

Coastal Wetland Responses to Warming

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Summary

Plant primary production is likely to increase with warming based on evidence from latitudinal gradients of tidal marsh biomass and experimental manipulations.

Rates of decomposition are likely to increase based on first principles and lab incubations, but microbial responses to temperature are poorly characterized and confidence in this forecast is low.

Models suggest that the net effect of warming on marsh carbon sequestration and the capacity to keep pace with relative sea-level rise will be small and related primarily to the indirect effect of temperature on rates of sea-level rise.

Temperature-driven displacement of tidal marsh plants by mangrove trees will increase carbon sequestration at the boundaries of these ecosystems.

Temperature will increase methane emissions through a combination of direct effects on the microorganisms that produce methane and indirect effects on microorganisms that consume methane or compete with methane producing microbes.

Introduction and Background

Despite the extraordinary leverage that coastal ecosystems exert over the global carbon cycle, the dynamics of coastal wetland carbon pools are not presently represented in earth system models. Compared to upland soils, the sequestration potential of tidal wetland soils is extremely high because rising sea level gradually increases the potential soil volume, and the rate at which carbon is transferred to deeper, more anoxic soil horizons. Thus, tidal wetlands are not subject to the limits on carbon storage typical of upland soils. Coastal wetlands have only recently been recognized as important carbon sinks, and therefore the response of carbon cycling to climate change in tidal wetlands is largely unexplored. The future sink strength and carbon stock stability of these systems is uncertain because global change drivers such as temperature and elevated CO₂ perturb the complex biotic and abiotic feedbacks that drive high rates of soil carbon sequestration, and biogeochemical processes such as decomposition, CH₄ emissions and hydrologic export. Thus, an important reason to study the effects of warming on coastal wetlands is to understand the stability of soil carbon pools, and to determine whether these important ecosystems will continue to gain elevation via carbon sequestration as rates of sea level rise accelerate.

Global air temperatures are projected to rise 0.3-4.8 °C by 2100, a range of outcomes that varies with assumptions about future greenhouse gas emissions (IPCC 2014). Warmer air temperatures will cause water bodies and soils to also warm. Over time this means that soil temperatures will rise to several meters depth (Huang *et al.*, 2000), a possibility that has particularly important implications for tidal marshes with deep, highly organic soils.

The direct effects of warming are accompanied by the direct effects of rising CO₂ levels on plants and a variety of indirect effects such as rising sea level. Carbon dioxide concentrations are projected to continue rising and may exceed 700 ppm by the year 2100 (IPCC 2014). There is evidence that elevated CO₂ acting alone can help stabilize tidal marshes by increasing elevation gain (Langley *et al.*, 2010, Ratliff *et al.* 2015, Reef *et al.* 2017), primarily through root production. Warming may either reinforce or negate the effects of elevated CO₂ on elevation, but there is little known about how the two global change factors interact in tidal marshes or tidal freshwater forests.

Rising temperatures are driving accelerated rates of sea-level rise. In addition, many sea coasts are experiencing land subsidence due to natural and anthropogenic phenomena that exacerbate sea-level rise by causing land to sink. The combination of these effects (i.e. relative sea level rise) tends to increase the frequency of tidal inundation, which in turn changes plant community composition and wildlife habitat value (Krauss *et al.*, 2009; Swanson *et al.*, 2014; Field *et al.*, 2017). When increasing rates of relative sea level rise cross a poorly-understood critical threshold, tidal marshes and forests are threatened with conversion to open water (Cadol *et al.*, 2013; Kirwan *et al.*, 2016b). The capacity of a marsh to respond to sea-level rise depends upon the availability of mineral and organic material to build soil and the availability of space for wetlands to migrate landwards with sea-level rise (Morris *et al.*, 2002; Orr *et al.*, 2003; Kirwan *et al.*, 2010; Spencer *et al.*, 2016).

Temperature and precipitation are coupled through regional and global-scale climate feedbacks that limit the distribution of plant species, and climate will ultimately constrain the responses of foundation plant species and ecosystems to climate change. Because of complex interactions among ecological, hydrological, geomorphological and biogeochemical processes that tend to maintain coastal wetlands in a state of quasi-equilibrium (Figure 1), shifts among functionally different plant community are likely to be non-linear and climate dependent (Gabler

et al. 2017). Temperature thresholds are expected to trigger shifts in ecosystem type under humid conditions (e.g. marsh to mangrove), precipitation under arid conditions (e.g. vegetated to unvegetated) (Osland et al. 2016). The influence of macroclimatic drivers on coastal wetlands would benefit from adding coastal processes to Earth System Models (USDOE 2017).

