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Tidal wetland stability in the face of human impacts and sea-level rise

Matthew L. Kirwan[1] & J. Patrick Megonigal[2]

Coastal populations and wetlands have been intertwined for centuries, whereby humans both influence and depend on the extensive ecosystem services that wetlands provide. Although coastal wetlands have long been considered vulnerable to sea-level rise, recent work has identified fascinating feedbacks between plant growth and geomorphology that allow wetlands to actively resist the deleterious effects of sea-level rise. Humans alter the strength of these feedbacks by changing the climate, nutrient inputs, sediment delivery and subsidence rates. Whether wetlands continue to survive sea-level rise depends largely on how human impacts interact with rapid sea-level rise, and socio-economic factors that influence transgression into adjacent uplands.

Coastal wetlands are simultaneously some of the most vulnerable and most economically important ecosystems on Earth. Marshes and mangroves protect coastal regions from storms, sequester carbon, transform nutrients and provide the organic matter and nursery grounds that support commercial fisheries[1]. Although these ecosystem services are valued at about US$10,000 per hectare[1], around 25–50% of the world's coastal tidal wetlands have been lost as a result of their direct conversion into land for agriculture and aquaculture uses[2–4]. Tidal wetland conversion to open water through sea-level rise is expected to accelerate, with regional assessments predicting a 20–45% loss of salt marsh during the current century[5]. However, forecasts of widespread wetland loss are difficult to defend on the basis of past accelerations of sea-level rise. There are relatively few examples of marsh loss in the historical record that are directly attributable to sea-level rise because feedbacks between flooding, plant growth and elevation change tend to stabilize submerging wetlands[6,7]. In fact, most coastal wetlands build vertically at rates similar to or that exceed the rate of historical sea-level rise[8,9]. Regions of the world with drastic wetland deterioration occur mainly in areas in which humans have accelerated subsidence rates and/or decreased sediment delivery rates to the coast (for example, coastal Louisiana, the Venice Lagoon and Chesapeake Bay). Nevertheless, past response to sea-level rise is an imperfect model for future response because the climate, water quality and sediment delivery rates continue to change with human activity. In this Review, we will discuss the processes that influence how tidal wetlands adapt to sea-level rise, and highlight how changing climate and socio-economic conditions may alter our emerging understanding of riveting feedbacks between ecology and geomorphology. We focus mainly on tidal marsh ecosystems for which the ecogeomorphic feedbacks are better understood, but also note instances in which data or general principles apply to mangroves. We argue that human impacts other than those that cause sea-level rise have dominated wetlands in the past, but that interactions between rapid sea-level rise and human impacts will drive wetland stability in the future. Whether these ecosystems continue to survive ever faster rates of sea-level rise depends principally on sediment availability, biotic responses to environmental change, the opportunity for wetlands to migrate inland, and environmental attitudes that influence land use, all of which are heavily determined by human socio-economic systems.

Biophysical feedbacks stabilize wetlands

Expansive tidal wetlands consisting of marshes and mangroves, and the channel networks that dissect them occupy about 20 million hectares worldwide[3], and have been a prominent component of coastal and estuarine landscapes for at least 4,000 years[10]. Over this period, the sea level has risen in most regions of the world by more than 2 metres[11,12]. However, observations of widespread wetland drowning are infrequent because of the fascinating interactions between plants and soil that allow wetlands to actively engineer their position within the intertidal zone in ways that enhance ecosystem persistence[7,13–15].

Vertical changes in wetland elevation

At the most basic level, a marsh or mangrove must build soil elevation at a rate faster than or equal to the rate of sea-level rise to survive in place[16]. Elevation gain occurs through biological and physical feedbacks that couple the rate of sea-level rise to the rate of vertical accretion (the increase in soil surface elevation) (Fig. 1). In their role as ecosystem engineers, plants set up distinct feedback loops above and below ground. Above ground, mineral sediment settles out of the water column and onto coastal wetland soils during periods of tidal flooding, so that deposition rates are highest in low elevation marshes that are inundated for long periods of time, and lowest in high elevation marshes that are more rarely flooded[17,18] (Fig. 2a). Plant shoots influence mineral sediment deposition by slowing water velocities[7], and add organic matter to the soil surface (Fig. 1). Below ground, the balance of plant root growth and decay directly adds organic matter to the soil profile, raising elevation by sub-surface expansion[19].

