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Feedbacks Regulating the Salinization of Coastal Landscapes

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Abstract

The impact of saltwater intrusion on coastal forests and farmland is typically understood as sea-level-driven inundation of a static terrestrial landscape, where ecosystems neither adapt to nor influence saltwater intrusion. Yet recent observations of tree mortality and reduced crop yields have inspired new process-based research into the hydrologic, geomorphic, biotic, and anthropogenic mechanisms involved. We review several negative feedbacks that help stabilize ecosystems in the early stages of salinity stress (e.g., reduced water use and resource competition in surviving trees, soil accretion, and farmland management). However, processes that reduce salinity are often accompanied by increases in hypoxia and other changes that may amplify saltwater intrusion and vegetation shifts after a threshold is exceeded (e.g., subsidence following tree root mortality). This conceptual framework helps explain observed rates of vegetation change that are less than predicted for a static landscape while recognizing the inevitability of large-scale change.

1. INTRODUCTION

Sea-level rise (SLR) is driving the landward movement of seawater into freshwater and terrestrial portions of the coastal landscape in a process known as saltwater intrusion (SWI). The impact of SWI on aquifers used for drinking water and irrigation has been studied for decades (Barlow & Reichard 2010, Werner et al. 2013), but an understanding of how shallow seawater intrusion affects coastal ecosystems is only beginning to emerge. SWI represents the leading edge of SLR, often preceding tidal inundation and active shoreline transgression and influencing landscapes far from the coast (Hein & Kirwan 2024, Tully et al. 2019a). Increasing salinity causes the stress and eventual mortality of a variety of coastal plants, with ghost forests and abandoned agricultural fields representing prominent visual indicators of ecosystem change (Kirwan & Gedan 2019) (**Figure 1**).

SWI is leading to vegetation mortality in a variety of natural and managed coastal ecosystems, including upland forests (Kirwan & Gedan 2019), wetland forests (White et al. 2021), mangroves (Sippo et al. 2018), agricultural fields (Fagherazzi et al. 2019), and lawns (Anisfeld et al. 2017). The extent of the SWI and its impact on inland ecosystems is controlled by several processes, including the position of sea level relative to land and the water table; the occurrence of storms, tides, and drought; and the influence of humans on water use and hydrologic connectivity (Tully et al. 2019a). Although vegetation mortality is globally distributed (McDowell et al. 2022), rates of ecosystem change tend to be fastest in regions with rapid rates of relative SLR and gently sloping topography, where small changes in sea level lead to salinization of large areas (Chen & Kirwan 2022). The Atlantic and Gulf of Mexico coasts of the United States are hotspots of forest loss, and rivers in Southeast Asia are hotspots of reduced crop production (**Figure 2**). Accelerating rates of SLR are driving increased rates of forest mortality (Schieder & Kirwan 2019) and displacing climate as the dominant factor influencing forest growth in the lowest-elevation portions of the terrestrial landscape (Chen & Kirwan 2022, S. Hall et al. 2022). The ecological impacts of SWI have large ramifications for coastal carbon cycling (Kirwan et al. 2023, Warnell et al. 2022), the provisioning of ecosystem services (Craft 2012, Feagin et al. 2010), and the vitality of rural communities (O'Donnell et al. 2024, Van Dolah et al. 2020). Therefore, accurate predictions of the impact of SWI on coastal ecosystems are needed.

The impacts of SLR and SWI on the terrestrial landscape are typically modeled according to simple, progressive inundation of a passive landscape where topography does not change and ecosystems do not adapt (Molino et al. 2022, Osland et al. 2022, Schuerch et al. 2018). This bathtub approach leads to predictions of widespread conversion of uplands to wetlands (Molino et al. 2022) and the salinization of freshwater ecosystems (Herbert et al. 2015, Osland et al. 2022), including loss of farms (Mondal et al. 2023) and forestland (White et al. 2021). In contrast to assumptions of a passive landscape, many coastal ecosystems respond to SLR with feedbacks that mitigate or amplify their vulnerability. Two-way couplings between biotic growth and sediment transport allow marshes, mangroves, and oyster reefs to build vertically with SLR up to some threshold rate, beyond which ecosystems collapse (Kirwan & Megonigal 2013, Saintilan et al. 2023). Humans modify natural processes in ways that alter coastal vulnerability (e.g., Armstrong & Lazarus 2019). These natural and anthropogenic feedbacks interact in complex ways, and characteristics

