2a), and the marsh becomes more organic-matter-rich (Fig. 2b). Thus, the effect of increased productivity on organic-matter accumulation depends on the background rate of sea level rise, and the elevation of the marsh relative to sea level. These processes suggest that predicting carbon cycling in rapidly accreting landscapes such as deltas, floodplains and wetlands requires knowledge not just of how plants respond to climate change, but also of how vegetation and geomorphic processes interact.

Given that sea-level-rise rates influence the net impact of warming on carbon accumulation, but are themselves a function of temperature, we considered a final experiment that simulated the evolution of a hypothetical marsh over the next century in which these variables interact (Fig. 3). Temperature projections followed the IPCC A2 scenario[19] (an increase of 3.7 °C by 2100), and drove the rate of sea level rise according to a second-order semi-empirical relationship[20]. The experiment began with a 100-year spin-up period in which carbon pools and marsh elevations grow and equilibrate with the historical rate of global sea level rise, which we take to be 1.7 mm yr^{-1} (ref. 19). Although plant productivity accelerated with inundation and temperature throughout the experiment, more complex behaviour related to the influences of temperature and carbon pool size on decay rates emerged late in the simulation. As in Fig. 2, warmer temperatures led to little change in the organic accumulation rate when the rate of sea level rise was 1.7 mm yr^{-1}. As sea level rise accelerated, and ambient productivity increased owing to relative marsh lowering, the effect of enhanced productivity became more pronounced. For most of the twenty-first century, warmer temperatures and faster sea level rise rates led to an increase in organic-matter production, carbon accumulation, and vertical accretion. This increasing organic production led to a growing carbon pool, and with it a growing loss of labile organic matter through decay. Eventually the combined effects of a larger carbon pool and enhanced decay outstripped organic production, leading to decelerating rates of organic accumulation after 2050 and declining rates of organic accumulation after 2075. Although enhanced plant productivity facilitated faster mineral sediment deposition, root zone processes dominated elevation change in this organic-matter-rich marsh, and vertical accretion rates also declined after 2075. With an accelerating rate of sea level rise and a declining rate of vertical accretion, the hypothetical marsh quickly lost elevation relative to sea level and vegetation drowned around 2085.

For more than 30 years, the debate on whether carbon stored in ecosystems will exacerbate or mediate climate change has focused on the biogeochemical evolution of terrestrial and open-ocean systems[21,22]. However, coastal ecosystems such as salt marshes have only recently been recognized as important components of the global carbon cycle[2,3]. Our results illustrate potential feedbacks between climate and carbon in the rapidly evolving coastal zone. We find that the net impact of temperature warming and sea level rise is to increase carbon burial rates in the first half of the twenty-first century (negative feedback with climate), but to slightly decrease carbon burial rates in the second half of the century (positive feedback with climate). In contrast, terrestrial ecosystems are likely to absorb a progressively smaller fraction of anthropogenic carbon dioxide emissions through the twenty-first century[23,24]. Thus, transient increases in carbon burial rates near the coast could potentially help offset the reduced uptake of carbon from terrestrial ecosystems. Interestingly, our model results suggest that a switch in feedback direction takes place even in marshes that are surviving sea level rise, and where rates of plant productivity accelerate in response to climate change. If sea level rises by more than a metre by 2100, most models of marsh evolution indicate that marshes will be submerged and lose productivity[25]. Our model considers only the temporal evolution of a single point within a hypothetical marsh. If the spatial extent of global marshes were to decline owing to sea level rise or anthropogenic modifications, then our prediction of long-term declining carbon burial rates would be amplified.

METHODS SUMMARY

To explore the temporal evolution of a hypothetical salt marsh platform, we coupled a model that simulates the influence of vegetation on the accumulation of mineral sediment[17] with a model that focuses on interactions between inundation, root zone processes, and carbon accumulation[12]. The model is generally suited to represent salt marshes in protected microtidal–mesotidal estuaries, most explicitly those colonized by *Spartina alterniflora*, the dominant macrophyte in North American marshes. In the model, inundation stimulates plant growth up to a threshold water depth[7,12,13] and increased temperatures tend to increase rates of productivity and decay[10,16]. Standing biomass varies throughout the growing season, and affects marsh accretion by trapping sediments during periods of marsh inundation and by depositing belowground carbon owing to root mortality. Belowground organic-matter production is estimated from aboveground biomass according to a depth-dependent root-to-shoot ratio[12]. Compaction is computed on the basis of sediment overburden and organic content[12]. Dead biomass decays according to a linear decay model, where decay is influenced by the concentration of organic carbon, its depth below the soil surface, and temperature. For simplicity, we consider only two pools of soil carbon in our simulations: a quickly decaying pool of organic matter that reflects the decomposition of cellulose and amino-acids (k_l), and a slowly decaying pool that reflects the decomposition of more refractory materials such as lignins (k_r).