Coastal wetlands are among the most productive ecosystems on Earth, and recent work suggests that vegetation tends to stabilize their relative elevation and seaward extent through feedbacks that vary with the depth and duration of flooding. For example, growth of the grass *Spartina alterniflora* is positively correlated with interannual variations in sea level, such that productivity peaks at intermediate elevations within the intertidal zone, and declines at higher or lower elevations[20] (Fig. 2a). Although the response of mangrove productivity to interannual sea-level variation is unknown, other marsh species show similar — but species-specific — patterns[21,22]. Faster rates of above-ground plant growth promote greater standing biomass, which in turn slows water velocities on the marsh platform[23], lowers wave height[24], reduces erosion and enhances mineral sediment deposition[25]. Collectively, these feedbacks allow tidal

[1]Virginia Institute of Marine Science, PO Box 1346, 1375 Greate Road, Gloucester Point, Virginia 23062, USA. [2]Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, Maryland 21037, USA.

marshes to survive accelerating rates of sea-level rise[6,20]. Similar feedbacks between flooding, plant growth and sub-surface expansion operate in the root zone, generating highly organic soils that persist for thousands of years[19,21,26] (Box 1). Together, these eco-geomorphic interactions suggest that more extensive flooding associated with sea-level rise should be accompanied by enhanced accretion. Indeed, vertical accretion rates approximately tripled in several marshes surrounding Long Island, New York, in response to twentieth century sea-level acceleration[27].

Spatial landscape-scale feedbacks

Landscape-scale geomorphic processes are also important in determining the stability of coastal wetlands. In regions where subsidence is limited and vertical drowning is relatively uncommon[8,9], the size of today's wetlands largely reflects the difference between the rate of lateral erosion at the seaward margin[28], and the rate of wetland creation (that is, migration) at the landward margin (Fig. 1). Erosion rates tend to increase with sea-level rise in shallow intertidal environments because increases in water depth reduce the amount of dissipation that occurs as incoming waves move across tidal flats[29]. Preliminary work suggests that rates of wetland expansion into adjacent forests may accelerate with future sea-level rise[30,31]. Therefore, coupling ecological models of the marsh–forest margin with geomorphic models of retreat at the seaward edge is an important direction for future research.

Sediment dynamics in submerging coastal landscapes can aid vertical accretion in tidal wetlands by delivering sediment from eroding portions of the landscape and depositing it in other portions. For example, rapid erosion of subtidal flats provides sediment to adjacent wetlands on the Yangtze River delta, China, allowing marshes to maintain their aerial extent[32]. Similarly, expansion of channel networks in response to accelerated sea-level rise may deliver more sediment to portions of the platform that were previously sediment deficient[33,34]. Together, these types of ecogeomorphic feedbacks probably explain the persistence of wetlands within the intertidal zone over thousands of years in the stratigraphic record[12], and observations of accretion rates that are highest in regions with historically high rates of sea-level rise[13].

Threshold rates of sea-level rise

Despite robust ecogeomorphic feedbacks that stabilize tidal wetlands, observations of wetland deterioration in places such as the Mississippi River Delta indicate that there are limits to the feedbacks that preserve wetlands within the intertidal zone. An emerging idea is that marshes survive increasing rates of sea-level rise by becoming lower in the tidal zone, which allows them to build elevations at progressively faster rates until they become so flooded that vegetation dies off, and stabilizing ecogeomorphic feedbacks are lost[6,20]. However, the rate of sea-level rise beyond which marshes tend to drown is highly site specific and heavily influenced by human impact, ranging from a few millimetres to several centimetres per year[6] (Fig. 2).

Wetland deterioration

Large areas of marsh are being converted to open water in the Gulf of Mexico, Venice Lagoon and along tributaries of the Chesapeake Bay[16,35,36]. In these regions, which are characterized by low elevations and/or fast rates of relative sea-level rise, increases in the duration of tidal inundation no longer stimulate plant productivity. Rather, progressive inundation reduces organic matter contributions from plants and accelerates erosion, causing a feedback that accelerates the deterioration of coastal wetlands[20,37,38] (Fig. 2a). A variety of numerical models suggest that the transition from a stable to unstable marsh is mainly regulated by the tidal range of an estuary (which sets the elevation range over which plants can grow) and the amount of sediment available for marsh accretion[6] (Fig. 2b). Each of these rapidly deteriorating systems is located in an estuary with small tidal ranges and sediment inputs.

A fundamental goal of tidal wetland research is to forecast the conditions under which tidal wetlands undergo a state change to open water or mud flat, and to relate this back to threshold rates of sea-level rise that can be measured and monitored. The geological record offers some insight. Submerged salt marshes are often preserved as layers of organic rich peat in the stratigraphy of bays, estuaries and the offshore continental shelf[10,39–41]. Although more work is needed to connect the collapse of these palaeo-marshes with historical rates of sea-level rise, peat from modern