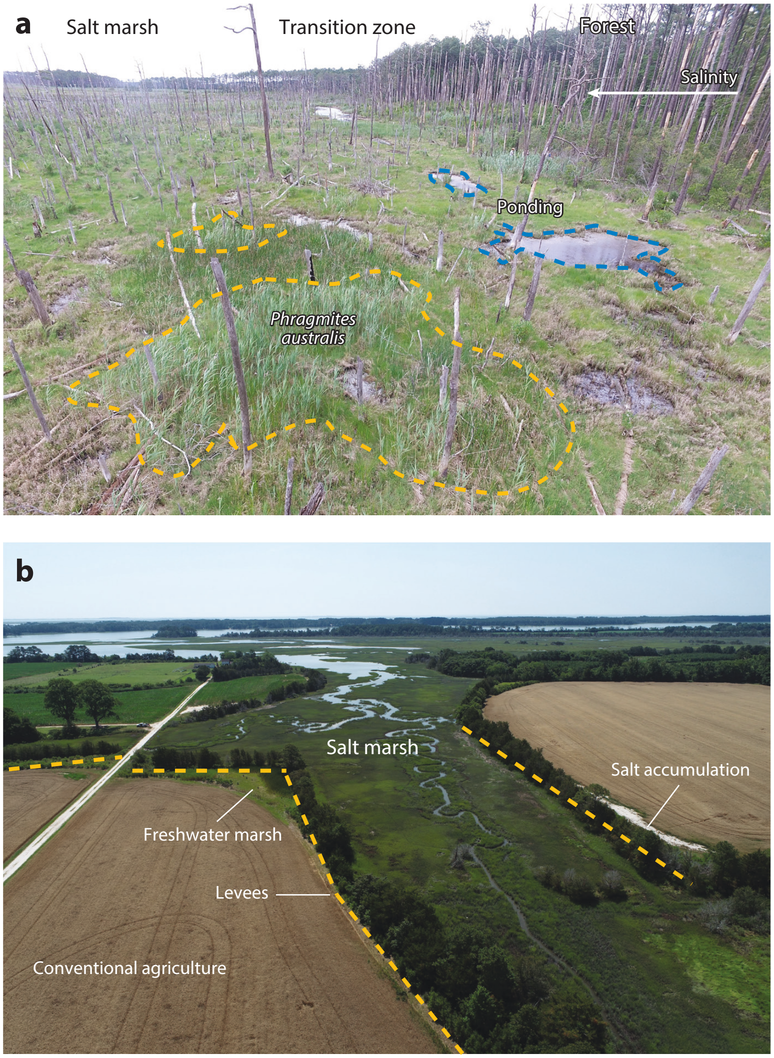


Figure 1

Photographs of salt-impacted forestland and farmland. (*a*) Transition from forest to salt marsh in Maryland, USA. The transition follows a progressively increasing salinity gradient from right to left. The transition zone is characterized by dead trees (ghost forest), invasive *Phragmites australis* (*yellow dashed lines*), and ponding (*blue dashed lines*). *P. australis* invasion and ponding may slow and enhance the pace of SWI, respectively. (*b*) Agricultural field experiencing SWI in Virginia, USA. Small levees (*yellow dashed lines*) designed to prevent tidal inundation and salt accumulation have restricted freshwater drainage and created a freshwater marsh. Abbreviation: SWI, saltwater intrusion. Photos provided by Tyler Messerschmidt.

of coastal ecosystems and landforms often lag behind changes in rates of SLR for decades to centuries (Kirwan & Murray 2008, Mariotti & Hein 2022). Only approximately half of coastal forests in the mid-Atlantic SLR hotspot retreated upslope between 1984 and 2021 (Chen & Kirwan 2024), suggesting that similar feedbacks may be at work in the terrestrial portion of the coastal landscape.

This review proposes several feedbacks that govern SWI and its impact on coastal landscapes. The first half considers hydrologic and geomorphic feedbacks that determine the pace and extent

