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Sea-level driven land conversion and the formation of ghost forests

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Ghost forests created by the submergence of low-lying land are one of the most striking indicators of climate change along the Atlantic coast of North America. Although dead trees at the margin of estuaries were described as early as 1910, recent research has led to new recognition that the submergence of terrestrial land is geographically widespread, ecologically and economically important, and globally relevant to the survival of coastal wetlands in the face of rapid sea level rise. This emerging understanding has in turn generated widespread interest in the physical and ecological mechanisms influencing the extent and pace of upland to wetland conversion. Choices between defending the coast from sea level rise and facilitating ecosystem transgression will play a fundamental role in determining the fate and function of low-lying coastal land.

Sea-level rise rates have been accelerating since the end of the nineteenth century, impacting low-elevation land along coasts and estuaries around the world[1]. Sea level rise enhances flooding and saltwater intrusion, and threatens coastal communities, infrastructure and ecosystems[2–4]. Ghost forests and abandoned farmland are striking indicators of sea-level driven land conversion. Dead trees and stumps surrounded by marshland, for example, represent relic forestland that has been replaced by intertidal vegetation. Similarly, bare soil and wetland plants at the edges of agricultural fields indicate the encroachment of wetlands into formerly productive farmland. These visual illustrations of land conversion are common along the North American Atlantic and Gulf of Mexico coasts, and reflect rapid ecosystem change and the inland migration of the intertidal zone in response to sea level rise (Fig. 1).

The ongoing conversion of uplands to wetlands is both economically and ecologically important. Eustatic sea level rise is predicted to increase by between 0.4–1.2 m by 2100 (ref. [5]). More than 600 million people live in low-lying coastal areas (<10 m elevation)[3], and approximately 50 million people live on land predicted to be permanently inundated with 0.5 m of sea level rise[6]. In the conterminous United States alone, 1 m of relative sea level rise would convert approximately 12,000–49,000 km^2 of dry land to intertidal land without flood-defence structures[7,8]. Heavily populated, low-lying regions including subsiding deltas and island nations will be most affected[6]. In Egypt and Bangladesh, sea level rise could cause a 15–19% loss in habitable land and displace 13–16% of the population[9]. In the United States, residential property values may decrease with proximity to wetlands[10], and the conversion of uplands to wetlands is perceived as highly undesirable by many landowners[11]. On the other hand, the marshes and mangroves that replace inundated forests and farmland are considered among the most valuable ecosystems in the world because they improve water quality, reduce coastal erosion, protect against flooding, sequester carbon and support marine fisheries[12]. Therefore, coastal sustainability in the face of sea level rise involves rapidly moving ecosystem boundaries and complex trade-offs between the direct and indirect values of different land uses[13].

Although ghost forests first appeared in the scientific literature over a century ago[14] and are a prominent feature of many coastal and estuarine landscapes from the Atlantic coast of Canada to the Gulf Coast of the United States[15–22], coastal change research has traditionally focused on more seaward environments, such as barrier islands, intertidal wetlands and subtidal ecosystems[23,24]. Extensive research into those portions of the coastal landscape has identified a number of feedbacks between flooding, vegetation growth and sediment transport, that allows them to resist sea level rise until some threshold rate is exceeded. For example, marshes, mangroves and oyster reefs are well known to resist sea level rise by accumulating sediment and growing vertically[24–26]. Although more work is needed to determine if analogous processes allow terrestrial land to resist sea level rise, observations of widespread land conversion[16,17,19] suggest terrestrial ecosystems largely lack mechanisms to engineer vertical soil growth. Therefore, forests and other terrestrial ecosystems are potentially more sensitive to sea level rise than better studied intertidal and subtidal portions of the coastal landscape[20].

Here, we review the natural and human mediated processes that influence sea-level driven land conversion. Although this Review considers a variety of land types, we emphasize the conversion of forests to marshes because it is the most common and well-studied conversion, and because it produces ghost forests that are a striking visual indicator of sea-level driven land conversion. The first section illustrates that historical land submergence is geographically widespread and has impacted terrestrial forests, agricultural fields and developed landscapes alike. The second section discusses the ecological processes linking sea level rise and land conversion, such as plant population demography and community reorganization, that shape the environmental consequences of land conversion. The third section argues that drowning of uplands is potentially the most important process determining future wetland area; and the fourth section considers the extent to which humans will prevent or facilitate coastal land submergence. The Review ends with implications for land management, and highlights uncertainty in local flood defence strategy as the key knowledge gap limiting our ability to predict future sea-level driven land conversion and its impact on coastal ecosystems.

Extent and control of historical land submergence

Ghost forests, abandoned agricultural fields and other indicators of historical land submergence occur throughout low-lying and

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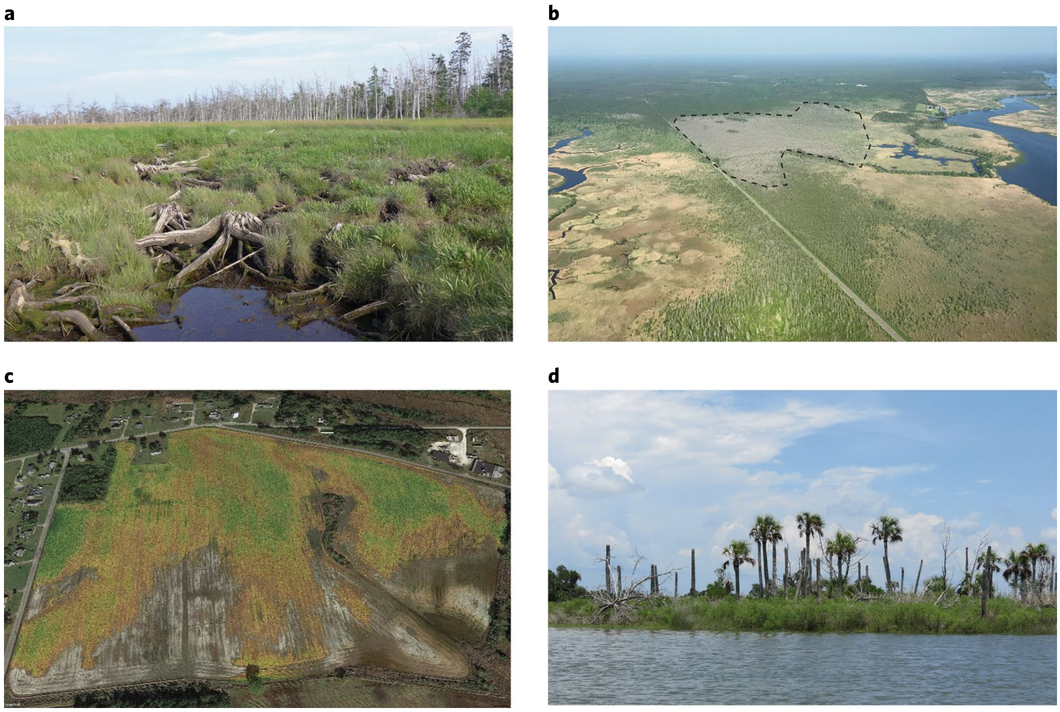