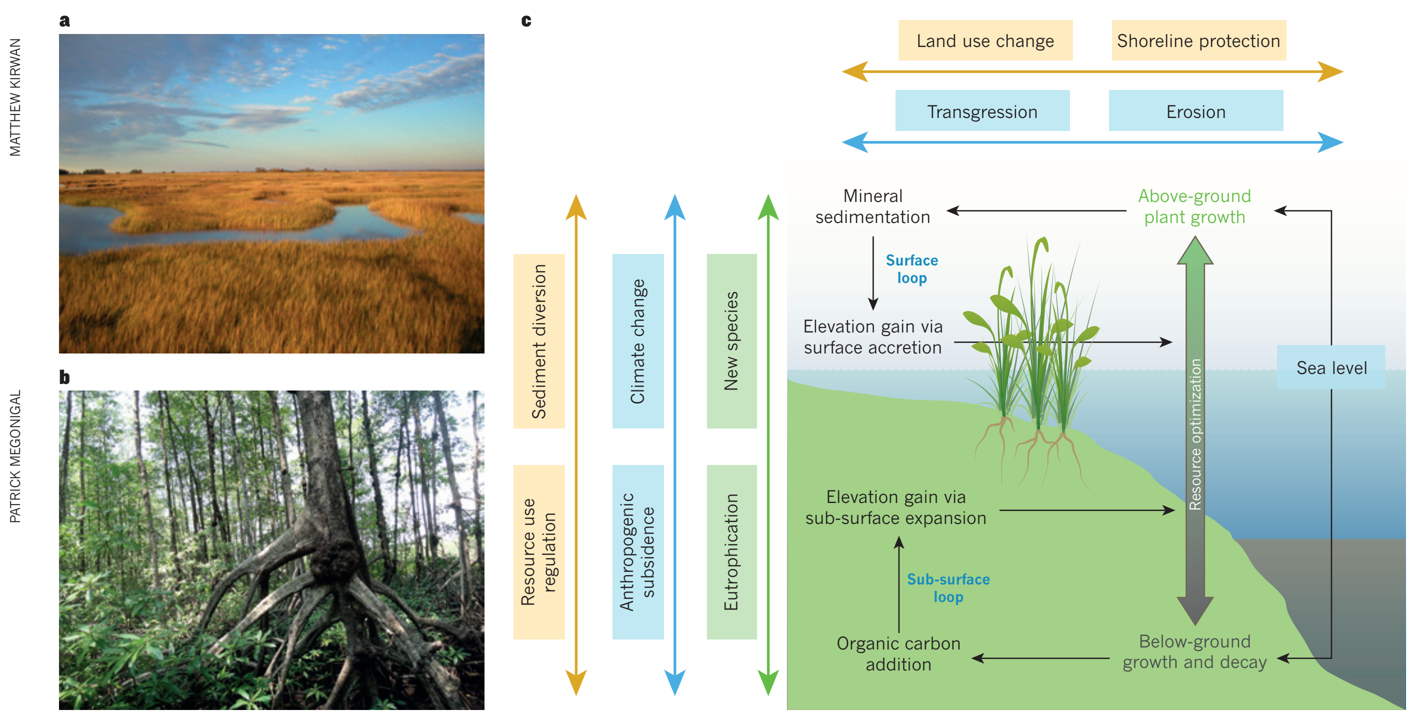

Figure 1 | Wetland feedbacks. Feedbacks in marshes (top left) and mangroves (bottom left) operate horizontally and vertically at different scales and with distinct sets of processes to influence the wetland stability. Feedbacks on vertical elevation change operate through natural processes above and below ground. These natural processes can be perturbed by local factors (green) such as eutrophication and new species; large-scale climatic and geomorphic processes (blue); and political, social and economic factors (orange), which affect the other processes.

marshes suggests that marshes form and persist when relative sea level rises at a rate of less than a couple of millimetres per year[12], but that existing marshes survive much faster rates. Most (>90%) basal peats from salt marshes along the US Atlantic Coast are less than 6,000 years old, implying that most modern marshes formed during a time when relative sea-level rise rates were slowing from 1–4 mm yr^{-1} to 0.5–2 mm yr^{-1} (ref. 12). This suggests that marshes mainly establish when rates of relative sea-level rise are quite low. However, rates of sea-level rise at marsh inception are a minimal estimate of threshold rates for survival because biophysical feedbacks (Fig. 1) allow established marshes to survive conditions in which they cannot form[42,43]. For example, mid-Holocene marshes that responded to rapid sea-level rise 8,200 ybp survived rates of about 7 mm yr^{-1} in Louisiana[44], and drowned in Chesapeake Bay only when rates exceeded 12 mm yr^{-1} (ref. 45).

Historical persistence

The response of salt marshes to sea-level rise can also be viewed in the context of more recent sea-level acceleration. Tide gauges and stratigraphic evidence indicate that relative sea-level rise rates were less than 1 mm yr^{-1} for most of the past 2,000 years, and began accelerating towards modern rates (about 2–3 mm yr^{-1}) around the end of the nineteenth century[11]. Perhaps in response, more flood-tolerant vegetation such as *Spartina alterniflora* invaded New England marshes, which had historically been dominated by flood-intolerant vegetation such as *Spartina patens,* at roughly the same time sea-level rise began to accelerate[46]. Although these are local observations, numerical models indicate that historical sea-level-rise acceleration would have led to a modest (around 5–15 cm) deepening of marsh surfaces relative to sea level[47]. Nevertheless, most models predict threshold rates of sea-level rise (5–50 mm yr^{-1}) that are much faster than what has occurred in the recent past[6] (Fig. 2b).