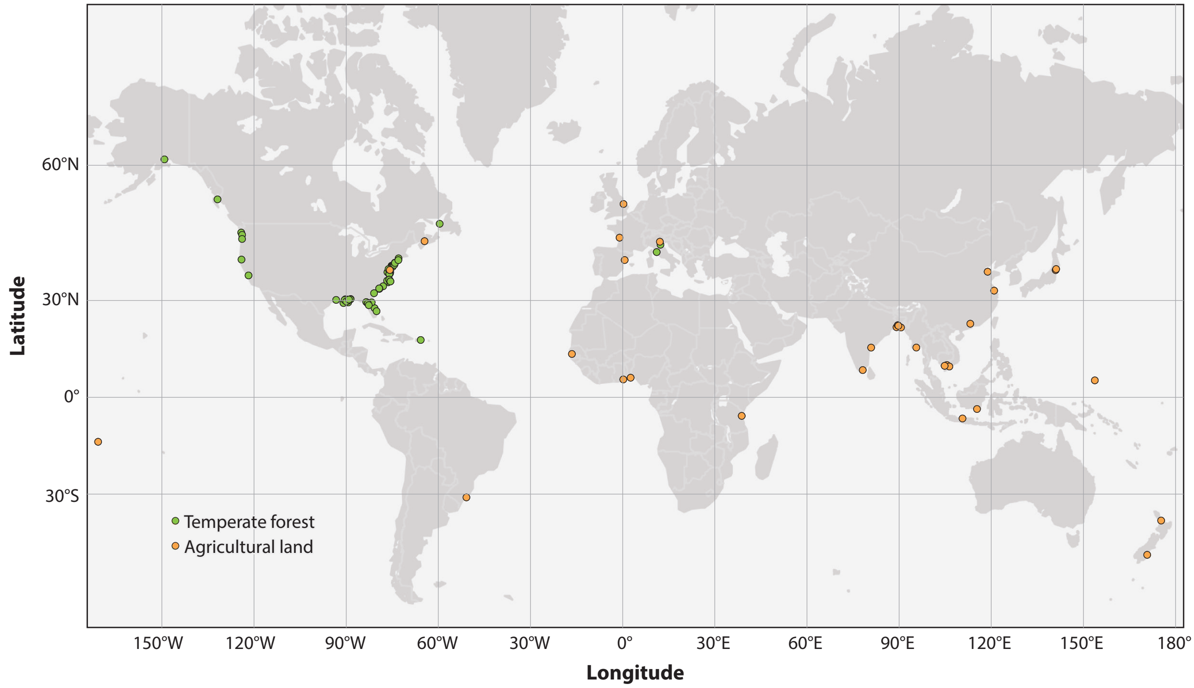


Figure 2

Global distribution of SWI into temperate forests (*green*) and agricultural land (*orange*) as reported in the literature (for details on each location, see the **Supplemental Data**). Data for temperate forests are focused on coastal ghost forests but in some cases may not be linked directly to SWI. Data for agricultural land focus on crop stress related to SLR and coastal flooding where the shallow, root-zone feedbacks discussed in this review are most likely to operate. Efforts were made to exclude examples related to irrigation from surface water and aquifers, though causation was difficult to determine. The dataset is not comprehensive, as SWI is likely occurring elsewhere but was not included due to limited research in some regions, private land ownership, and human impacts that obscure its effect. Abbreviations: SLR, sea-level rise; SWI, saltwater intrusion. Figure updated from McDowell et al. (2022) (CC BY 4.0) to include salinized agricultural land.

Supplemental Material >

of SWI; the second half considers the biotic and anthropogenic feedbacks that determine how SWI influences ecosystem change, with an emphasis on the fate of coastal forests and farmland. In each section, we consider negative and positive feedbacks that stabilize and amplify sea-level-driven SWI, respectively. We hypothesize that the net impact of these feedbacks is to slow the impact of SWI on coastal ecosystems, so that predictions based on passive responses may overestimate actual changes to the coastal landscape. However, we also hypothesize that negative feedbacks are most impactful in early stages of SWI and identify research priorities to help determine when and where tipping points may occur.

2. HYDROLOGIC FEEDBACKS

SWI into coastal ecosystems is determined by the balance between saline ocean water and fresh groundwater that together influence soil and groundwater salinity distributions. Although salinity distributions depend on regional hydrologic settings (Michael et al. 2013), shallow SWI often occurs from the surface—a result of flooding during high tide and storm events. Floodwater infiltrates the unsaturated zone and reaches the water table, salinizing shallow groundwater. SWI can also occur from subsurface pathways. Sea-level-driven increases in both salinity and soil moisture (hypoxia) cause stress and mortality of terrestrial vegetation (McDowell et al. 2022), leading to extensive migration of wetlands into uplands (Fagherazzi et al. 2019, Kirwan & Gedan 2019) and changes in the water balance of coastal soils (Mollema et al. 2012). Although ecohydrologic feedbacks involve both soil saturation and salinity, we focus on salinity as the driver of vegetation change, assuming that vegetation is more tolerant of inundation by freshwater than by saltwater (Krauss et al. 2009, Williams et al. 1999).

In the absence of hydrologic feedbacks, the rate of the inland movement of salt is expected to occur in proportion to SLR. As mean sea level and mean high-water elevation increase, the salt front on the land surface moves inland at the rate of SLR divided by the topographic slope. If the fresh groundwater table is static in response to SLR, the subsurface freshwater–saltwater interface would move upward and landward to a position governed by the aquifer permeability and density difference between fresh and saline groundwater. In theory, this density difference would result in the movement of the interface 40 times faster than the magnitude of SLR (Post et al. 2018) in coastal areas with limited topographic relief (Michael et al. 2013).

2.1. Stabilizing Feedbacks

An increase in the elevation of the groundwater table driven by SLR leads to two negative feedbacks that potentially reduce salinization. First, water-table rise reduces the thickness of the unsaturated zone (**Figure 3*a*,*b***), which limits vertical infiltration of saline floodwater during storms and high tides because there is less soil pore volume available to be filled (**Figure 3*c***). As a result, more of the floodwater is rejected recharge that drains off the landscape when surface waters recede, and a lower salt mass is introduced to the soil zone, therefore reducing tree stress