Fig. 1 | Geographic distribution of sea-level driven land conversion in North America. a, Red spruce ghost forest and buried stumps, New Brunswick, Canada. **b**, Atlantic white cedar ghost forest in New Jersey (indicated by dashed line). **c**, Salt damaged agricultural field in Virginia, where white and grey areas indicate bare ground, and yellow-red colours represent stressed crops. **d**, Palm tree ghost forest in Florida. Credit: David Johnson (**a**), Kenneth W. Able (**b**), USDA Farm Service Agency (**c**) and Amy Langston, Virginia Institute of Marine Science (**d**)

gently sloping portions of the Atlantic and Gulf Coasts of North America[15–20] (Fig. 1). Land submergence is most extensive within the mid-Atlantic sea-level rise hotspot that stretches from North Carolina to Massachusetts, where relative sea level is rising three times faster than eustatic rates[27]. For example, 400 km^2 of uplands in the Chesapeake Bay region have converted to tidal marsh since the mid-1800s[19], and large tracts of hardwood and cedar forest death have been observed in Delaware Bay[16]. However, ghost forests are not confined to the sea level rise hotspot; they have also been documented throughout the Florida Gulf Coast[17,18], the St. Lawrence estuary in Canada[15], and tidal freshwater forests in South Carolina, Georgia and Louisiana[21,28]. There has been 148 km^2 of forest conversion over 120 years along the Florida Gulf Coast[17], and near complete loss of pine forests in the Lower Florida Keys[29]. Surprisingly, the phenomenon has not been widely documented on coastal plains outside of the United States. There are no reports of ghost forests from low-lying tropical regions where the phenomenon would be predicted, such as the Yucatan Peninsula, Mexico[30], or from the Pacific Ocean's western margin, such as along eastern China, due to the prevalence of seawalls there[31].

Observations of historical land submergence indicate that topography and relative sea level rise are the two most important controls on the rate of lateral forest retreat[32]. Migration rates are substantially lower in United States Pacific coastal regions and New England estuaries (<10 cm yr^{-1})[33,34] than in the mid-Atlantic coastal plain (up to 7 m yr^{-1})[16,19,35], where rates of land conversion are inversely correlated with slope[16,19]. Although mortality of canopy trees may depend on punctuated disturbance events, such as storms, and therefore lag behind sea level rise[30,36], land conversion is tightly tied to sea level over decadal timescales[16,18,30]. For example, the elevation of coastal treelines has increased in parallel with late-Holocene sea level rise, and lateral rates of forest retreat are 2–14 times higher than pre-industrial rates[20,35] (Fig. 2).

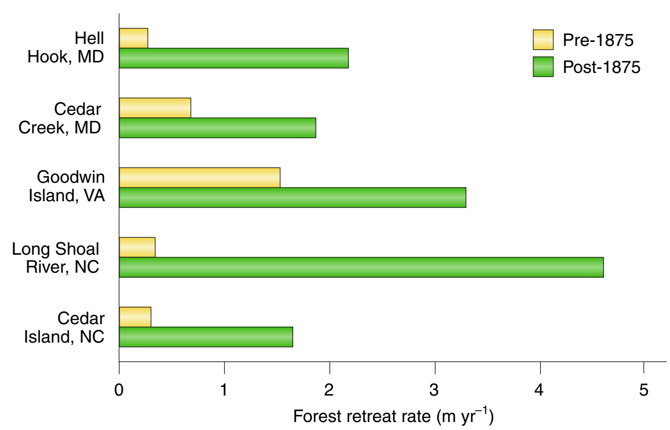

Fig. 2 | Accelerating forest retreat rates. Lateral forest retreat rates for five US mid-Atlantic sites, where gold bars represent late-Holocene rates (pre-1875) inferred from sediment cores and historical maps, and green bars represent modern rates (post-1875) inferred from historical maps and aerial photographs. 1875 was chosen to approximate the initiation of accelerated sea level rise on the Atlantic coast[1]. Modern forest retreat rates are 2–14× higher than late-Holocene rates, and generally increase through time. Adapted from ref. [20], Virginia Institute of Marine Sciences.

The conversion of agricultural fields and residential lawns to wetlands is less visually striking than ghost forests, as one herbaceous plant community is replaced by another, but is much more economically damaging. Marshes migrate rapidly into urban and suburban lawns, where mowed marshes look similar to mowed lawns[37]. Abandonment of agricultural land due to salinization is prevalent in low elevation coastal regions around the world, including large

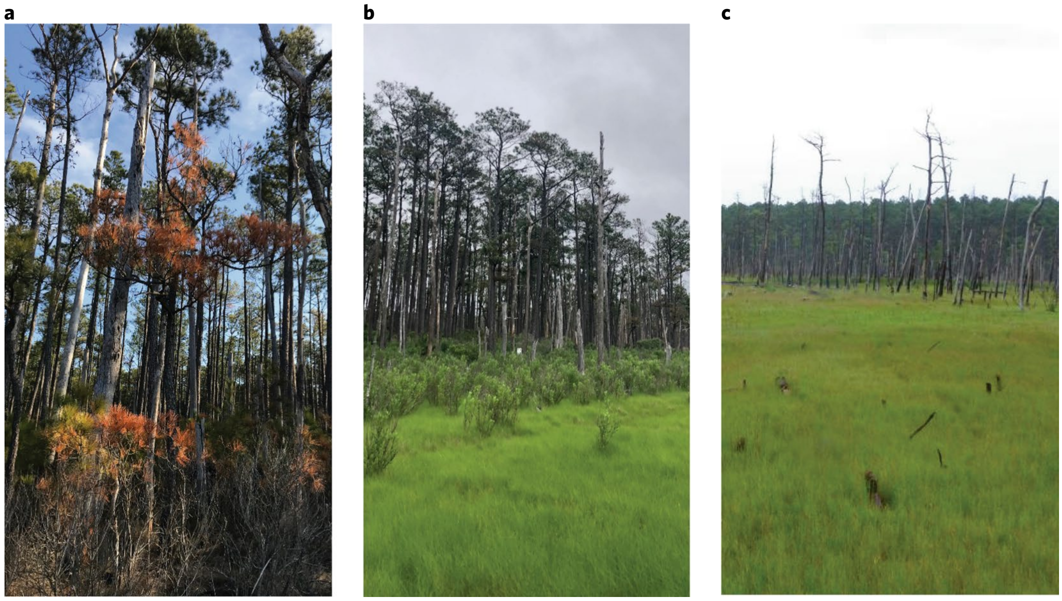

Fig. 3 | Stages of ghost forest creation. a–c, Photos show forest-to-marsh conversion in the Chesapeake Bay region (MD, USA) characterized by (**a**) death of tree saplings, (**b**) opening of canopy and invasion of *Phragmites* and shrubs, and (**c**) adult tree death and conversion to marsh, indicated by stumps in foreground and ghost forest in background. Image in **c** courtesy of Lennert Schepers, UAntwerpen.

areas of North Carolina[38,39], Italy[40], Mexico[41] and Bangladesh[42]. In Bangladesh, saltwater intrusion has salinized 10,000 km^2 of land in the last four decades, including an estimated 3,000 km^2 of arable land[42]. Bangladeshi farmers responded by increasing fertilizer applications to compensate for losses in yields, switching crops and converting 1,380 km^2 of farmland to shrimp ponds[42]. Sea level rise is forecasted to result in major losses in agricultural area over the next century in nations with agricultural production in deltaic or coastal regions (for example, 1,000 km^2 will be lost within the Pearl River Delta region of China)[43]. The Mekong Delta of Vietnam stands to be one of the most affected areas in the world, where losses in rice production threaten global food supply[44].