Measurements of vertical accretion rates in tidal wetlands around the world are consistent with models that predict relatively fast threshold rates of sea-level rise. Although some tidal wetlands are flooded for longer durations, as evidenced by changes in vegetation type, there seems to be no evidence of widespread wetland loss that is directly related to sea-level rise[8,9]. These data emphasize that threshold rates of sea-level rise have rarely been crossed in recent decades. However, it remains unclear how anthropogenic impacts will shift thresholds.

Human interference with ecosystem feedbacks

Historical observations yield clues as to the maximum rate of sea-level rise that tidal wetlands can tolerate, but are ultimately limited by substantial differences between past, present and future environmental conditions. Compared with the last period of rapid sea-level rise 8,200 ybp[45], the present and future are characterized by higher atmospheric carbon dioxide concentration, plant-available nitrogen, temperature and introductions of new plant and animal species, all of which influence the major natural feedback processes that stabilize tidal wetland ecosystems (Fig. 1).

Deterioration of tidal wetlands often begins with plant stress, and the disruption of the stabilizing feedbacks that plants provide. For example, plant mortality associated with the BP Deepwater Horizon oil spill triggered order-of-magnitude increases in marsh edge erosion rates[48], historically stable channel networks became strongly erosive when crabs disturbed plants and substrate[49], herbivory caused an accreting marsh on an actively building delta to become strongly erosive[34], and tree mortality wrought by Hurricane Mitch caused mangrove peat collapse[50]. Even temporary, climatically driven episodes of vegetation die-off[51,52] sometimes lead to geomorphic change, including rapid subsidence, platform erosion and diminished deposition rates[23,53]. Thus, factors that influence the growth rate of plants (for example, climate and nutrients) are likely to influence the ability of a marsh to survive sea-level rise.

Climate change and eutrophication

The effect of any given perturbation on tidal wetland stability depends a great deal on the extent to which it affects above ground compared with below-ground feedbacks (Fig. 1). For example, elevated CO_2 increases the photosynthetic efficiency of above-ground (C_3) plant tissues, plant demand for root-acquired soil nutrients and root growth[54,55]. Plants with C_4 photosynthetic pathways show little response to elevated atmospheric CO_2 because their photosynthetic apparatus naturally concentrates CO_2 at the site of the primary CO_2-fixing enzyme[26]. Although elevated CO_2 may also accelerate the decay of soil organic matter, the net effect is to increase soil mass, subsurface expansion and elevation gain (Fig. 1), all of which can occur without an increase in mineral sediment deposition. Thus, elevated CO_2 probably either enhances wetland stability through increased root production (C_3-dominated wetlands such as mangroves, brackish marshes and tidal freshwater marshes) or has no effect on stability (C_4-dominated systems such as *Spartina* salt marshes).

Latitudinal gradients suggest that warming will increase tidal wetland productivity[56] and decomposition[57,58], with the net effect that carbon storage and vertical accretion will be enhanced — at least initially[58]. The few experimental manipulations of temperature in tidal marshes confirm this pattern[59,60], but suggest that long-term temperature responses will be more complex owing to species replacement[60] and interactions with rates of sea-level rise[58]. The effects of warming on