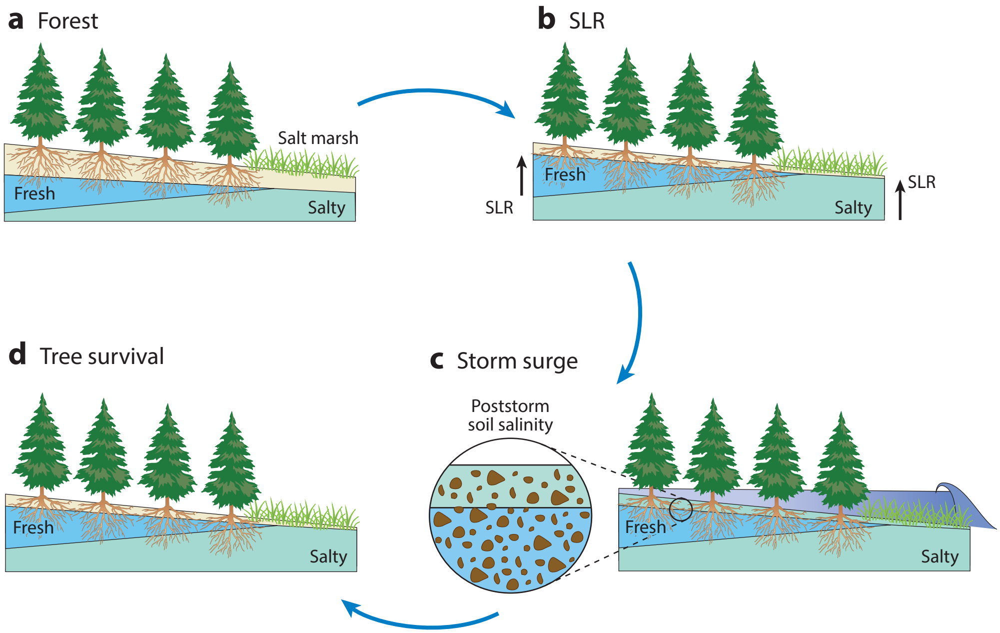


Figure 3

Potential negative feedback between SLR and storm surge that stabilizes the impact of SWI. (*a*) A coastal forest bordering a salt marsh is characterized by a large unsaturated zone (*beige*) that is prone to salinization during storm surge. (*b*) SLR leads to an increase in the height of the fresh groundwater table (*blue*) and a reduction in the thickness of the unsaturated zone. (*c*) During a storm surge, the higher groundwater table limits salt infiltration because the pore space is already occupied by groundwater (*inset*). (*d*) Reduced salinization favors tree survival. Abbreviations: SLR, sea-level rise; SWI, saltwater intrusion.

(Cantelon et al. 2022, Chui & Terry 2012, Liu & Tokunaga 2020) (**Figure 3*d***). Second, water-table rise reduces the inland movement of the subsurface freshwater–saltwater interface because extra freshwater prevents saline water from rising from below. In this scenario, a rising water table results in minimal inland movement of the interface and would tend to enhance the persistence of vegetation adapted to freshwater in settings with sufficient topographic relief and rainfall (Michael et al. 2013).

2.2. Uncertain or Conditional Feedbacks

Vegetation has a strong capacity to affect the balance between water and salt at the terrestrial–aquatic interface wherever plants are significant water users (Schlesinger & Jasechko 2014). Hydrologic feedbacks caused by vegetation shifts are complex and can either amplify or stabilize salinization. Mortality of upland vegetation tends to reduce transpiration (Duberstein et al. 2020, Krauss & Duberstein 2010) but increase evaporation due to a loss of canopy cover (S. Hall et al. 2022, Whitcraft & Levin 2007). At the same time, encroachment of marsh vegetation into the retreating forest will relatively increase transpiration and reduce evaporation. If these two processes—woody plant loss and marsh migration—result in a net increase in evapotranspiration, then reductions in soil saturation and water-table elevation could lead to increasing salt infiltration during floods and increased evapoconcentration of salt (Shen et al. 2023, Yu et al. 2021). This would promote a positive feedback with vegetation change, where increased evapotranspiration favors soil salinization and leads to further loss of canopy cover. Conversely, if a shift from forest to marsh vegetation results in a net decrease in evapotranspiration, then increased water-table elevations could reduce salinization. In this scenario, reduced evapotranspiration simultaneously creates more saturated and less saline conditions in the root zone (Ding et al. 2023). This potentially represents a negative feedback because vegetation tends to be more sensitive to salt than to hypoxia (Krauss et al. 2009, Williams et al. 1999).

Vegetation responses to SLR can also enhance or reduce salinization through flood mitigation effects. Marsh loss due to SLR could reduce flood mitigation, allowing storm surges to propagate further into the upland (Al-Attabi et al. 2023, Sheng et al. 2022) (**Figure 4*a***). Conversely, if marshes expand due to migration or progradation, flooding effects could be mitigated, reducing the extent of surface salinization (Guimond & Michael 2021) (**Figure 4*b***). Subsurface salinization is also influenced by the development of marsh soils, since organic-rich marsh sediments have hydraulic conductivity values two to three orders of magnitude lower than those of terrestrial soils (Knott et al. 1987). Low-conductivity marsh soils limit infiltration of saline water during storm surges and lateral flow of saline water from adjacent estuaries (Guimond & Michael 2021, Guimond et al. 2020). However, shallow marsh sediments that cap higher-conductivity terrestrial sediments near the upland boundary also prevent the infiltration of freshwater into the root zones of trees during precipitation events, enhance the retention of saltwater near the surface, and divert freshwater flows to deeper soils, where they bypass the marsh soils altogether (Harvey & Odum 1990).

Hydrologic feedbacks may slow the retreat of coastal forests, but SLR and SWI eventually lead to forest mortality. As forests retreat, tree and shrub root mortality can leave open pathways for water infiltration, especially in low-permeability soils (Guo et al. 2019). Although the impacts on coastal salinization have not been studied, these preferential flow conduits could promote infiltration of saltwater into the root zone and groundwater during flooding events, a positive feedback that could amplify salinization (Xu et al. 2024). However, preferential flow through the soil zone can also accelerate soil drainage (Xu et al. 2024), which would enhance flushing of salt and excess moisture from the root zone, representing a negative feedback that mediates both salt and hypoxia stress.