Ecosystem Responses to Warming

Warming is expected to influence the aboveground and belowground feedback loops that regulate soil carbon sequestration, elevation gain, methane emissions and hydrologic export of carbon and nitrogen (Figure 1). Temperature effects on plant production will influence processes that regulate carbon inputs, outputs, and burial, with implications for soil carbon sequestration and marsh stability against sea-level rise. Changes in production will lead to different outcomes for ecosystem function depending on the relative responses of shoots versus roots. Changes in decomposition affect soil organic matter pools directly through mass loss, or indirectly through mass gain if increased soil organic matter decomposition increases nitrogen availability and therefore plant growth. Finally, changes in plant and microbial metabolism will have consequences for methane (CH₄) emissions to the atmosphere, and dissolved or particulate forms of carbon and nitrogen to adjacent aquatic ecosystems.

Primary production

The effects of temperature on plant production have been explored through latitudinal gradients and experimental manipulations (Figure 3). All of the experimental manipulations to date have been through passive warming using chambers (Figure 2, left panel), which typically causes a 2-4 °C increase in air temperature, but have negligible effects on soil temperature. In general, warming tends to increase production rates (Gray and Mogg, 2001; Loebel *et al.*, 2006; Charles and Dukes, 2009; Gedan and Bertness, 2009), but the effects tend to be specific to the location and plant species. A latitudinal gradient of *Spartina alterniflora*-dominated salt marshes showed an increase of 27 g m⁻² yr⁻¹ per 1°C increase in temperature (Kirwan *et al.*, 2009). Similarly, experimental air warming in a *S. alterniflora* marsh in NE United States suggests an increase in biomass on the order of about 50 g m⁻² per degree of warming (Gedan *et al.*, 2010). Experimentally warming a *Spartina patens*-dominated NE United States salt marsh also increased biomass (Gedan and Bertness, 2009), while warming a different NE United States salt marsh increased biomass in some species (e.g. *S. alterniflora*), but not others (e.g. *S. patens* and *Distichlis spicata*) (Charles and Dukes, 2009). By contrast, warming increased *D. spicata* biomass by ~250±70 g m⁻² yr⁻¹ (mean±SD, averaged over 2 years) in a SE United States brackish marsh, representing a doubling of salt marsh plant biomass (Coldren *et al.*, 2016). These three *in-situ* warming experiments span a large latitudinal range. The observation that warmer air temperatures resulted in more plant growth in one or more plant species at each site studied indicates that saltmarsh plants may respond positively to warming across their full latitudinal range, and thus may exhibit increased carbon storage in a future, warmer climate.

Warmer air temperatures may also alter salt marsh root biomass and depth distribution, although this response has rarely been measured in the few existing temperature manipulation experiments. In Coldren *et al.* (2016), wetland plant root mass declined at depths of 40-60 cm in warming chambers and showed a trend towards declines at the surface (0-20 cm). In a greenhouse experiment, *Spartina anglica* increased in belowground biomass with a rise in temperature (Gray and Mogg 2001). Because belowground plant production plays a dominant role in determining surface elevation (Nyman *et al.* 2006, Mudd *et al.* 2009), understanding the

influence of temperature on both root growth and decomposition is essential. Root growth responses to soil warming are yet unknown (fig 2B), but may be especially important drivers long-term carbon stocks in organic soils.

Few experimental manipulations in wetlands have tested hypotheses about the effects of warming on ecological interactions. Bertness and Ewanchuk (2012) studied the role of climate in regulating species interactions by transplanting nine locally common saltmarsh plant species into unvegetated mudflats on the north side (cool) and south side (warm) of Cape Cod, U.S. Soil surface temperature in the two regions differ by 2-3°C. Species were planted with and without neighbors. The presence of plant neighbors tended to improve growth rates on the south (warm) side of Cape Cod, but reduce growth rates on the north (cool) side of Cape Cod. This difference in plant interactions seemed to be mediated by the effects of temperature on soil salinity, both of which are greater in the southern sites. The study suggests that interspecific interactions can switch from competitive to facultative in a warming environment, which may help plant communities adapt to climate change. But this conclusion only applies in the aggregate. Another lesson of the study is that predicting the response of such interactions for a given plant species or plant functional group will be exceedingly difficult, limiting forecasts of warming on plant community composition.