Processes linking sea level and land conversion

Dead trees underlain by wetland vegetation are a striking final indicator of uplands that have been displaced by sea level rise and saltwater intrusion (Fig. 3). However, the creation of ghost forests and the wholesale reorganization of ecosystems begins with more subtle changes that can be anticipated with a deeper understanding of the ecological processes that link sea level rise and land conversion. In the early stages of groundwater salinization, live trees may exhibit reduced sap flow[45] and annual growth[46,47], although reduced growth is not always observed[34,48]. During the next phase of ghost forest formation, forest distress becomes more visible. Young trees die conspicuously and tree recruitment ceases[30,46] (Fig. 3a). Because recruitment ceases prior to the death of mature trees[30,46,48], tree age distributions skew towards older trees at lower elevations[36,46], and relict trees stand as ghost forests in-waiting[18]. Salt-tolerant species establish in the understory as adult trees die[30], aided by increased light penetration and seed delivery from storm wrack deposits[49]. Shrubs often dominate the transition from forest to tidal wetland[18,21,50] (Fig. 3b). Of the 148 km^2 of converted forest land in Big Bend, Florida, 55% converted to marsh while 45% converted to a shrub-dominated habitat[17] that persisted for 20 years[18]. These areas may be particularly persistent in formerly agricultural areas, where land is graded flat during cultivation. Finally, dead tree trunks and stumps persist in tidal marshes for decades, a lasting remnant of the forests displaced by sea level rise and saltwater intrusion (Fig. 3c).

Upland ecosystem mortality is driven by the synergistic impacts of salinity and inundation, which are more challenging for plants than either stress alone[21,51–53]. Generally, plants that tolerate flooding are more resistant to low-level salinity stress[21]. Variation in stress tolerances between plant species can explain differences in the rate of transition of different forest types. For example, in Delaware Bay, Atlantic white cedar (*Chamaecyparis thyoides*) forests died back at faster rates than hardwood forests (typical species: red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*)). Eastern red cedar (*Juniperus virginiana*) is among the most tolerant tree species; the species outlasted loblolly pine (*Pinus taeda*), winged elm (*Ulmus alata*) and Florida maple (*Acer floridanum*) during forest dieback in Florida[54]. Trees and crops are most vulnerable to salinity stress during germination and as seedlings[51,55,56]. Mortality of relatively salt-tolerant tree seedlings occurs when salinity exceeds about 5 ppt (ref. [57]), and most crops cannot tolerate sustained salinities over 2 ppt (refs. [58,59]).

The transition of uplands to wetlands can be either gradual or punctuated by disturbance events, such as hurricanes, fires and insect outbreaks. Pulses of high salinity water during storms often trigger mortality[60,61]. Although storm waters recede in hours, salinity effects can linger for years to decades in the groundwater[62,63], and individual storms have lasting impacts on tree growth[47]. Storm floods can reach tens of kilometres inland and are accompanied by wind, erosion and wrack disturbances. Correspondingly, shifts in upland land cover occur suddenly, when storm-related disturbance destroys an upland ecosystem[61]. In the absence of major disturbance, change may occur more gradually, as elevated groundwater salinities slowly take their toll on a plant community that is intolerant to salinity. Moreover, the impact of storms increases with sea level rise, leading to the progressive inland retreat of upland ecosystems over time[15]. Terrestrial water budgets can also affect the rate of change, as saltwater intrusion resulting from sea level rise is exacerbated by drought[54], surface and groundwater withdrawals[41], and hydrological connectivity from dams, ditching and canals[64].

Ecosystem transitions affect the provision of ecosystem services, though the exact nature of these shifts varies based on trade-offs in services between upland and wetland ecosystems[13,65]. Tidal wetlands exhibit much higher areal rates of carbon sequestration and storage than terrestrial environments[7]. Therefore, the conversion of forests and croplands to tidal wetlands will increase total carbon sequestration of a region, provided that gains are not offset by concurrent losses in tidal wetland area (see 'Implications for the survival of adjacent wetlands'). Similarly, upland conversion of agricultural lands (a nutrient source to adjacent waterways and estuaries[66]) to tidal wetlands (a nutrient sink[12]) should ultimately increase nutrient uptake. During transition, however, salinization of uplands can result in short-lived[21] releases of massive amounts of legacy nutrients that have accumulated in cultivated soils over prior decades. In North Carolina, saltwater intrusion into former farmland is predicted to release 18×10^6 kg of ammonium, or approximately half the annual ammonium flux of the Mississippi River to the Gulf of Mexico[39]. In Maryland, high releases of phosphate occur during saltwater intrusion into agricultural land[67]. These nutrient releases contribute to coastal eutrophication and associated algal blooms and dead zones[68].

Upland conversion may reduce biodiversity provisioning, as wetland migration represents an opportunity for invasive species expansion. In Delaware Bay, 30% of converted forest area became native tidal marsh habitat, while 60% became dominated by the invasive common reed (*Phragmites australis*)[16]. The conversion of uplands to the invasive common reed during ghost forest formation is of particular concern for Atlantic tidal marsh endemic species with narrow habitat requirements, such as the diamondback terrapin (*Malaclemys terrapin*)[69] and the saltmarsh sparrow (*Ammodramus caudacutus*), predicted to go extinct by 2030 due to sea level rise[70]. In Florida, the invasive Brazilian pepper (*Schinus terebinthifolius*) inhabits a similar niche to the common reed in that it outcompetes native species in the ecotone and exhibits wide salinity tolerance, and is also expected to spread during upland conversion[18,71]. Thus, sea-level driven land conversion will affect both the composition and function of the coastal landscape.

Implications for the survival of adjacent wetlands

The conversion of uplands to wetlands is a primary mechanism for wetland survival in the face of sea level rise, and counterintuitively leads to predictions that wetlands may expand with sea level rise under certain conditions[2,8,17]. At the most basic level, wetlands must migrate to higher elevations faster than they erode laterally and drown vertically in order to maintain their size[32]. Although marshes and mangroves build soil vertically, there are limits to the rate of sea level rise that wetlands can survive in place. Numerical models predict that maximum possible vertical accretion rates overlap with the range of predicted sea level rise rates for 2100 (generally 5–30 mm yr^{-1})[72], and observations of wetland drowning indicate that these limits have already been exceeded in some places[73,74]. When these threshold rates of sea level rise are exceeded, wetlands must migrate laterally into submerging uplands to survive.

Historical observations and simple analyses of coastal topography indicate that upland drowning has the potential to create large areas of new wetlands that are comparable in size to existing wetlands. For example, historical maps of the Chesapeake Bay suggest that approximately 1/3 of all marshland today formed as a result of migration into drowning uplands since the mid-nineteenth century, and that upland drowning compensated for historical erosion of marshes in the region[19]. On the Florida Gulf Coast, marsh formation in submerging uplands has outpaced historical loss, and led to net marsh expansion[17]. More work is needed to infer how future sea level rise will alter the timescales associated with wetland loss and migration, but these historical trends together with observations of ghost forests underlain by marsh vegetation, suggest that wetland migration can occur on the decadal–century timescales relevant to wetland loss. Across the conterminous United States, there are ~26,000 km^2 of saline wetlands[75], and sea level rise of 1.2 m would inundate ~12,000–49,000 km^2 of uplands[7]. Thus, the formation of new wetlands in drowning uplands has the potential to compensate for even large losses of existing wetlands.