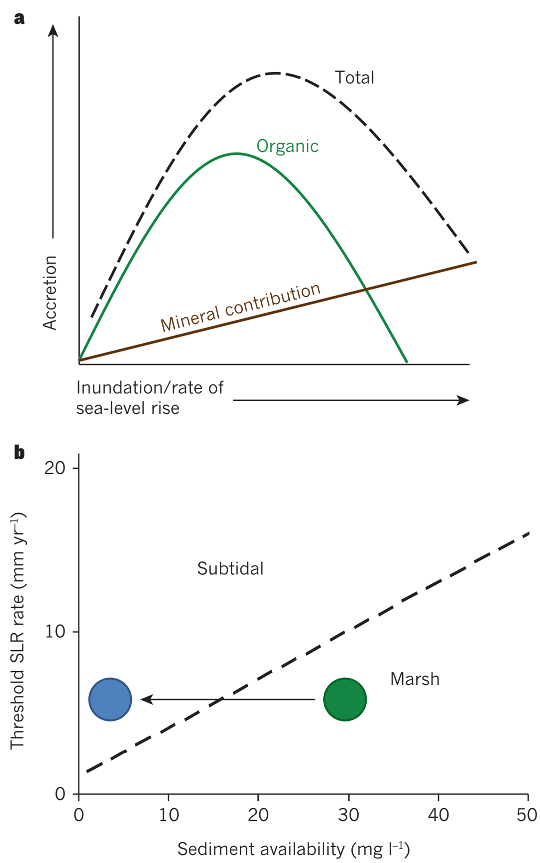

Figure 2 | Conceptual links between sea-level rise and marsh accretion. a, The hypothetical contribution of organic and mineral matter to accretion as a function of inundation in a sediment-deficient marsh. Organic matter dominates total accretion for infrequently flooded marshes that are typical of high-elevation marshes and/or periods of slow sea-level rise (left). However, the same marsh becomes progressively more mineral rich as inundation duration and rate of sea-level rise increase (right). Therefore, the threshold rate of sea-level rise tends to be a function of sediment availability. **b,** Threshold rates of sea-level rise (SLR) beyond which marshes cannot survive as a function of suspended sediment concentration in an estuary. Dashed line represents threshold rates from the 1-m tidal range case from ref. 6. Under moderately rapid sea-level rise (5 mm yr^{-1}), a marsh that is stable under historical sediment loads (green circle) submerges if sediment loads are reduced (blue circle). This suggests that land use change and dam construction may cause marshes to become less stable in the future, even if sea-level rise rates remain constant.

BOX 1

Organic contributions to elevation

Soil elevation is the result of of complex interactions between the three components of soil volume: mineral matter, organic matter, and water- or gas-filled pore space. Soil accretion is sensitive to both mineral and organic deposition (Figs 1 and 2), but the ephemeral nature of organic matter makes it particularly sensitive to disturbance. Depending on the geomorphic setting, organic matter accounts for between 1 and 80% of the dry mass of tidal wetland soils, commonly forming peat soils (histosols)[94]. Organic matter particles occupy about twice the volume of mineral particles on a mass-normal basis (about 0.8 $cm^3 g^{-1}$ compared with 0.4 $cm^3 g^{-1}$), and soil organic matter contributes 2–5 times more to bulk soil volume than an equal mass of minerals[94,95]. Accretion rates often have a stronger correlation with organic matter accrual than mineral accrual in North American tidal marshes[94,95], although the reverse is sometimes true and the relationship is site and region dependent. Organic matter accrual is the main process by which tidal wetlands become perched high in the tidal frame, which reduces their vulnerability to rapid sea-level rise or decreased plant productivity.

Organic matter derived from roots, shoots and allocthonous inputs accumulate in wetland soils because a large fraction is recalcitrant to decay in the absence of oxygen, the overwhelming agent of preservation in wetland soils. The molecular composition of plant tissue is an important secondary factor, but many mechanisms of organic matter preservation in upland soils[96] are unimportant in wetlands. For example, physical protection by mineral armouring is largely absent in organic soils and of little consequence in tidal mineral soils, which lack aggregates owing to limited fungal activity and wet–dry cycles.

There are limits to the suggestion that slow decay in wetlands is explained by the low free-energy yield of anaerobic respiration. For example, accumulation of phenolic compounds in peat-land soils can directly inhibit microbial biodegradation[97]. Most effort has been devoted to the terminal steps of anaerobic decomposition, rather than the fermentation processes that precede it[98]. We know little about the factors that regulate fermentative bacteria, enzyme activity, substrate feedbacks and microbial community interactions — all of which affect organic matter volume.

The delivery of salts and sulphates to brackish and freshwater coastal wetlands through sea-level rise may destabilize soil organic matter pools. Organic accretion rates tend to be highest in freshwater tidal wetlands[99], and studies report accelerated decomposition rates with saltwater intrusion[100], but these results are equivocal and we lack the mechanistic insight to explain such responses. Finally, most studies of decomposition focus on the decay of relatively labile, leaf and root litter over timescales of less than 3 years. The fraction of net primary production that is preserved after a decade or more is much more crucial for the accumulation of soil carbon and the maintenance of wetland elevation[30].

mangrove productivity are far less certain because even a relatively small rise in local temperatures (less than 1.3 °C) will expose these systems to year-round temperatures well outside (more than 2 standard deviations) current variability[61].

Coastal eutrophication might be expected to enhance elevation gain owing to higher rates of plant growth, but nutrient enrichment experiments show the full spectrum of elevation responses from gain to loss[19,55,62,63]. In a single Caribbean mangrove swamp, nitrogen addition decreased or reversed elevation gain at fringe and interior sites, but had no effect on sites transitional between the two; likewise, adding phosphorus stimulated elevation gain in areas other than the fringe, at which it suppressed elevation gain[62]. In this low-sediment environment, these seemingly enigmatic responses were driven solely by below-ground processes, and mainly by differences in fine-root growth[62], which increased, decreased or remained unchanged depending on the initial state of nitrogen and phosphorus limitation. Similar observations were reported for a peat-forming tidal marsh[55]. This is in contrast with sediment-rich systems in which any increase in plant growth — root or shoot — is likely to enhance elevation gain because biomass enhances mineral sediment deposition[19] (Fig. 1). Nutrient-induced elevation loss may be caused by a shift in plant growth from nutrient-acquiring roots to light-harvesting shoots, competitive replacement of a high-biomass species by a low-biomass species[54], or enhanced organic matter decay rates[64]. Of these, decay responses to nutrient enrichment are the most poorly understood because studies often fail to distinguish between root respiration and soil organic-matter respiration in field studies; artificially interrupt interactions between microbial and root processes by separating the two in laboratory incubations; or focus on short-term litter decay, which has little relevance to organic-matter preservation (Box 1). Reconciling the direction of eutrophication effects on elevation will require an understanding of the processes that operate over long timescales (decades) and large areas (square kilometres). It has been suggested that eutrophication reduces soil strength in wetlands[64,65], but the effect of such change may take decades or a major storm event to become apparent[64,66]. This topic is controversial[63] and ripe for new experimental approaches.