Collectively these studies suggest that warming has the potential to affect organismal-level processes such as physiological adaptation to temperature; population-level processes such as reproduction, dispersal, and genetic selection; community-level processes such as interspecific competition and introduction of invasive species; and ecosystem-level functional group shifts such as from herbaceous species to woody shrubs. It is difficult to predict changes in the distributions of species and the consequences of such changes because they are highly dependent on the traits of individual species and on ecological interactions among species in often novel plant community associations. A great deal of further research on these topics is needed to develop robust forecast models of tidal marsh and forest responses to warming.

Decomposition

Most carbon stored in coastal wetlands lies belowground, yet the critical belowground responses of roots and microbial respiration to warming are far more difficult to assess than the aboveground responses. Though warming-induced increases in plant production are expected to increase carbon inputs to soils, warming may simultaneously increase microbial respiration and decomposition of soil organic matter.

Latitudinal gradient studies suggest that warming will increase decomposition rates at the same time it increases production (Kirwan *et al.*, 2014; Kirwan *et al.*, 2009). The net effect of higher carbon input and output in the short term (decades) will be for warming to enhance carbon storage (Kirwan and Mudd, 2012). However, the long term effects of warming are more complex than latitudinal patterns suggest, and will be strongly mediated by sea-level rise and gradual increases in total soil-profile decomposition rates as carbon accumulates in the soil profile. Model simulations of a typical *Spartina alterniflora* marsh suggest that carbon storage is enhanced for several decades, followed by weakening and potentially declining carbon storage rates. This pattern is supported by two experimental manipulations of air temperature in New England marshes (Charles and Dukes, 2009; Gedan *et al.*, 2011), but these studies suggest that long-term ecosystem responses to warming will also be controlled by ecological interactions in the form of changes in plant functional groups (Charles and Dukes, 2009; Gedan *et al.*, 2011).

Changes in plant community composition are as important for decomposition rates as for productivity. Plants exert a strong control over soil organic matter decomposition rates in tidal wetlands (Mueller et al., 2015; Ouyang et al., 2017), most likely due to a combination of labile carbon and O₂ additions from plants, and effects vary dramatically across plant species. Bernal *et al.* (2017) demonstrated that an invasive genotype of *Phragmites australis* accelerates soil organic matter decomposition compared to rates in native North American plant communities. Furthermore, plant stimulation of decomposition differed by soil depth depending on the plant species, with *Schoenoplectus americanus* enhancing soil organic matter decomposition at the soil surface, *Phragmites australis* at greater depths, and *Spartina patens* having no discernable effect on decomposition (Bernal *et al.* 2017). The potential of warming and ensuing sea-level rise to alter plant community composition represents a large uncertainty for predicting future ecosystem carbon dynamics in tidal marshes and tidal forests.

Initial attempts to measure the sensitivity of organic matter decomposition to warming in marshes range from no responses (Charles and Dukes, 2009) to responses that are larger than those reported in most terrestrial temperature response studies (Kirwan and Blum, 2011). Interestingly, a recent meta-analysis found that decomposition rates in marshes varied with temperature but not latitude (Ouyang et al., 2017). Some models of the process have used a relatively high temperature sensitivity ($Q_{10}=3.44$), but more recent analyses suggest a much lower sensitivity to warming ($Q_{10}=1.3-1.5$, Kirwan *et al.*, 2014). Because the sensitivity of refractory carbon to warming has never been evaluated in coastal wetlands, the initial models have assumed that both labile and refractory pools respond identically to warming, even though strong differences in temperature effects on labile versus recalcitrant have been observed in upland soils (Frey *et al.*, 2013). Therefore, the precise response of soil carbon decomposition to warming represents a key knowledge gap, and new model experiments informed by field experiments are critical for accurate forecasts of coastal carbon cycling (Figure 2). It is important that warming experiments heat both aboveground and belowground portions of the ecosystem.