Rates of marsh migration generally increase in parallel with sea level rise[20,35,37], but existing marsh is relatively resistant to sea level rise because enhanced flooding leads to faster vertical accretion[76]. Upland migration, therefore, allows marshes to potentially expand, rather than contract, in response to sea level rise[13,76]. Numerical modelling suggests that marshes adjacent to gently sloping uplands will expand under moderate increases in sea level rise, followed by inevitable contraction when high rates of sea level rise lead to widespread drowning of existing marshland[76]. The particular rate of sea level rise that leads to a transition from marsh expansion to marsh contraction depends principally on the slope of adjacent uplands[32], anthropogenic barriers to migration[77], and factors such as tidal range and sediment supply that control the resistance of existing marsh to sea level rise and edge erosion[24]. Nevertheless, numerical models that consider both dynamic marsh accretion and the potential for marshes to migrate inland suggest that many marshes will expand under moderate rates of sea level rise, and then contract under higher rates[13,76,78,79] (Fig. 4).

These types of simple landscape models based on topography and land use have thus far assumed a binary response of land types to sea level rise (for example, complete conversion of inundated forestland and no conversion of inundated urban land; see 'Opportunities and barriers to coastal submergence'), and that wetlands will migrate into uplands as soon as they become sufficiently inundated (for example, without ecological lags; see 'Processes linking sea level and land conversion'). Other work identifies additional caveats. For example, the response of low-lying land to sea level rise will vary both within and across regions[19,80–82], where regions with steep upland topography and anthropogenic barriers to migration may see near complete loss of marshes[81]. In places where marshes persist, the proportion of flood-tolerant vegetation types will increase[78,79,81] and newly created wetlands may themselves be vulnerable to sea level rise[10]. Salt water intrusion into freshwater soils increases organic matter decomposition rates so that soil elevation loss could limit wetland migration and/or survival in submerging forests with organic-rich soils[4,28]. Finally, interactions between multiple facets of climate change and socioeconomic factors (for example, changing hurricane frequencies and flood protection strategies) may influence sea-level-driven land conversion in unanticipated ways. Nevertheless, recent global modelling suggests wetland migration into submerging uplands is the single biggest factor influencing wetland area through time, and that global wetland area could increase by up to 60% by 2100 for a 1.1 m sea level rise (Fig. 5)[83].

Opportunities and barriers to coastal submergence

Although there is abundant land that could be inundated by sea level rise, anthropogenic structures and coastal development may prevent land conversion in many regions of the world. Ghost forests, abandoned farmland and other indicators of land submergence are most common in the south-eastern and mid-Atlantic United States, in part because these coastal regions are largely rural and devoid of large, systematic flood control structures outside of major cities. In contrast, ghost forests are rare in western Europe and China because extensive seawalls and dykes protect uplands from sea level rise and coastal flooding[31,84]. Large flood control structures are less common in the United States, but migration of wetlands into submerging uplands may instead be prevented by local barriers including berms, bulkheads, roads, ditches with floodgates and impervious surfaces[80,85]. For example, 42% of all land less than 1 m above spring high water is currently developed along the United States Atlantic coast, whereas less than 10% is currently protected against development[86].

Human impacts are typically perceived as barriers to wetland migration, but people also facilitate sea-level driven land

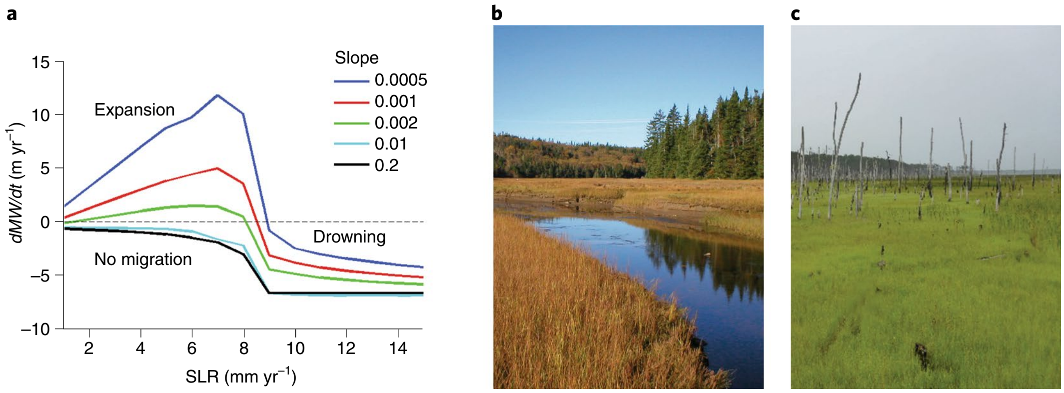

Fig. 4 | Effect of topographic slope and human impacts on marsh size. a, Model simulations showing change in marsh width (*dMW/dt*) for different rates of sea level rise (SLR) and slopes of adjacent land (coloured lines). For gently sloping, natural coasts, marshes expand with increasing SLR rates until a threshold rate is exceeded. Marshes inevitably decline in size when uplands are steep or protected by anthropogenic barriers (black line represents a case with no migration). **b**, Steep uplands prevent landward marsh migration and favour small and/or shrinking marshes (Bay of Fundy, Nova Scotia, Canada). **c**, Gently sloping uplands facilitate landward marsh migration and favour large and/or expanding marshes (Chesapeake Bay, MD, USA). Panel **a** reproduced from ref. [76], John Wiley & Sons. Image in **c** courtesy of Lennert Schepers, UAntwerpen.

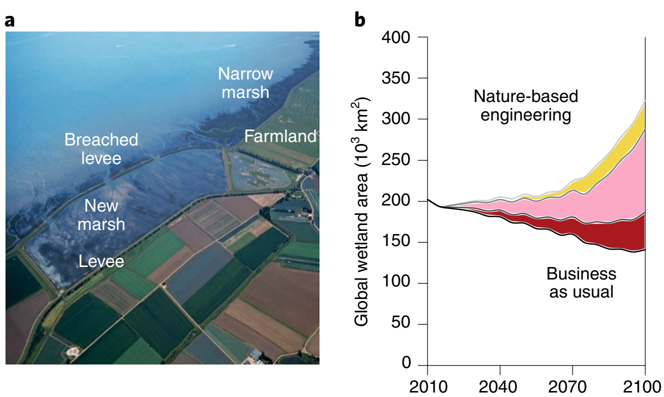

Fig. 5 | Effect of flood defence strategy and land conversion on wetland size. a, Nature-based engineering to create marsh in front of leveed agricultural fields in the Wash Estuary, UK. The levee was intentionally breached in 2002, marsh vegetated colonized naturally, and now protects the more inland levee. **b**, Modelled global wetland area for the Intergovernmental Panel on Climate Change RCP 8.5 sea-level rise scenario. Colours represent different flood-defence scenarios, where the model assumes no landward wetland migration where the projected human population in the 100-year floodplain exceeds 5–20 people km^{-2} (red, reflecting business as usual), 20–150 people km^{-2} (pink), and 150–300 people km^{-2} (yellow, reflecting extensive nature-based engineering). Credit: Anglian Coastal Monitoring Programme (**a**). Panel **b** adapted from ref. [83], Springer Nature Ltd