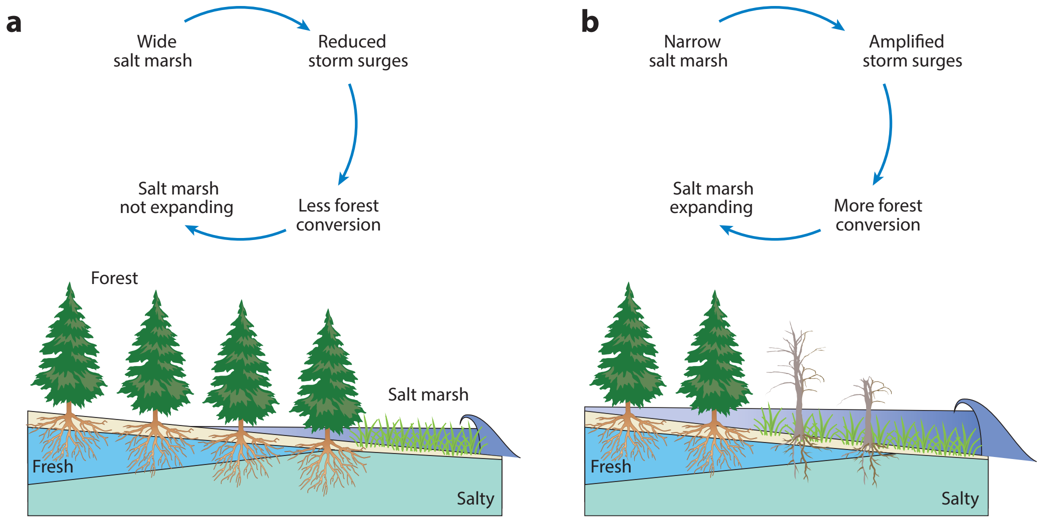


Figure 4

Potential negative feedback between salinization and changes in marsh width. (*a*) The presence of a wide marsh in front of a forest dissipates storm surges, reducing salinization and forest conversion to salt marsh. (*b*) A narrow marsh does not protect the forest from storm surge, so that storm surge facilitates more extensive forest mortality and marsh encroachment. These feedbacks are amplified by the development of organic-rich marsh soils with low hydraulic conductivity that limit subsurface propagation of saline water during storm surges (Guimond & Michael 2021).

2.3. Net Impact

Many of the proposed hydrologic feedbacks are inferred from a generalized process-level understanding of coastal hydrology but lack the direct observations that would be required to assess their magnitude and net impact on the salinization of coastal ecosystems. Hydrologic observations at the marsh–upland transition are geographically sparse and do not typically extend over the timescales (years to decades) necessary to quantify feedbacks between hydrologic conditions and the slow mortality of mature trees. Further, stabilizing feedbacks on salinity, such as reduction of saltwater infiltration with water-table rise, may have concurrent amplifying feedbacks on vegetation, such as soil hypoxia.

Process-based numerical models and space-for-time substitution can enable longer-timescale analysis over a broader range of conditions. For example, numerical modeling indicates that reduced evapotranspiration from forest stress leads to simultaneous increases in hypoxia and decreases in salinity (Ding et al. 2023), consistent with the hydrologic feedback proposed herein. High-resolution measurements at the forest–marsh ecotone show that salinity increases with groundwater levels, a clear sign of salt concentration due to evapotranspiration (Nordio & Fagherazzi 2022). Space-for-time substitution suggests that hydrologic gradients are driven mostly by vegetation–hydrology interactions, since salinization by storm surges is often uniform (Nordio et al. 2024). On the other hand, uniform hydrologic characteristics across a coastal forest fronted by an expansive marsh during storm surges (Nordio et al. 2024) and observed rates of forest retreat that are not correlated with distance to open water (Chen & Kirwan 2024) are perhaps in opposition to the feedback between marsh width and salinization proposed in **Figure 4**. In any case, observations across lateral gradients of forest health indicate that SWI leads to wetter and more saline soils and that the proposed hydrologic feedbacks that stabilize salinity are eventually overcome (Gardner & Reeves 2002, Nordio et al. 2024).

3. GEOMORPHIC FEEDBACKS

In the absence of geomorphic feedbacks, coastal forest retreat and marsh migration occur steadily, follow gradients in topography, and allow for the study of hydrologic and ecological processes via simple space-for-time substitution (Brinson et al. 1995, Smith & Kirwan 2021). This conceptual framework relies on the assumption that SWI does not alter the elevation of the soil surface through time. Some observations suggest a relatively stable upland topography during SWI (Powell et al. 2022). However, assumptions of a static topography contrast with the general understanding that SLR results in dynamic changes to the topography of more seaward coastal landforms (e.g., beaches, deltas, and marshes), where surface elevations evolve according to the balance between erosion and sediment deposition (Anthony 2015, FitzGerald et al. 2008, Kirwan & Megonigal 2013). Geomorphic change is likely to be more subtle in landward portions of the coastal zone (i.e., the leading edge of SWI) and determined by processes that alter the balance between soil formation (e.g., plant productivity) and soil losses (e.g., organic matter decomposition) (Hein & Kirwan 2024). Feedbacks between geomorphology and SWI are potentially strong because elevation and topographic slope directly affect groundwater discharge and inundation frequency (Michael et al. 2013, Yu et al. 2016).