A largely unexplored question is whether changes in salinity and associated increases in sulfate concentration will influence rates of soil organic matter decomposition (Sutton-Grier *et al.*, 2011, Craft 2007, Stagg et al. 2017). The limited evidence available is equivocal. In many cases sulfate addition has caused an increase in decomposition rates (Weston *et al.*, 2006), and a meta-analysis suggests that decomposition is slower in mangrove soils with higher salinity (Ouyang et al., 2017). However, in a comparison of 10 wetland soils, D'Angelo and Reddy (1999) did not find a difference in decomposition rates under sulfate-reducing or methanogenic conditions. This result may be explained by the fact that the terminal step in microbial respiration where sulfate acts does not necessarily control all of the earlier steps in organic matter degradation, such as depolymerization (Sutton-Grier *et al.*, 2011). There has been limited work on the impacts of different terminal electron acceptors on organic carbon mineralization in soils that differ in organic matter quality.

Microbial metabolism

Temperature accelerates enzymatic reactions that breakdown organic substrates. Indeed, this is the mechanism by which Arrhenius-based models traditionally forecast changes in soil carbon pools – generally declines – due to warming (Wieder *et al.*, 2013). More recent decomposition models incorporate mechanistic details of microbial population dynamics such as extracellular enzymes, carbon use efficiency (CUE), and turnover, with a wider range of outcomes from declines to gains in soil carbon (Hagerty *et al.*, 2014; Li *et al.*, 2014). These new

models show that predicting changes in soil carbon pools in response to temperature requires detailed knowledge of microbial biomass, physiology and ecology, and that the understanding of these processes is not presently sufficient to predict whether warming will increase or decrease soil carbon pools.

Changes in microbial metabolism induced by temperature affect the efficiency with which organic matter is converted into microbial biomass, a property known as carbon use efficiency (CUE). Theoretically, warming should reduce CUE by changing the balance between energy production and biosynthesis; at higher temperature, the demand for cell maintenance energy increases, leaving less substrate for biosynthesis of new cell materials (Allison *et al.*, 2010, Manzoni *et al.*, 2012, Sinsabaugh *et al.*, 2013, Cotrufo *et al.* 2015). However, experimental results are variable with some showing the expected decrease (Steinweg *et al.* 2008; DeVêvre and Horwáth 2000) and some find no effect of temperature on CUE (Dijkstra *et al.*, 2011, Hagerty *et al.*, 2014). By comparison, the turnover rate of microbial products does respond strongly to temperature (Hagerty *et al.*, 2014), indicating that it may be important to understand temperature effects on microbial growth as well as death. In freely drained soils dominated by aerobic conditions, microbial mortality is caused by predation and grazing by specialized bacteria and fungi, protozoa, nematodes, and other organisms; the role of such eukaryotic microbes in dominantly anaerobic wetland soils is unexplored. Also relatively less studied in soils is microbial turnover caused by viruses (Kimura *et al.*, 2008), which may be important as controls on microbial turnover in low and mid-latitude marine ecosystems (Fuhrman, 1999; Mojica *et al.*, 2016). The temperature sensitivity of CUE and its underlying biochemistry in terrestrial ecosystems have mostly been determined under aerobic conditions in mineral soils. Because tidal marshes and forests contain large stores of soil C, it is essential to consider fundamental microbial processes such as CUE and turnover in anaerobic soils.

Methane emissions

Methane (CH₄) emissions are an important feature of the tidal wetland carbon budget because CH₄ is a powerful greenhouse gas and relatively small rates of release can offset large rates of CO₂ sequestration (Poffenbarger *et al.*, 2011). Each gram of CH₄ released from a marsh into the atmosphere offsets 32-45 grams of sequestered CO₂ in terms of the climate impact these gases (Neubauer and Megonigal, 2015). The balance between rates of CO₂ sequestration and CH₄ emissions is important to understand when the goal is to quantify the effects of an activity such as restoration, creation or management on greenhouse gases. Warming also has the potential to change the balance of CO₂ and CH₄ fluxes.

Subjecting anaerobic soils to a range of temperatures typically shows that warming will increase microbial production of CH₄ (Fung *et al.*, 1991, Meng *et al.*, 2012). Similarly, measuring CH₄ emissions in the field as temperature changes across seasons suggests that warming will increase CH₄ emissions from tidal wetlands (Dunfield *et al.*, 1993; Megonigal and Schlesinger, 2002; Yvon-Durocher *et al.*, 2014). However, the value of such studies is limited either by the absence of real field conditions (soil incubations) or by the assumption that seasonal variation is entirely due to temperature (field studies). Because of complex interactions between many processes, *in situ* temperature manipulation experiments are needed to determine whether warming will increase or decrease CH₄ emissions.