conversion, and the net-impact can be difficult to discern. Historical marsh migration rates likely decrease with the degree of coastal development in the Chesapeake Bay region, but the relationship is weak and highly site specific[19,85]. Elsewhere, suburban lawns convert to marsh as quickly as adjacent forests[37], and reclaimed agricultural areas are particularly susceptible to salinization and land conversion[40]. Wetland restoration projects commonly remove berms to reconnect agricultural fields and other land types with tidal flooding[87,88]. Barrier removal has mixed effects. Since barriers enhance land subsidence and limit sedimentation, the land behind the barriers may require substantial restoration to be suitable for wetlands[87–90]. Indeed, accidental or poorly planned breaches after significant subsidence can rapidly drown wetlands[89]. In other cases, large levees are carefully removed or moved further inland to create wetlands that contribute to natural flood protection, in a concept known as nature-based engineering or managed realignment[84,90] (Fig. 5a). Finally, human actions sometimes unintentionally accelerate land submergence by increasing rates of saltwater intrusion via groundwater withdrawal and/or subsidence[4,91], or building canals that input saltwater[64]. Nevertheless, anthropogenic barriers block substantial wetland migration today in many regions[80,81], and wholesale submergence and abandonment of low-lying coastal land is unlikely because in most cases the cost of conventional flood control structures is far less than the cost of economic damages associated with flooding[92].

The United States Gulf Coast represents an interesting case study for how population growth and flood-control structures might interact to determine the extent of upland land conversion (Fig. 6a). This region contains approximately 50% of United States saline wetlands[75], high variability in human population densities and rates of relative sea level rise, and the most extensive flood protection system in the United States[77,82,93]. Analysis of topography and land use across the entire Gulf Coast indicate that 39,000 km^2 of land is vulnerable to submergence under a 1.2 m sea level rise, and that barriers projected under population growth will prevent conversion in an additional 6,000 km^2 (ref. [77]). This work highlights that there are strong spatial gradients in both opportunities and barriers to migration within the Gulf Coast region, such that the absence of land conversion in highly urbanized areas may result in large reductions in local wetland area[77,82]. Nevertheless, these analyses have three fundamental implications at the regional scale. First, current and projected barriers to wetland migration are small relative to the total amount of land available for migration (~15%), such that the total area of land that will be inundated will be large regardless of protection of urban areas. Second, only 35% of land available for migration is currently owned by government and private conservation organizations[77], suggesting that most land conversion will take place on private land and depend on local decisions not fully considered in analyses based on urbanization and levee construction. Finally, the area of land potentially available for saline wetland migration (39,000 km^2)[77] is nearly three times the area of land currently occupied by saline wetlands on the Gulf Coast (13,600 km^2)[75] and larger than the current extent of saline wetlands in the entire conterminous United States (26,000 km^2). Together, these observations emphasize that sea-level-driven land conversion will be

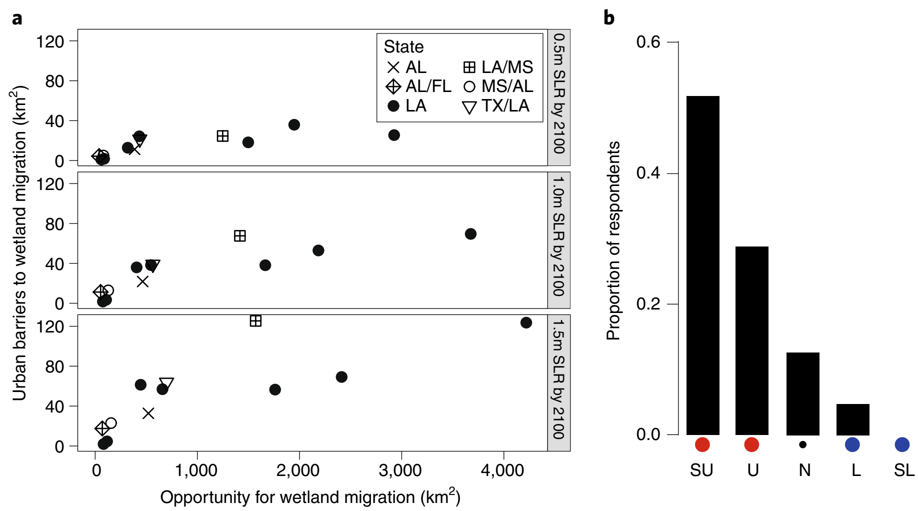

Fig. 6 | Land conversion in the face of human barriers. a, Projected urban barriers and opportunities for wetland migration for US Gulf Coast estuaries[82]. Opportunities for wetland migration are an order of magnitude greater than urban barriers to migration in each estuary, and potential wetland migration increases with increasing sea level rise (SLR) scenario (top to bottom). **b**, Preferences of 1,002 landowners regarding conservation easements to allow marsh migration in the north-eastern United States. Responses are strongly unlikely (SU), unlikely (U), neutral (N), likely (L) and strongly likely (SL). Adapted from ref. [82], British Ecological Society (**a**); ref. [11], PNAS (b).

widespread and a fundamental determinant of wetland area at regional scales, even in the presence of urban barriers.

Moving beyond static models based on topography and land use is difficult because adaptation to coastal flooding depends not only on the rate of sea level rise, but also on a variety of human decisions influenced by complex socio-economic factors. There are strong landowner attitudes against wetland migration[11] (Fig. 6b), growing coastal populations[94], and it is economically rational to build flood defence structures for most of the world's coasts[92]. On the other hand, rising sea level and energy costs suggest that building and maintenance costs will increase through time, such that conventional engineering may be unsustainable in the long term[95,96]. Rising costs may especially prevent engineering solutions in developing countries and poorer regions[3]. Interestingly, highly developed deltaic regions, including the Mississippi, Rhone and East Asian deltas, are the most vulnerable to rising energy costs[96]. Therefore, regions with large areas of currently protected land are also the most likely to incorporate nature-based engineering approaches that would allow submergence of some land for the first time in centuries[84,90].

While the factors that contribute to flood defence are ultimately quite complex, levees generally occur where population densities in the 100-year coastal flood plain exceed 20 people per km^2, and global modelling suggests this threshold represents a key determinant of wetland fate under sea level rise and population growth[83]. Lower population thresholds (reflecting nature-based engineering) lead to wetland expansion, whereas higher thresholds (reflecting conventional engineering) lead to wetland contraction (Fig. 5b). Therefore, decisions to defend or abandon portions of the coast represent a fundamental, if not primary, determinant of coastal submergence and the migration of wetlands into uplands[24,83].

Recommendations for future research

Our Review suggests that widespread sea-level driven submergence of low-lying land will continue in the future, even under scenarios of coastal population growth and large-scale defence of urban areas. However, land conversion will largely take place on privately owned land[82,86], where landowner attitudes and adaptation efforts suggest local resistance[70]. We, therefore, pose the following questions to guide future research and land management decisions.

First, is land-conversion inevitable on privately owned, rural land? Research in the last five years has identified and mapped large barriers to wetland migration, such as urban land and publically owned levees at regional scales[77,80–82]. However, the majority of vulnerable land is located on private property in rural areas[38,82,87]. Future research should investigate the efficacy of local and privately maintained barriers, such as berms, ditches and secondary roads, and the probability and consequences of barrier failure. Barriers influence the adaptive capacity of coastal systems by enhancing land subsidence and limiting sedimentation. Therefore, this research should quantify key thresholds in the timing of barrier removal/failure that minimize both the cost of abandoned land and the cost of restoration. Government and conservation organizations are increasingly preserving wetland 'migration corridors' but understanding of if and how landowners influence land submergence will help prioritize conservation efforts.