Full Methods and any associated references are available in the online version of the paper.

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Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to M.L.K. (mlk4n@virginia.edu).

METHODS

Vegetation modelling. To explore the temporal evolution of a hypothetical salt marsh platform, we coupled a model that simulates the influence of vegetation on the accumulation of mineral sediment[17] with a model that focuses on interactions between inundation, root zone processes, and carbon accumulation[12]. The model is generally suited to represent salt marshes in protected microtidal–mesotidal estuaries, most explicitly those colonized by *Spartina alterniflora*, the dominant macrophyte in North American marshes. In the model, inundation stimulates plant growth up to a threshold water depth[7,12,13] and increased temperatures tend to increase rates of productivity[10]. Between a minimum and maximum depth, measured below mean high high water (MHHW), the biomass during the peak growing season is:

$$B_{\text{peak}} = \frac{B_{\max}}{D_{\max} - D_{\min}}(D - D_{\min})(1 + \Delta T \sigma_{\text{B}}) \quad (1)$$

(Dimensions are denoted in square brackets of [M] for mass, [L] for length and [T] for time). Here, $D_{\min}$ [L] and $D_{\max}$ [L] are the minimum and maximum depths below MHHW, B_{peak} is the peak season biomass [M L^{-2}], $B_{\max}$ [M L^{-2}] is the biomass at the optimal depth below mean high tide, ΔT is the change in temperature from a reference temperature, and σ_{B} is a factor that accounts for the increase in biomass due to an increase in temperature. From a latitudinal gradient of *S. alterniflora* productivity in 56 North American marshes[10], we determine that $\sigma_{\text{B}} \approx 0.06\ ^{\circ}\text{C}^{-1}$, in general agreement with experimental warming studies that also demonstrate a positive response to warming[11,26,27]. The time-varying standing biomass B [M L^{-2}] is calculated on the basis of on a sinusoidal approximation of the annual variation in marsh productivity (B fluctuates between 0 and B_{p} during the year)[12]. Standing biomass can then affect marsh accretion by trapping sediments during periods of marsh inundation and by depositing belowground carbon owing to root mortality.

Sediment trapping. We model the trapping of mineral sediment as the sum of plant-mediated particle settling Q_{s} [M L^{-2} T^{-1}]) and direct capture of sediment by plant stems Q_{c} [M L^{-2} T^{-1}] using the method of ref. 16. In *S. alterniflora* marshes, the mass flux from plant mediated settling is much greater than that from direct particle capture under typical flow conditions (<10 cm s^{-1}) (ref. 17). The particle settling flux is:

$$Q_{\text{s}} = (w_{\text{s}} - w_{\text{up}})C \quad (3)$$

where C [M L^{-3}] is the suspended sediment concentration, w_{s} [L T^{-1}] is the settling velocity of particles in still water and w_{up} [L T^{-1}] is the upward velocity of particles due to turbulence. The upward velocity of particles is:

$$w_{\text{up}} = \kappa_{\text{vK}} \sqrt{\frac{0.20\alpha_{\text{k}}^2 u^2 (C_{\text{D}} a_{\text{c}} d_{\text{c}})^{2/3}}{\rho_{\text{w}}}} \quad (4)$$

where u [L T^{-1}] is the flow velocity, κ_{vK} is von Karman's constant, assumed to be 0.4, α_{k} is a coefficient reported to be 0.9 (ref. 28) and C_{D} is the depth-averaged drag coefficient. a_{c} [L^{-1}] is the projected plant area per unit volume, calculated as $a_{\text{c}} = \alpha B^{\beta}$, and d_{c} is the stem diameter calculated by $d_{\text{c}} = \mu B^{\varphi}$. The drag coefficient is calculated using:

$$C_{\text{D}} = 2\left(\frac{\alpha_0 v}{u \mu B^{\phi}} + \chi + \zeta \frac{\alpha \mu \pi}{4} B^{\beta + \phi}\right) \quad (5)$$

where χ and ζ are empirical coefficients reported to be 0.46 ± 0.11 and 3.8 ± 0.5, respectively[29]. During the rising limb of the tide we make the simplification that sediment concentrations are fixed owing to a supply of sediment-laden water from tidal creeks, and during the falling limb of the tide suspended sediment concentrations are calculated by solving the sediment continuity equation[17].