Experimental design limits our ability to forecast tidal wetland response to change. The limited duration and spatial scale of most designs does not capture the tendency of ecosystems to resist perturbation until they reach a crucial threshold, after which they undergo a rapid change in state[64]. The simplicity of factorial designs can be at the expense of defining response curves that are more useful for modelling. Experimental designs that support modelling are important because models can identify hysteresis or specific sets of initial conditions that influence vulnerability. For example, warming can inhibit accretion when initial rates of sea-level rise and primary production are low, or stimulate accretion when the rate of sea-level rise is initially high[58]. A challenge for tidal wetland research is to define the suite of initial conditions, and interactive variables that generate complex patterns of tidal wetland stability. One such factor is plant species composition.

Vegetation shifts

The consequences of gaining or losing plant species are often more drastic than changes in the growth or physiology of existing plant species. New species influence tidal wetland stability by adding or subtracting new physiological and morphological traits that contribute to ecogeomorphic feedbacks. Low-salinity marshes of the Mississippi River delta sustained more damage from Hurricane Katrina and Hurricane Rita than high-salinity marshes because they are dominated by species with relatively shallow root profiles and consequently lower resistance to surging water and waves[66]. Genotypes of the grass *Phragmites australis* introduced to North America from Europe are likely to stabilize tidal wetlands because of traits that support higher below-ground productivity than the vegetation they are replacing[67,68]. The subsidy in soil-elevation gain provided to C_3-dominated wetlands by elevated CO_2 can be diminished when other factors, such as eutrophication, favour C_4 species[54]. As these examples show, forecasting marsh vulnerability to sea-level rise requires attention to key functional attributes of tidal wetland species such as root depth distributions and responses to perturbation.

Subsidence and sediment delivery

Humans also indirectly threaten the survival of coastal wetlands by altering subsidence rates and restricting sediment delivery (Fig. 1).

Groundwater withdrawal and artificial drainage of wetland soils contribute to rapid subsidence such that 8 of the world's 20 largest coastal cities now experience relative sea-level rise rates that greatly exceed any likely climate-driven projection[69], and most of the world's major river deltas are sinking much faster than the historical rate of sea-level rise[70]. Although subsidence from isostatic flexure and the compaction of young unconsolidated sediment has a sizable natural component, subsidence caused by artificial drainage and groundwater extraction near metropolitan areas such as New Orleans, Louisiana, and Venice, Italy, can be up to an order of magnitude faster[71]. Temporal variations in recent subsidence rates also correlate with estimates of hydrocarbon extraction[72]. Spatial patterns of wetland loss in coastal Louisiana correlate with the density of canals built by oil and gas companies[73], and temporal patterns of wetland loss correlate with variation in subsidence rates[72].

Dams and reservoirs now prevent about 20% of the global sediment load from reaching the coast[74]. Because mineral sediment availability is a primary driver of wetland building, changes in sediment delivery rates have large impacts on marsh sustainability[43,75]. An ensemble of numerical models predicts that threshold rates of sea-level rise respond linearly to changes in suspended sediment concentration, where marshes in sediment-rich estuaries survive rates of sea-level rise much greater than projected climate-driven scenarios[6]. Indeed, regions of the world with rapid wetland conversion to open water (for example, the Gulf of Mexico, Venice Lagoon and along tributaries of the Chesapeake Bay) are all located in sediment-deficient areas[16,35,36]. Dam construction, reforestation and agricultural sediment-control practices continue to lower sediment yields to the coast[74], so these observations suggest that historically stable coastal wetlands may become increasingly prone to collapse in the future, even if sea-level rise rates were to remain steady[6] (Fig. 2b). Marshes on the Yangtze River delta, for example, have expanded seaward since the seventh century, surviving subsidence-generated sea-level rise rates of more than 50 mm yr^{-1}. After sediment restriction associated with the construction of more than 50,000 dams on Yangtze River tributaries, marshes in several areas are now eroding landward, and overall rates of marsh expansion have declined to near zero[31,76].