Second, can transitional land uses and nature-based engineering compensate for trade-offs between private property and ecosystem service values? Sea-level-driven land conversion leads to simultaneous loss in value for private landowners and gain in ecosystem services for the general public[13,97]. Future research should focus on whether transitional land and water management decisions, such as planting salt-tolerant crops[98], leasing land to hunt clubs, early harvest of susceptible timber lands and groundwater manipulations[4], could significantly offset economic losses and influence the function of newly forming wetlands. Future research should also consider the viability of nature-based engineering, where limited wetland migration could simultaneously enhance natural flood protection and reduce levee maintenance costs[84,91].

Finally, how can policy incentives shape the future of coastal upland conversion? There are few programs in the United States that provide assistance or recommendations to landowners affected by sea level rise, and they are harshly criticized for providing perverse subsidies[99] and benefiting repeatedly flood damaged and reconstructed properties[100]. Programs such as the United States Department of Agriculture's Conservation Reserve Program, that subsidize remediating salinity damage on farm fields, could be repurposed as instruments for adaptation to sea level rise. Regional predictions for tidal wetland habitat gain or loss should set the context for management and policy incentives to either prioritize wetland migration or upland protection[100].

In summary, our Review highlights extensive sea-level-driven land conversion, marked by ghost forests and abandoned agricultural land that represent relict features of a rapidly submerging coast. Accelerated sea level rise over the next 80 years could potentially create new wetlands equivalent in size to current ones, even under scenarios of coastal population growth and urban levee construction. These changes will happen disproportionately on rural and private lands, where efforts to prevent or promote land conversion are poorly understood. Given the extent of historical change, the magnitude of forecasted change, and an unpredictable human response, sea-level-driven land submergence is likely to lead to wholesale reorganization of coastal ecosystems and economies within this century.

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References

1. Kemp, A. C. et al. Climate related sea-level variations over the past two millennia. *Proc. Natl Acad. Sci. USA* **108**, 11017–11022 (2011).
2. Hopkinson, C. S., Lugo, A. E., Alber, M., Covich, A. P. & Van Bloem, S. J. Forecasting effects of sea-level rise and windstorms on coastal and inland ecosystems. *Front. Ecol. Environ.* **6**, 255–263 (2008).
3. Neumann, B., Vafedis, A. T., Zimmermann, J. & Nicholls, R. J. Future coastal population growth and exposure to sea-level rise and coastal flooding: a global assessment. *PLoS ONE* **10**, e0118571 (2015).
4. White, E. & Kaplan, D. Restore or retreat? Saltwater intrusion and water management in coastal wetlands. *Ecosyst. Health Sust.* **3**, e01258 (2017).
5. Horton, B. P., Rahmstorf, S., Engelhart, S. E. & Kemp, A. C. Expert assessment of sea-level rise by AD 2100 and AD 2300. *Quat. Sci. Rev.* **84**, 1–6 (2014).
6. Rasmussen, D. J. et al. Extreme sea level implications of 1.5° C, 2.0° C, and 2.5° C temperature stabilization targets in the 21st and 22nd centuries. *Environ. Res. Lett.* **13**, 034040 (2018).
7. Morris, J. T., Edwards, J., Crooks, S. & Reyes, E. in *Recarbonization of the biosphere: Ecosystems and the Global Carbon Cycle* (eds Lal, R. et al.) 517–531 (Springer, 2012).
8. Haer, T., Kalnay, E., Kearney, M. & Moll, H. Relative sea-level rise and the conterminous United States: consequences of potential land inundation in terms of population at risk and GDP loss. *Glob. Environ. Chang.* **23**, 1627–1636 (2013).
9. Milliman, J. D., Broadus, J. M. & Gable, F. Environmental and economic implications of rising sea level and subsiding deltas: the Nile and Bengal examples. *AMBIO* **18**, 340–345 (1989).
10. Bin, O. & Polasky, S. Evidence on the amenity value of wetlands in a rural setting. *Am. J. Agric. Econ.* **37**, 589–602 (2005).
11. Field, C. R., Dayer, A. A. & Elphick, C. S. Social factors can influence ecosystem migration. *Proc. Natl Acad. Sci. USA* **114**, 9134–9139 (2017).
Landowner surveys indicate resistance to incentive programs allowing for marsh migration on private property.
12. Barbier, E. B. et al. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* **81**, 169–193 (2011).
13. Feagin, R. A., Martinez, M. L., Mendoza-Gonzalez, G. & Costanza, R. Salt marsh zonal migration and ecosystem service change in response to global sea level rise: a case study from an urban region. *Ecol. Soc.* **15**, 14 (2010).
14. Shreve, F., Chrysler, M. A., Blodgett, F. H. & Besley, F. W. *The plant life of Maryland* (Johns Hopkins Press, 1910).
15. Robichaud, A. & Begin, Y. The effects of storms and sea level rise on a coastal forest margin in New Brunswick, Eastern Canada. *J. Coast. Res.* **13**, 429–439 (1997).
16. Smith, J. A. The role of *Phragmites australis* in mediating inland salt marsh migration in a mid-Atlantic estuary. *PLoS ONE* **8**, e65091 (2013).
Invasive *Phragmites* is the dominant species in submerged forests.
17. Raabe, E. A. & Stumpf, R. P. Expansion of tidal marsh in response to sea-level rise: Gulf Coast of Florida, USA. *Estuaries Coasts* **39**, 145–157 (2016).