3.1. Stabilizing Feedbacks

Several geomorphic processes are likely to increase the elevation of coastal forest soils during SWI. Like marshes and mangroves, forested wetlands build soil through mineral sediment deposition by tides, in situ litterfall and root growth, and allochthonous organic matter deposition (Ensign et al. 2014) (**Figure 5**). Vertical accretion rates in tidal freshwater forests range from approximately 1 to 10 mm y^{-1}, which are higher than those of terrestrial forests but typically less than those of adjacent salt marshes (Craft 2012, Ensign et al. 2014, Krauss et al. 2024) (**Figure 6**). Interestingly, rates of soil accretion and elevation change have no clear relationship with forest health along estuarine salinity gradients (Craft 2012, Ensign et al. 2014, Krauss et al. 2024), such that the impacts of SWI are unclear. Numerical models of sea-level-driven land conversion assume that forested uplands do not accrete vertically (Molino et al. 2022, Osland et al. 2022). Nevertheless, observations of rapid accretion rates in forested wetlands at least illustrate the potential for forest soils to build elevation through time.

Mineral sediment deposition and allochthonous organic matter deposition by tides are unlikely to be strong contributors to terrestrial forest soil elevation during the initial stages of SWI, as reflected by low rates of elevation change in upland forests of the York River (~1 mm y^{-1}) (**Figure 6**). Nevertheless, terrestrial soil elevations impacted by SWI may be enhanced by the rapid colonization of *Phragmites australis*, an invasive species that dominates retreating coastal forests along the mid-Atlantic coast (Langston et al. 2021, Smith 2013, Smith & Kirwan 2021) (**Figure 1*a***). *P. australis* is known for exceptionally rapid biomass production, mineral sediment trapping, and leaf litter accumulation (Langston et al. 2021, Rooth et al. 2003). Accretion rates of mature *Phragmites* stands approach 10 mm y^{-1}, perhaps double that of adjacent native species (Rooth et al. 2003). *P. australis* survives partial shade and a wide range of salinities, so that it colonizes the understory of stressed forests well before mortality occurs (Shaw et al. 2022, Sward et al. 2023), thus potentially raising the elevation of terrestrial soils and slowing rates of SWI. However, high rates of subsidence may offset accretion in the transition zone between forest and salt marsh, resulting in negligible if not negative rates of elevation change (**Figure 6**). Hurricanes, floods, and other high-water inundation events may increase rates of forest and marsh soil accretion by delivering sediment and organic matter (i.e., wrack) to portions of the coastal landscape that are rarely inundated (Tate & Battaglia 2013). Collectively, these processes

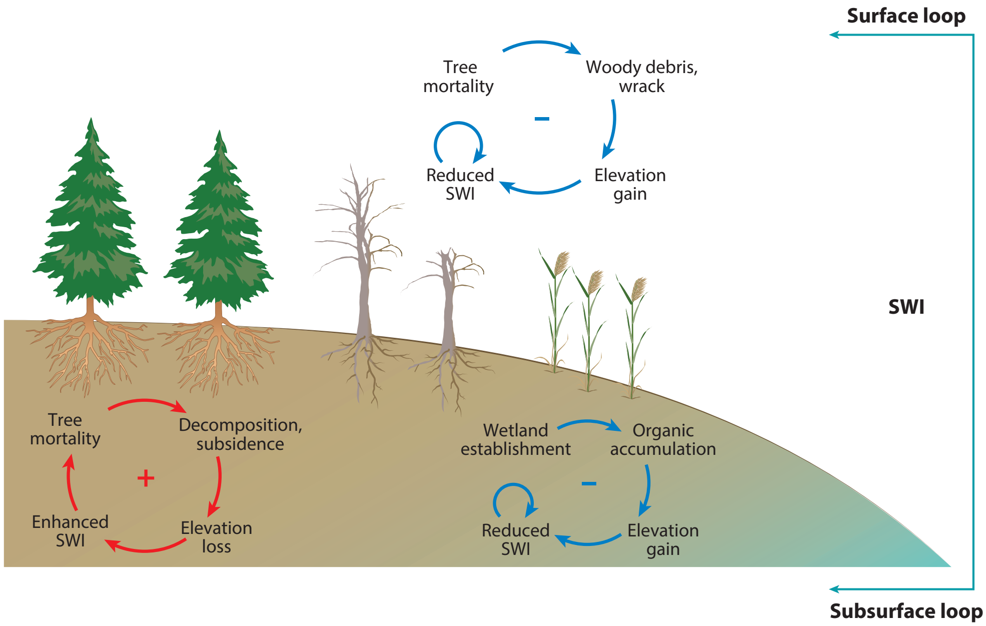


Figure 5

Summary of the geomorphic feedbacks that influence SWI through changes in soil elevation, highlighting surface and subsurface processes. (*Top*) Tree mortality is accompanied by woody debris and wrack deposition on the soil surface, which contributes to elevation gain and potentially reduces the impact of SWI in a stabilizing (−) feedback. (*Bottom*) Tree mortality is accompanied by decomposition of soil organic matter and root-zone subsidence, which contributes to elevation loss and potentially enhances the impacts of SWI in an amplifying (+) feedback. However, establishment of wetland plants in the transition zone between forest and marsh (e.g., *Phragmites australis*) is accompanied by increased soil organic matter accumulation, which contributes to elevation gain and potentially reduces the impact of SWI in a stabilizing feedback. Erosion and deposition of mineral sediment are not depicted because SWI typically takes place far from waves and tidal channels. Abbreviation: SWI, saltwater intrusion.

tend to increase the elevation of forested wetlands and salt marshes (**Figure 6**) and could contribute to a negative feedback that results in reduced SWI and reduced rates of ecosystem migration.