The effect of temperature on CH₄ emissions is more complex than the effect on CH₄ production alone for several reasons. One is that emissions of CH₄ are the net outcome of two separate microbial processes -- production and oxidation -- that can have different temperature

responses. Because the amount of CH₄ consumed in oxidation can exceed the amount emitted (Meronigal and Schlesinger, 2002), both must be considered in predictions of future CH₄ emissions. The few Q₁₀ values reported for CH₄ oxidation are near 2.0, a value similar to other aerobic biochemical processes, while the Q₁₀ values reported for net CH₄ emissions in field and laboratory studies are often much higher (Dunfield *et al.*, 1993). Meronigal (1996) proposed that even a modest difference in the apparent activation energy (equivalent to Q₁₀) of CH₄ production (60 kJ mol⁻¹) versus oxidation (50 kJ mol⁻¹) causes CH₄ oxidation to consume an increasingly smaller fraction of CH₄ production as soils warm (Figure 3). The implication is that warming may increase CH₄ emissions from tidal marshes by decreasing percent CH₄ oxidation.

In principle, warming can influence CH₄ emissions indirectly by affecting other coupled aerobic-anaerobic processes that regulate CH₄ emissions. Methanogens compete with a variety of other microorganisms for the organic compounds that support respiration (Meronigal *et al.*, 2004). These organisms generally outcompete the methanogens and suppress CH₄ production wherever there is an abundance of nitrate (denitrifying bacteria), oxidized iron (iron-reducing bacteria) or sulphate (sulphate-reducing bacteria) (Neubauer *et al.*, 2005). Bullock *et al.* (2013) demonstrated that rising temperature increases iron reduction rates faster than iron oxidation rates, with the result that the abundance of iron oxides declines with warming. Thus, warming may cause increased rates of CH₄ production by releasing methanogens from competition with iron-reducing bacteria.

Climate warming will also change CH₄ emissions through other indirect mechanisms that regulate the supply of metabolism-regulating compounds. Methane production is sensitive to the supply and quality of organic carbon (Meronigal and Schlesinger, 1997; Vann and Meronigal, 2003; Mozdzer and Meronigal, 2012), which can vary due to temperature-driven changes in plant growth or plant species replacement (Gough and Grace, 1998; Baldwin *et al.*, 2001; Langley and Meronigal 2010; Mueller *et al.*, 2016). Sea-level rise will increase the supply of sulfate -- a critical substrate for the respiration of sulfate-reducing bacteria -- which typically outcompete methanogens for organic compounds, thereby suppressing CH₄ production (Neubauer *et al.*, 2005; Weston *et al.*, 2006).

Finally, warming will influence CH₄ emissions by increasing the diffusion rate of gases through soil water or plant tissue, which exhibits a temperature sensitivity similar to biological processes (Kirwan *et al.* 2014). The net effect increased diffusion rates on CH₄ emissions is complex, and will depend on the relative change in CH₄ versus O₂ diffusion rates, and whether rates of aerobic methanotrophy are limited by CH₄ versus O₂. For example, a scenario in which CH₄ emissions would increase is where CH₄ oxidation is CH₄-limited (e.g. Meronigal & Schlesinger 2002), and the Q₁₀ of CH₄ diffusion exceeds the Q₁₀ of oxidation.

Model forecasts

Numerical models are one approach to forecasting temperature effects on tidal marsh elevation and carbon sequestration. There are several robust tidal marsh elevation models (Fagherazzi *et al.*, 2012), but only a few attempt to mechanistically model soil organic matter (SOM) accumulation. The Callaway model (Callaway *et al.*, 1996; Callaway and Takekawa, 2013) and the modification named WARMER (Swanson *et al.*, 2014) simulate burial by varying SOM decay rates as a function of age and soil depth, but there are no feedbacks of temperature or flood duration on decomposition rate. The Marsh Equilibrium Model (MEM) of Morris *et al.*, (2002) and similar models add a constant fraction of annual primary production to the SOM pool, which means that SOM storage (the inverse of decomposition) effectively varies only

indirectly as a function of flooding on plant production. The Kirwan and Mudd (2012) marsh elevation-carbon model is the only model in this group to date in which SOM decomposition rates respond to temperature.