Direct human modification of wetlands

Direct human modification, rather than sea-level rise, is by far the major cause of historical and contemporary coastal wetland loss. Although more robust estimates are needed, conversion of wetlands into other land uses claimed about 25–50% of the world's coastal wetlands during the twentieth century alone[2–4]. Wetland habitat conversion is an ongoing phenomenon despite several decades of investment in research, policy, education, laws and treaties aimed at understanding and conserving these resource-rich ecosystems. The history of coastal wetland degradation tracks human population growth, industrialization and development, with marginally sustainable use of coastal resources giving way to rapid decline 150–300 ybp[77]. Tidal marshes were among the earliest coastal wetlands to be modified on a large scale[78] because they dominate the temperate zone where industrialization began. Intentional conversion of tidal marshes has slowed in developed countries with the adoption of laws and conservation efforts, leaving unintentional conversion to open water as the major cause of loss[79]. However, developing countries are at present converting coastal wetlands to other land uses at high rates[80], substituting agriculture, aquaculture and tourism for the natural capital and ecosystem services these systems provide. For example, between 1975 and 2005, countries in the tsunami-affected

Figure 3 | Human disturbance of tidal wetland ecosystems. **a**, Fisherman's and Manatee's Cays, Belize, where mangroves were cut and filled with substrate dredged from nearby patch reefs to create white beaches. **b**, Aerial image of mangrove swamps that have been converted into shrimp ponds. **c**, Tidal marsh prevented from migrating landward by a sea wall. **d**, Subsidence of a tidal freshwater peat land in California after being dyked (embankment created), drained and farmed.

region of Asia converted 12% of their mangrove forests to agriculture and aquaculture[81], despite some evidence that these systems provide protection against tsunamis and storm surge[82–84]. A challenge is to fully quantify the socio-economic and ecological costs of wetland conversion and bio-engineering activities, and incorporate these costs in policy, planning and restoration activities[82,85].

Socio-economic factors

Economic incentives to expand arable land, harvest resources and protect infrastructure investments have long motivated humans to actively alter the land–sea margin[78] (Fig. 3). Such activities have generally served to degrade tidal wetlands, and to do so at an increasingly global scale that is certain to intensify with ongoing global population growth and economic development[77]. The future vulnerability of tidal wetlands to degradation and loss will be a function of interacting natural and socio-economic phenomena[86] that must be reconciled through informed decision making. For example, it may be possible to simultaneously accommodate limited conversion of mangrove to shrimp ponds and maintain certain ecosystem services such as wave attenuation that scale non-linearly with wetland size[85]. Thus, it is no longer sufficient to focus separately on the natural processes that sustain coastal systems, the economic incentives for human activities that disrupt these processes, and the social dimensions of human behaviour.

During the millennial period in which people's interactions with the sea have been most intense, sea-level rise rates have remained low. Only now are we beginning to learn how to respond to accelerating sea-level rise. Historical strategies for protecting coastal property have favoured use of vertical, often hardened structures such as dykes, sea walls, revetments and bulkheads[87,88] (Fig. 3). Because intertidal wetlands lie between these structures and the sea, such measures contribute to wetland loss through 'shoreline squeeze', in which erosion removes the wetland area at the margin and structures prevent the addition of area by migration onto adjacent uplands[87]. Because rates of marsh-edge erosion increase with rates of sea-level rise[28], the impacts of these barriers will accelerate with climate change, and the effect of coastal defence on the trajectory of coastal wetland area is potentially large. In the absence of anthropogenic barriers, a 1 m rise in sea level would create around 11,000 km^2 of new intertidal area in the conterminous United States alone[31]. This is a significant percentage of the existing US intertidal zone (about 16,000 km^2)[31], suggesting that sea-level-induced losses of existing wetlands may be offset by transgression if anthropogenic barriers are minimal. However, alternatives to flood defence structures that allow wetland migration require the cooperation of stakeholders on adjacent uplands, and creating these alternatives will become more difficult as the coast is developed.

The non-market value of ecosystem services is being used to promote the conservation, restoration and creation of coastal wetlands, and to protect adjacent uplands for wetland transgression. For example, the 1990 US Coastal Wetlands Planning, Protection and Restoration Act (Public Law 101-646) invests $30–80 million annually in coastal restoration. An emerging strategy is to market the substantial capacity of coastal wetlands to store and retain carbon[3,89]. Mangroves, salt marshes and sea grasses — blue carbon ecosystems — are global carbon hot spots where area-based carbon pools and fluxes far exceed those of other terrestrial and aquatic ecosystems[4]. Because the highest wetland loss rates and area-based carbon pools converge in mangroves, the highest potential for generating carbon credits is in developing countries where financial resources for climate mitigation are most limited. Forecasts of global wetland loss owing to sea-level rise alone are small when compared with forecasts of loss owing to the combined effects of sea-level rise and human activities related to adaptation[86]. Therefore, the fate of wetlands in the twenty-first century fundamentally depends on socio-economic conditions, policy decisions and perceptions about the value of coastal wetlands[4,90].