3.2. Amplifying Feedbacks

Other processes may decrease the elevation of terrestrial soils during SWI, resulting in a positive feedback where geomorphic processes amplify the impacts of SWI on migrating ecosystems. Because the leading edge of SWI is typically located far inland from waves and tidal currents (Hein & Kirwan 2024, Hingst et al. 2023, Tully et al. 2019b), degradation of organic-rich soils is more likely to result in loss of elevation than physical erosion of sediment. Two processes are likely to contribute to losses of soil elevation (**Figure 5**). First, SWI into freshwater marshes often results in increased organic matter decomposition rates through enhanced sulfate reduction, and potentially peat collapse (Chambers et al. 2019, Charles et al. 2019, Noe et al. 2013). Second, a loss of root volume following storm-induced tree mortality leads directly to subsidence of organic-rich soils, as observed in mangroves and freshwater wetlands (Cahoon et al. 2003, Middleton & David 2022). An increasing ionic strength of salinized porewater may also lead to shrinkage of clays, reducing soil volume (Cai et al. 2023). Together, these processes may help explain inferred subsidence rates of 3.7–19.6 mm y^{-1} that accompanied SWI into a forested wetland in eastern North Carolina

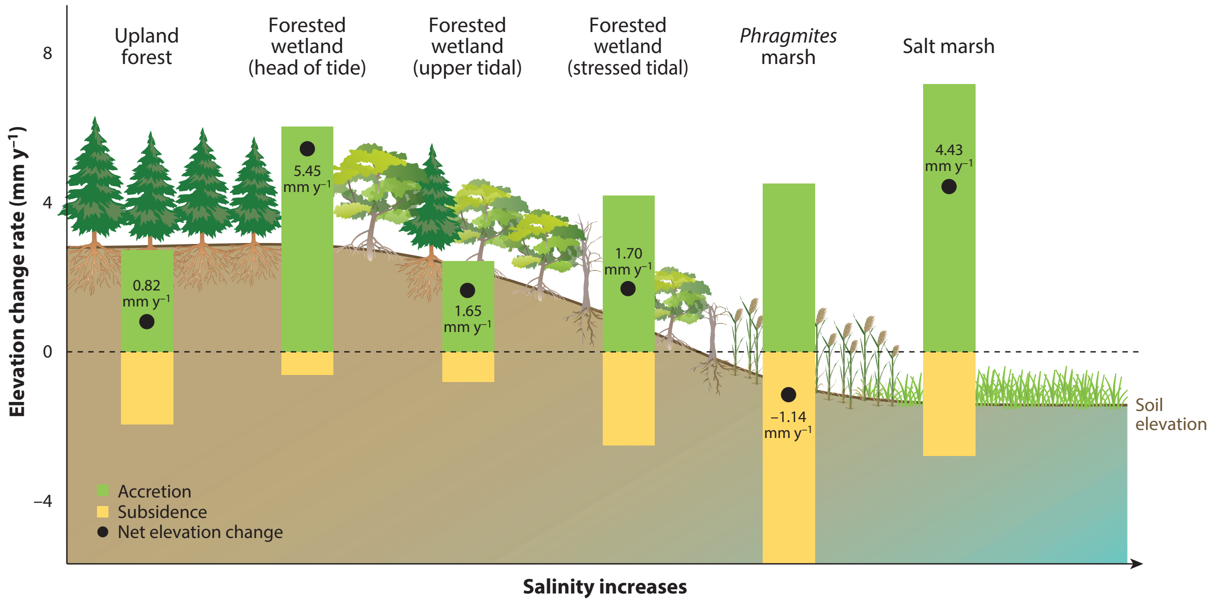


Figure 6

Comparison of elevation change rates along a salinity gradient in the York River watershed (Virginia, USA). The net elevation changes (*black circles*) reflect the difference between accretion (*green*) and subsidence (*yellow*) as measured by sediment elevation tables. The freshwater forested wetland data represent the average rate for each zone measured on hummocks along the Mattaponi and Pamunkey Rivers as reported by Krauss et al. (2024). The elevation change rates for the upland forest, *Phragmites* marsh, and salt marsh were measured on Goodwin Island, York River. The *Phragmites* marsh represents a transition zone between upland forest and salt marsh. The salt marsh data represent the average rate for salt marsh on Goodwin Island as reported by Saintilan et al. (2023); the upland forest and *Phragmites* marsh data are unpublished.

(Miller et al. 2021). These processes may also explain shallow subsidence rates that generally increase along a salinity gradient in the York River estuary, peaking in the *Phragmites*-dominated zone, where tree mortality is highest and net elevation change rates are negative (**Figure 6**).