18. Langston, A. K., Kaplan, D. A. & Putz, F. E. A casualty of climate change? Loss of freshwater forest islands on Florida's Gulf Coast. *Glob. Chang. Biol.* **23**, 5383–5397 (2017).
19. Schieder, N. W., Walters, D. C. & Kirwan, M. L. Massive upland to wetland conversion compensated for historical marsh loss in Chesapeake Bay, USA. *Estuaries Coasts* **41**, 940–951 (2018).
100,000 acres of marsh migration since 1850 in Chesapeake region.
20. Schieder, N. W. *Reconstructing coastal forest retreat and marsh migration response to historical sea level rise*. MSc thesis, College of William and Mary, Virginia Institute of Marine Science (2017).
21. Conner, W. H., K. W. Krauss & T. W. Doyle. in *Ecology of Tidal Freshwater Forested Wetlands of Southeastern United States* (Conner, W. H. et al.) 223–253 (Springer, 2007).
22. Noe, G. B., Krauss, K. W., Lockaby, B. G., Conner, W. H. & Hupp, C. R. The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands. *Biogeochemistry* **114**, 225–244 (2013).
23. Fitzgerald, D. M., Fenster, M. S., Argow, B. A. & Buynevich, I. V. Coastal impacts due to sea-level rise. *Annu. Rev. Earth Planet Sci.* **36**, 601–47 (2008).
24. Kirwan, M. L. & J. P. Megonigal, J. P. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* **504**, 53–60 (2013).
Proposes that wetland fate largely depends on how humans respond to sea level rise and influence transgression into adjacent uplands.
25. McKee, K. L., Cahoon, D. R. & Feller, I. C. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob. Ecol. Biogeogr.* **16**, 545–556 (2007).
26. Rodriguez, A. B. et al. Oyster reefs can outpace sea-level rise. *Nat. Clim. Change* **4**, 493–497 (2014).
27. Sallenger, A. H. S., Doran, K. S. & Howd, P. A. Hotspot of accelerated sea-level rise on the Atlantic coast of North America. *Nat. Clim. Change* **2**, 884–888 (2012).
28. Craft, C. B. Tidal freshwater forest accretion does not keep pace with sea level rise. *Glob. Change Biol.* **18**, 3615–3623 (2012).
29. Ross, M. S., O'Brien, J. J. & Sternberg, S. L. Sea-level rise and the reduction in pine forests in the Florida Keys. *Ecol. Appl.* **4**, 144–156 (1994).
30. Williams, K. et al. Sea-level rise and coastal forest retreat on the west coast of Florida, USA. *Ecology* **80**, 2045–2063 (1999).
Recruit failure precedes mortality of adult trees in retreating coastal forests.
31. Ma, Z. J. et al. Rethinking China's new great wall. *Science* **346**, 912–914 (2014).
32. Brinson, M. M., Christian, R. R. & Blum, L. K. Multiple states in the sea-level induced transition from terrestrial forest to estuary. *Estuaries Coasts* **18**, 648–659 (1995).
Changes in marsh size determined by the balance between erosion and forest retreat.
33. Wasson, K., Woolfolk, A. & Fresquez, C. Ecotones as indicators of changing environmental conditions: rapid migration of salt marsh-upland boundaries. *Estuaries Coasts* **36**, 654–664 (2013).
34. Field, C. R., Gjerdrum, C. & Elphick, C. S. Forest resistance to sea-level rise prevents landward migration of tidal marsh. *Biol. Conserv.* **201**, 363–369 (2016).
35. Hussein, A. H. Modeling of sea-level rise and deforestation in submerging coastal ultisols of Chesapeake Bay. *Soil Sci. Soc. Am. J.* **73**, 185–196 (2009).
36. Clark, J. S. Coastal forest tree populations in a changing environment, Southeastern Long Island, New York. *Ecol. Monogr.* **56**, 259–277 (1986).
37. Anisfeld, S. C., Cooper, K. R. & Kemp, A. C. Upslope development of a tidal marsh as a function of upland land use. *Glob. Chang. Biol.* **23**, 755–766 (2017).
Marsh vegetation develops rapidly in submerging suburban lawns and is not inhibited by mowing.
38. Bhattachan, A. et al. Sea level rise impacts on rural coastal social-ecological systems and the implications for decision making. *Environ. Sci. Policy* **90**, 122–134 (2018).
39. Ardón, M., Morse, J. L., Colman, B. P. & Bernhardt, E. S. Drought-induced saltwater incursion leads to increased wetland nitrogen export. *Glob. Chang. Biol.* **19**, 2976–2985 (2013).
40. Da Lio, C., Carol, E., Kruse, E., Teatini, P. & Tosi, L. Saltwater contamination in the managed low-lying farmland of the Venice coast, Italy: an assessment of vulnerability. *Sci. Total Environ.* **533**, 356–369 (2015).
41. Vanderplank, S., Ezcurra, E., Delgadillo, J., Felger, R. & McDade, L. A. Conservation challenges in a threatened hotspot: agriculture and plant biodiversity losses in Baja California, Mexico. *Biodivers. Conserv.* **23**, 2173–2182 (2014).
42. Khanom, T. Effect of salinity on food security in the context of interior coast of Bangladesh. *Ocean Coast. Manag.* **130**, 205–212 (2016).
43. Kang, L., Ma, L. & Liu, Y. Evaluation of farmland losses from sea level rise and storm surges in the Pearl River Delta region under global climate change. *J. Geogr. Sci.* **26**, 439–456 (2016).
44. Wassmann, R., Hien, N. X., Hoanh, C. T. & Tuong, T. P. Sea level rise affecting the Vietnamese Mekong Delta: water elevation in the flood season and implications for rice production. *Climatic Chang.* **66**, 89–107 (2004).
45. Teobaldelli, M., Mencuccini, M. & Piussi, P. Water table salinity, rainfall and water use by umbrella pine trees (*Pinus pinea* L.). *Plant Ecol.* **171**, 23–33 (2004).
46. Begin, Y. The effects of shoreline transgression on woody plants, Upper St. Lawrence Estuary, Québec. *J. Coast. Res.* **6**, 815–827 (1990).
47. Fernandes, A., Rollinson, C. R., Kearney, W. S., Dietze, M. C. & Fagherazzi, S. Declining radial growth response of coastal forests to hurricanes and nor'easters. *J. Geophys. Res. Biogeosci.* **123**, 82–849 (2018).