Kirwan and Mudd (2012) simulated the response of a tidal marsh to a step change in air and soil temperature (Figure 4). The model was parameterized for a tidal marsh dominated by *Spartina alterniflora* in a setting with low suspended sediment concentrations and a constant rate of sea-level rise. The model found that warming increased soil carbon accumulation rates in the years immediately following a sudden increase in in temperature. Warming increased plant productivity, which led to enhanced mineral deposition rates, soil elevation gain, and soil organic matter accumulation. However, several factors caused the initial increase in accumulation to decline over time. Warming increased the total pool of soil organic matter over time, which in turn increased the total amount of carbon lost to decomposition. At the same time, gains in marsh surface elevation became too high for optimum plant growth. The net result of these changes was that warming had little impact on net carbon gain after a century in model runs with both plant and decomposition effects (Figure 4, black line, Kirwan and Mudd, 2012). Warming increased organic matter accumulation more when the decomposition response was taken out of the model, highlighting the need for research on decomposition responses to temperature, which are poorly understood (Kirwan and Megonigal, 2013).

The Kirwan and Mudd (2012) model forecasts that the positive impact of temperature on *S. alterniflora* production increases with the rate of sea-level rise. This behavior arises for three reasons. First, plant productivity increases with inundation frequency, so proportional increases in growth caused by warming are larger in absolute terms when the rate of sea level is faster. Second, faster rates of sea level rise tend to offset gains in surface elevation that would otherwise decrease inundation frequency and eventually limit primary production. Third, sea-level rise enhances sediment deposition, so that the carbon concentration in the soil profile and its impact on decomposition is reduced (Mudd *et al.*, 2009, Kirwan and Mudd, 2012). However, these model results are based on simple parameterizations that apply to a specific wetland type, and they remain untested in natural environments.

Mangrove invasion of tidal marsh

Mangroves are invading marsh-dominated ecosystems around the world (Figure 6), representing one of the most dramatic plant range shifts occurring today (Perry and Mendelsshon, 2009; Doyle *et al.*, 2010; Record *et al.*, 2013; Saintalin *et al.*, 2014). This shift indicates that warming-driven changes in carbon storage are already occurring (Kelleway *et al.*, 2016) or are imminent (Doughty *et al.*, 2015). The expansion of mangroves into higher latitudes on a global scale is driven predominantly by declining frequency of severe freeze events (Osland *et al.*, 2013, Cavanaugh *et al.*, 2014). For example, in North America, the black mangrove, *Avicennia germinans*, intermingles with salt marsh species and can expand its distribution during freeze-free intervals (Stevens *et al.*, 2006) or when saltmarsh vegetation is stressed or killed (McKee *et al.*, 2004). Though air temperatures drive global patterns of mangrove expansion, finer-scale changes in mangrove extent respond to many other environmental factors such as erosion, land subsidence and accretion (Giri and Long, 2014). Thus, some mangrove expansion may be due to re-emergence from previous populations that had disappeared due to disturbance. Regardless, the declining frequency of freeze-related disturbances has generated an overall trend of poleward mangrove range expansion (Saintilan *et al.*, 2014). Woody mangroves encroaching

into herbaceous marshes will likely significantly increase wetland carbon storage at these ecotones between temperate marshes and tropical mangroves.

Mangrove area in southeastern Florida (U.S.) has doubled over the past three decades at the northern edge of the historical mangrove range, with a corresponding loss of salt marsh (Cavanaugh *et al.*, 2014). Mangroves are also expanding into vast areas of marshland on the Louisiana and Texas U.S. coasts (Comeaux *et al.*, 2012; Osland *et al.*, 2013), rendering a large portion of the U.S. coastline subject to dramatic change in the next few decades. At a site in northeastern Florida, Doughty *et al.* (2015) showed that mangrove area increased by 69% in only 7 years, driving a 25% increase in carbon storage over the landscape in less than a decade (Doughty *et al.*, 2015). Kelleway *et al.* 2016 quantified the lateral encroachment of mangroves into two south-eastern Australian salt marshes over a period of 70 years, increasing soil carbon sequestration rates by as much as 230 Mg C km² yr⁻¹. This is one example of a mechanism by which warming may increase carbon storage in a tidal wetland, thereby counteracting global warming.