Compaction plays a significant part in determining the absolute elevation of marsh surfaces because the sediments that make up salt marsh soils are compressible. Here we use a constitutive equation verified by laboratory experimentation to model the compaction of the vertical soil profile. Following ref. 12:

$$E = E_0 - \text{CI} \log\left(\frac{\sigma_{\text{eff}}}{\sigma_0}\right)$$

where E [dimensionless] is the void ratio, CI [dimensionless] is the compression index, E_0 [dimensionless] is the void ratio at the reference stress, σ_0 [M T^{-2} L^{-1}], and σ_{eff} [M T^{-2} L^{-1}] is the effective stress. Following ref. 12, we assume the column is under hydrostatic pressure and that the effective stress at any depth below the surface is simply the buoyant weight of the material above it. The compression index and reference void ratio depend on the substrate, where organic material in the modelled soil column is far more compressible than inorganic material[12].

Organic-matter production. Carbon is deposited in the subsurface via root mortality. The belowground biomass B_{bg}, [M L^{-2}] is related to the aboveground biomass through:

$$\frac{B_{\text{bg}}}{B} = \theta_{\text{bg}} D + D_{\text{mbm}} \quad (6)$$

where θ_{bg} and D_{mbm} are the slope [L^{-1}] and the intercept [dimensionless] of the relationship between the roots-to-shoots ratio and the depth below MHHW. These parameter values were determined from field experiments that examined the change in roots-to-shoots ratio with inundation for *S. alterniflora*[12].

The difference between growth rate and mortality rate determines the change in standing biomass through the year. Mudd *et al.*[12] approximated the measured growth of *S. alterniflora* as a sinusoidal function based on field data from North Inlet, South Carolina. This yields a mortality rate, M [M L^{-2} T^{-1}] of:

$$M = \frac{1}{2}\left[G_{\min} + G_{\text{peak}} + (G_{\text{peak}} - G_{\min}) \cos\left(\frac{2\pi[\text{JD} - \text{JD}_{\text{peak}} + \varphi]}{365}\right)\right] + \frac{\pi}{365}(B_{\text{peak}} - B_{\min}) \sin\left(\frac{2\pi[\text{JD} - \text{JD}_{\text{peak}}]}{365}\right) \quad (7)$$

where JD is the Julian day (1 Jan = 1, 31 Dec = 365), JD_{peak} is the day of the year when aboveground biomass is at its peak and $B_{\min}$ [M L^{-2}] is the minimum aboveground biomass, G_{ag} [M L^{-2} T^{-1}] is the rate of aboveground biomass production per unit area, $G_{\min}$ [M L^{-2} T^{-1}] is the minimum growth rate, G_{peak} [M L^{-2} T^{-1}] is the peak growth rate, ϕ is the phase shift (in days) between the peak growing season and the date of peak biomass[7]. The mortality rate is then integrated over a time step and multiplied by the ratio between aboveground and belowground biomass.

Organic-matter decay. Fresh organic matter enters the soil profile upon mortality. Dead biomass decays according to a linear decay model ($\partial C_i / \partial t = -k_i C_i$) where C_i [M L^{-3}] is the concentration in pool *i*, and k_i [T^{-1}] is the decay coefficient in pool *i* (refs 12, 30). The decay coefficient of pool *i* is calculated as $k_i = (1 + \Delta T \sigma_k) k_{i,0} \exp[d/\mu_i]$ where $k_{i,0}$ is the decay coefficient at a reference temperature, σ_{k} is a coefficient that describes the increase in decay coefficient as temperature increases, d [L] is the depth below the marsh surface and μ_i (0.4 m) is a coefficient that describes the reduction in decomposition with depth as organic sediments are buried under anoxic conditions[12]. Kirwan and Blum[16] found the coefficient σ_{k} to be about 0.25 °C^{-1} for a mid-Atlantic *S. alterniflora* marsh. This result is qualitatively consistent with other observations of decay that are more rapid in marshes during warmer portions of the year, and with observations from terrestrial ecosystems (see references within ref. 16). In our simulations, we consider two pools of soil carbon: a quickly decaying pool of organic matter that reflects the decomposition of cellulose and amino acids (k_{l}), and a slowly decaying pool that reflects the decomposition of more refractory materials such as lignins (k_{r}). Experimental studies of decay in salt marshes are limited to durations less than five years, so this approach is necessarily guided by terrestrial models of carbon dynamics[31]. Nevertheless, slow decay over timescales of decades to millennia is apparent in the salt marsh stratigraphic record[32].

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