Priorities for future research

For more than 30 years, point-based comparisons between rates of sea-level rise and elevation change have dominated wetland vulnerability research. However, many of the most fundamental questions pertaining to coastal wetland stability and value are inherently spatial in nature. Will wetlands transgress landward at a rate that exceeds seaward displacement? Could sea-level rise actually cause wetlands to expand? What factors explain spatial and geographical variations in tidal wetland vulnerability? To answer these questions will require integrating studies of wetland processes in the vertical dimension with research on the factors that control the lateral position of wetland boundaries. This research will require accessible sources of high-resolution digital elevation models, and data layers on the prevalence of important landscape features such as anthropogenic barriers and population density. It will also require more process-level research on the factors that control edge erosion[28], rates of forest-to-marsh conversion[91] and land use change[88]. For example, in the absence of anthropogenic barriers in the conterminous United States, preliminary work suggests that even complete drowning of existing wetlands may result in only a 22% decrease in potential wetland area because significant upland area could be available for wetland migration[31]. Thus, a systematic evaluation of the amount of land where humans restrict marsh transgression, or are likely to do so in the future, represents a simple and crucial step towards understanding whether the world's wetlands will expand or contract with sea-level rise.

In coastal regions, where the world's population continues to converge, two-way couplings between society and ecosystems are particularly captivating. Humans now have an impact on every major process influencing wetland stability (Fig. 1). Upstream land use change and dam construction alter sediment delivery rates to the coast, fluid withdrawal accelerates relative sea-level rise, eutrophication affects plant growth and decay of organic matter, and climate affects every biogeochemical process. But humans are themselves influenced by the enormous ecosystem services wetlands provide, including coastal protection from storms and rising water[83–85]. These human impacts interact with each other, and with sea-level rise. Because of these new interactions, threshold rates of sea-level rise for marsh submergence predicted by numerical models and observed in the stratigraphic record will probably be poor indicators of future wetland vulnerability. Incorporating the indirect effects of humans on climate, sediment availability and nutrient loads into biophysical models of coastal wetland evolution is an important challenge. Indeed, preliminary work indicates that even the direction of change they induce may be site specific (for example, eutrophication). Thus, more process-level research is needed before quantitative assessments of global wetland vulnerability can hope to account for the indirect effects of human modification. For example, we have identified the processes that regulate organic matter accumulation in tidal wetland soils as one area in which more research is needed (Box 1). Large-scale manipulative experiments that push the limits of wetland survival and incorporate human actions also seem especially relevant, because most natural wetlands have adapted to historic sea-level rise alone.

Coastal population growth and accelerating rates of sea-level rise will intensify the tight interactions between society and coastal wetlands. The effect of decisions that determine how governments and landowners conserve wetlands and defend uplands from rising seas may dwarf the effect of sea-level rise alone[86]. Thus, new socio-economic research examining perceptions of wetland value is needed to fully understand coastal sustainability[90]. Here again, integrating direct (for example, barriers and land conversion) and indirect (for example, climate, sediment supply and nutrients) human impacts into numerical models of wetland vulnerability remains challenging. Large-scale coastal vulnerability models largely ignore the biophysical feedbacks that are known to aid marsh persistence, whereas process-oriented models are highly site specific and do not include human components[7]. The disconnect between these modelling approaches must be bridged to predict how the size and global distribution of wetlands will change in response to climate and future human activity.

The historical loss of coastal wetlands has been dominated by the direct conversion of wetlands to agriculture and aquaculture, rather than by climate change. However, recent disasters such as Hurricane Katrina and Hurricane Sandy, the Indian Ocean tsunami and the Deepwater Horizon oil spill have renewed public interest in wetland restoration as a mechanism to provide economically valuable coastal protection[82]. Towards these efforts, our Review provides two insights. First, biophysical feedbacks allow coastal wetlands to survive conditions under which they cannot develop[42,43]. Such a hysteresis is challenging to overcome in efforts to restore severely degraded landscapes[92], but may bode well for the longevity of creation and restoration activities. Relying on plants to modify their environment and build wetland elevations is an intriguing strategy that should be pursued in future research. However, in some cases the biophysical environment in which these systems formed may no longer support restoration to their recent condition. For example, there is no longer enough sediment delivered to the Mississippi River Delta to fully restore the landscape to an elevation at which plants can grow and initiate these feedbacks[93], forcing value-laden decisions about which portions of the landscape to restore. Second, historical adaptation to sea-level rise indicates that the loss of wetlands is not an inevitable outcome of climate change. Although very rapid rates of sea-level rise may drown some marshes regardless of indirect human impacts, numerical models predict that many wetlands will survive in places in which dams and embankments do not restrict sediment transport[6] (Fig. 2b). Preliminary topographic analyses suggest that wetland migration could largely offset even a complete loss of existing coastal wetlands in the absence of anthropogenic barriers[31]. Thus, we propose that the fate of coastal wetlands is perhaps more intrinsically linked to the complex economic and sociological decisions aimed at protecting coastal infrastructure from the impacts of climate change, than the rates and magnitude of the change itself. ■

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