Though extreme climatic events (i.e. reduction of freezes) are driving wetland plant community composition changes, chronic warming will likely continue to alter the carbon sequestration potential of these rapidly shifting ecotones. Root dynamics in transitional wetlands are of particular interest because mangrove roots can potentially oxygenate the soil more than marsh roots, increasing microbial decomposition of organic matter and increasing carbon release. Understanding these dynamics is an important challenge where organic matter is a driver of surface elevation maintenance to SLR (Krauss *et al.* 2017). As coastal ecosystems provide some of the highest carbon sequestration rates on earth, understanding their shifting carbon storage capacity holds particular importance (Chmura *et al.*, 2003, Donato *et al.*, 2011, Atwood *et al.* 2017).

Sea-level rise

Temperature is a major driver of accelerated sea-level rise. The impact of sea-level rise on tidal wetlands is to shift spatial boundaries, the vertical and horizontal ranges in the coastal zone that wetlands occupy (Woodroffe *et al.* 2016, Lovelock *et al.* 2017). The response of an individual wetland to sea-level rise is nested within the larger landscape response as estuaries, open coasts, barrier systems and other large landforms adjust to the changing balance between increased wave energy (including tides) and the redistribution of sediment (Pethick and Crooks, 2000). If tidal wetlands are unable to adjust to this progressive and accelerating shift, they will drown out and transition to subtidal habitat such as mud flat or seagrass meadows.

The persistence of tidal wetlands in the face of accelerated sea-level rise is favored by a high mineral sediment supply and low slopes (Woodroffe *et al.* 2016). Settings with low sediment supply and limited space for marshes to migrate to will see a progressive conversion of vegetated wetland area to mudflat and open water (Spencer *et al.*, 2016; Kirwan *et al.*, 2016b). Field observations and numerical models suggest that tidal range also regulates the transition from a stable to unstable marsh by setting the elevation range over which plants can grow (McKee and Patrick, 1988; Kirwan *et al.*, 2010; Kearney and Turner, 2016). Relative sea-level rise is most rapid in large river deltas and other areas of rapid subsidence (Kirwan and Megonigal, 2013). Thus, the most sensitive marshes to sea-level rise are those with rapid relative sea-level rise, and small tidal ranges and sediment inputs. Though there is a great deal known about the processes by which tidal marshes gain elevation, large gaps remain in our understanding about how these interact with hydrogeomorphic phenomena and land use patterns

at large spatial scales. As a result, current forecasts of marsh loss due to sea level rise may be overestimated (Kirwan *et al.*, 2016). Tidal freshwater marshes and forests as a rule occur at the head of tidal rivers where the nearby uplands have relatively steep slopes. As a result of this geomorphic setting, these systems may be particularly vulnerable to loss of area with accelerated sea level rise.

Conclusions

Warming is one of many global changes that affect the structure and function of tidal wetland ecosystems, and forecasting the effects of warming is hampered by limitations in observational data, experimental evidence, and models. Key among these is information on how plant growth and interspecies competition are influenced by temperature. Temperature-driven shifts in species composition will dramatically alter tidal marsh ecology, biogeochemical cycling, and ecosystem services. Such shifts will arise from species-specific responses of which very little is known. Changes in plant production caused directly by temperature or indirectly by species shifts will fundamentally alter carbon cycling and storage. Forecasting these effects will require information on changes in belowground production and depth distributions, which are not commonly measured.

The processes that regulate decomposition rates are poorly understood. Perhaps the most important consequence of this gap is the challenge of forecasting the effects of warming on marsh stability against sea-level rise. Because soil carbon is a large fraction of tidal wetland soil volume (Morris *et al.*, 2016), an increase in decomposition rate caused directly by warming or indirectly by increased plant production (Wolf *et al.*, 2007; Mueller *et al.*, 2015), has the potential to destabilize existing soil organic matter pools. The feedbacks between plant activity, microbial activity, and carbon storage are complex and will remain a research challenge for decades.

Ultimately, forecasts of tidal marsh responses to warming will require improved models informed by manipulative experiments and process-level observations. Presently there are few wetland warming experiments, and none of these manipulate soil temperature deeper than a few centimeters. Manipulative experiments should focus on observations that inform models (and vice versa) and seek to elucidate feedbacks between plant responses, microbial responses, nutrient cycling and elevation change.

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