48. Kirwan, M. L., Kirwan, J. L. & Copenheaver, C. A. Dynamics of an estuarine forest and its response to rising sea level. *J. Coast. Res.* **23**, 457–463 (2007).
49. Tate, A. S. & Battaglia, L. L. Community disassembly and reassembly following experimental storm surge and wrack application. *J. Veg. Sci.* **24**, 46–57 (2013).
50. Gedan, K. B. & Fernández-Pascual, E. Salt marsh migration into salinized agricultural fields: a novel assembly of plant communities. *J. Veg. Sci.* (in press).
51. Pezeshki, S. R., DeLaune, R. D. & Patrick, W. H. Jr. Flooding and saltwater intrusion: potential effects on survival and productivity of wetland forests along the US Gulf Coast. *Ecol. Manag.* **33**, 287–301 (1990).
52. Barrett-Lennard, E. G. The interaction between waterlogging and salinity in higher plants: causes, consequences and implications. *Plant Soil* **253**, 35–54 (2003).
53. Conner, W. H. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. *J. Coast. Res.* **10**, 1045–1049 (1994).
54. Desantis, L. R., Bhotika, S., Williams, K. & Putz, F. E. Sea-level rise and drought interactions accelerate forest decline on the Gulf Coast of Florida, USA. *Glob. Chang. Biol.* **13**, 2349–2360 (2007).
55. Hosseini, M. K., Powell, A. A. & Bingham, I. J. Comparison of the seed germination and early seedling growth of soybean in saline conditions. *Seed Sci. Res.* **12**, 165–172 (2002).
56. Ashraf, M. & Waheed, A. Screening of local/exotic accessions of lentil (*Lens culinaris* Medic.) for salt tolerance at two growth stages. *Plant Soil* **128**, 167–176 (1990).
57. Tolliver, K. S., Malxin, D. W. & Young, D. R. Freshwater and saltwater flooding response for woody species common to barrier island swales. *Wetlands* **17**, 10–18 (1997).
58. Katerji, N., Mastrorilli, M., Lahmer, F. Z. & Oweis, T. Emergence rate as a potential indicator of crop salt-tolerance. *Eur. J. Agron.* **38**, 1–9 (2012).
59. Tanji, K. K. & Kielen, N. C. *Agricultural drainage water management in arid and semi-arid areas* (FAO, 2002).
60. Chapman, E. L. et al. Hurricane Katrina impacts on forest trees of Louisiana's Pearl River basin. *Ecol. Manag.* **256**, 883–889 (2008).
61. Middleton, B. A. Differences in impacts of Hurricane Sandy on freshwater swamps on the Delmarva Peninsula, Mid-Atlantic Coast, USA. *Ecol. Eng.* **87**, 62–70 (2016).
62. Yu, X. et al. Impact of topography on groundwater salinization due to ocean surge inundation. *Water Resour. Res.* **52**, 5794–5812 (2016).
63. Elsayed, S. M. & Oumeraci, H. Modelling and mitigation of storm-induced saltwater intrusion: improvement of the resilience of coastal aquifers against marine floods by subsurface drainage. *Environ. Model. Soft.* **100**, 252–277 (2018).
64. Poulter, B., Goodall, J. L. & Halpin, P. N. Applications of network analysis for adaptive management of artificial drainage systems in landscapes vulnerable to sea level rise. *J. Hydrol.* **357**, 207–217 (2008).
65. Craft, C. et al. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Front. Ecol. Environ.* **7**, 73–78 (2009).
66. Jordan, T. E. & Weller, D. E. Human contributions to terrestrial nitrogen flux. *BioScience* **46**, 655–664 (1996).
67. Tully, K., Weissman, D., Wyner, W. J., Miller, J. & Jordan, T. E. Soils in transition: saltwater intrusion alters soil chemistry in agricultural fields. *Biogeochemistry* **142**, 339–356 (2019).
68. Smith, V. H. & Schindler, D. W. Eutrophication science: where do we go from here? *Trends Ecol. Evol.* **24**, 201–207 (2009).
69. Cook, C. E., McCluskey, A. M. & Chambers, R. M. Impacts of invasive *Phragmites australis* on diamondback terrapin nesting in Chesapeake Bay. *Estuaries Coasts* **41**, 966–973 (2018).
70. Field, C. R. et al. High-resolution tide projections reveal extinction threshold in response to sea-level rise. *Glob. Chang. Biol.* **23**, 2058–2070 (2017).
71. Spector, T. & Putz, F. E. Biomechanical plasticity facilitates invasion of maritime forests in the southern USA by Brazilian pepper (*Schinus terebinthifolius*). *Biol. Invasions* **8**, 255–260 (2006).
72. Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R. & Fagherazzi, S. Overestimation of marsh vulnerability to sea level rise. *Nat. Clim. Change* **6**, 253–260 (2016).
73. Lovelock, C. E. et al. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. *Nature* **526**, 559–563 (2015).
74. Crosby, S. C. et al. Salt marsh persistence is threatened by predicted sea-level rise. *Estuar. Coast. Shelf Sci.* **181**, 93–99 (2016).
75. Dahl, T. E. & Stedman, S. M. *Status and trends of wetlands in the coastal watersheds of the Conterminous United States 2004 to 2009* (US Department of the Interior, Fish and Wildlife Service & National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 2013).
76. Kirwan, M. L., Walters, D. C., Reay, W. G. & Carr, J. A. Sea level driven marsh expansion in a coupled model of marsh erosion and migration. *Geophys. Res. Lett.* **43**, 4366–4373 (2016).
77. Enwright, N. M., Griffith, K. T. & Osland, M. J. Barriers to and opportunities for landward migration of coastal wetlands with sea-level rise. *Front. Ecol. Evol.* **14**, 307–316 (2016).
Large areas of land are available for migration on the Gulf Coast, but with large geographic variability due to anthropogenic and topographic barriers.
78. Schile, L. M. et al. Modeling tidal marsh distribution with sea-level rise: evaluating the role of vegetation, sediment, and upland habitat in marsh resiliency. *PLoS ONE* **9**, e88760 (2014).
79. Cadol, D., Elmore, A., Guinn, S., Engelhardt, K. A. M. & Sanders, G. Modeled tradeoffs between developed land protection and tidal habitat maintenance during rising sea levels. *PLoS ONE* **11**, e0164875 (2016).
80. Torio, D. D. & Chmura, G. L. Assessing coastal squeeze of tidal wetlands. *J. Coast. Res.* **29**, 1049–1061 (2013).
81. Thorne, K. et al. US Pacific coastal wetland resilience and vulnerability to sea-level rise. *Sci. Adv.* **4**, eaao3270 (2018).
82. Borchert, S. M., Osland, M. J., Enwright, N. M. & Griffith, K. T. Coastal wetland adaption to sea level rise: quantifying potential for landward migration and coastal squeeze. *J. Appl. Ecol.* **55**, 2876–2877 (2018).
83. Schuerch, M. et al. Future response of global coastal wetlands to sea level rise. *Nature* **561**, 231–234 (2018).
Marsh loss is not inevitable but depends on anthropogenic barriers to marsh migration.
84. Temmerman, S. et al. Ecosystem-based coastal defense in the face of global change. *Nature* **504**, 79–83 (2013).
85. Mitchell, M., Herman, J., Bilkovic, D. M. & Hershner, C. Marsh persistence under sea-level rise is controlled by multiple, geologically variable stressors. *Ecosyst. Health Sustain.* **3**, 1379888 (2017).
86. Titus, J. G. et al. State and local governments plan for development of most land vulnerable to rising sea level along the US Atlantic coast. *Environ. Res. Lett.* **4**, 044008 (2009).
87. Gray, A., Simenstad, C. A., Bottom, D. L. & Cornwell, T. J. Contrasting functional performance of juvenile salmon habitat in recovering wetlands of the Salmon River estuary, Oregon, USA. *Restor. Ecol.* **10**, 514–526 (2002).
88. Williams, P. B. & Orr, M. K. Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. *Restor. Ecol.* **10**, 527–542 (2002).
89. Smith, J. A., Hafner, S. F. & Niles, L. J. The impact of past management practices on tidal marsh resilience to sea level rise in the Delaware Estuary. *Ocean Coast. Manag.* **149**, 33–41 (2017).
90. Temmerman, S. & Kirwan, M. L. Building land with a rising sea. *Science* **349**, 588–589 (2015).
91. Syvitski, J. P. et al. Sinking deltas due to human activities. *Nat. Geosci.* **2**, 681–686 (2009).
92. Hinkel, J. et al. Coastal flood damage and adaptation costs under 21st century sea-level rise. *Proc. Natl Acad. Sci. USA* **111**, 3292–3297 (2014).
93. Doyle, T. W. et al. Predicting the retreat and migration of tidal forests along the northern Gulf of Mexico under sea-level rise. *Ecol. Manag.* **259**, 770–777 (2010).
94. Wong, P. P. et al. in *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C. B. et al.) Ch. 5 (Cambridge Univ. Press, 2014).
95. Renaud, F. G. et al. Tipping from the Holocene to the Anthropocene: how threatened are major world deltas? *Curr. Opin. Environ. Sustain.* **5**, 644–654 (2013).
96. Tessler, Z. D. et al. Profiling risk and sustainability in coastal deltas of the world. *Science* **349**, 638–643 (2015).
97. Schmidt, J. P., Moore, R. & Alber, M. Integrating ecosystem services and local government finances into land use planning: a case study from coastal Georgia. *Landsc. Urban Plan.* **122**, 56–67 (2014).
98. Voutsina, N., Seliskar, D. M. & Gallagher, J. L. The facilitative role of *Kosteletzkya pentacarpos* in transitioning coastal agricultural land to wetland during sea level rise. *Estuaries Coasts* **38**, 35–44 (2015).
99. Neal, W. J., Pilkey, O. H., Cooper, J. A. G. & Long, N. J. Why coastal regulations fail. *Ocean Coast. Manag.* **156**, 21–34 (2018).
100. Calil, J. et al. Aligning natural resource conservation and flood hazard mitigation in California. *PLoS ONE* **10**, e0132651 (2015).
Explores conservation and buyout programs for flood prone land.

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