3.3. Net Impact

The net impact of SWI on processes that build and destroy the elevation of terrestrial forest soils is difficult to assess. Although SWI is thought to cause a net decrease in the elevation of organic-rich freshwater wetland soils (Herbert et al. 2015), it remains unknown whether the same pattern would be observed in terrestrial soils with a lower organic content. Decomposition rates along terrestrial forest dieback gradients may not be sensitive to salinity (Smith et al. 2024), even though salinity is a strong driver of decomposition in organic-rich freshwater wetlands (Herbert et al. 2015). Anecdotal evidence suggests that root collapse may trigger subsidence during terrestrial forest mortality, including the observation of extensive ponding at the marsh–forest boundary (Taylor et al. 2020) (**Figure 1*a***). Salt addition and other disturbance experiments in terrestrial coastal forests remain in their infancy (Hopple et al. 2023, Tate & Battaglia 2013, Walters et al. 2021). Nevertheless, vegetation recovery was rapid in one of the few terrestrial forest disturbance experiments, suggesting that subsidence was not extensive enough to prevent regeneration (Walters et al. 2021). Long-term monitoring of elevation through time in healthy and degraded coastal forests is therefore necessary to tease out the net impact of processes that lead to accretion and subsidence of terrestrial soils experiencing SWI.

4. BIOTIC FEEDBACKS

Forested uplands and forested wetlands together account for approximately 80% of the historical marsh migration area along the mid-Atlantic coast (Chen & Kirwan 2024) and approximately 80% of the nonmarsh areas vulnerable to future saline wetland intrusion in the continental United States (Osland et al. 2022). In the absence of feedbacks, SWI results in tree stress and mortality (Kirwan & Gedan 2019, Taillie et al. 2019). Primary mechanisms for decline include osmotic stress (Méndez-Alonzo et al. 2016, Munns & Tester 2008, Zhang et al. 2021) and salt toxicity (Munns & Tester 2008, Zhang et al. 2021), which together lead to carbon starvation (Matallana-Ramirez et al. 2021, McDowell et al. 2022) and impaired hydraulic function (McDowell et al. 2022, Zhang et al. 2021). Some field observations suggest an ordered pattern of forest retreat, characterized by the steady replacement of salt-intolerant species, that can be predicted by space-for-time substitution in the absence of feedbacks (Conner et al. 2007, Williams et al. 1999). In general, deciduous tree species (variable species, <2–3 ppt; Conner et al. 2007) are less salt tolerant than coniferous tree species (*Pinus taeda*, <4 ppt, Poulter et al. 2008) and the shrubs (*Morella cerifera*, <10 ppt; Young et al. 1994) and marsh species (*P. australis*, <20–30 ppt; Achenbach & Brix 2014) that replace them. Yet trees are powerful ecosystem engineers due to their water usage, effects on understory light and temperature, and control over ecosystem processes such as decomposition and nutrient cycling (Ellison et al. 2005). Changes in species distributions are not necessarily well explained by salinity (Ury et al. 2020), and rates of forest retreat are slower than would be predicted by SLR in the absence of feedbacks (Chen & Kirwan 2024, Field et al. 2016).

4.1. Stabilizing Feedbacks

Several negative feedbacks potentially explain patterns of surprising forest stability (**Figure 7**). Thinning and mortality of some trees may reduce light competition and provide an unexpected, positive tree growth response during early- and mid-stage salinization. Both *P. taeda* and *Juniperus virginiana* are shade-intolerant pioneer species that dominate the margins of many coastal forests (Ferguson et al. 1968, Schultz 1997). As more salt-sensitive trees die, surviving trees, particularly those growing on elevated hummocks or with deep roots to obtain freshwater (Williams et al. 1999, 2007), benefit from increased light availability due to gap creation and possibly reduced competition for nutrients. Storms or other disturbance events that accompany SWI may amplify these effects. Dominant trees, such as longleaf pine, *Pinus palustris*, exhibit increased seed production (masting) in response to hurricane disturbance (Cannon et al. 2023). Therefore, storms or other climate variables can result in pulses of tree recruitment in these pioneer species, followed by long periods of little to no recruitment (Kirwan et al. 2007).

Ecohydrologic feedbacks may also help explain slower-than-expected patterns of forest retreat. As trees become stressed, the leaf area index, canopy cover, and basal area decline (Conner et al. 2007, Zhang et al. 2021), which is accompanied by a decline in transpiration (Krauss & Duberstein 2010). Trees preferentially utilize freshwater, so reduced transpiration could lead to lower soil salinity concentrations, as discussed in Section 2 (Ding et al. 2023). Shrubs and tall grasses that are more light demanding and salt tolerant than trees become more common as the tree canopy opens (Sward et al. 2023). Shading by dense understory plants, such as the invasive common reed *P. australis*, affects salinity in surface soils by reducing evaporation rates and can shape the nature of species interactions (Bertness & Ewanchuk 2002). In low-salinity environments, shading by grasses can reduce salinities enough to promote tree seedling survival (Poulter et al. 2009). However, this is likely a context-dependent effect, as tree mortality preceded grass colonization without tree regeneration in a more saline system (Williams et al. 1999).

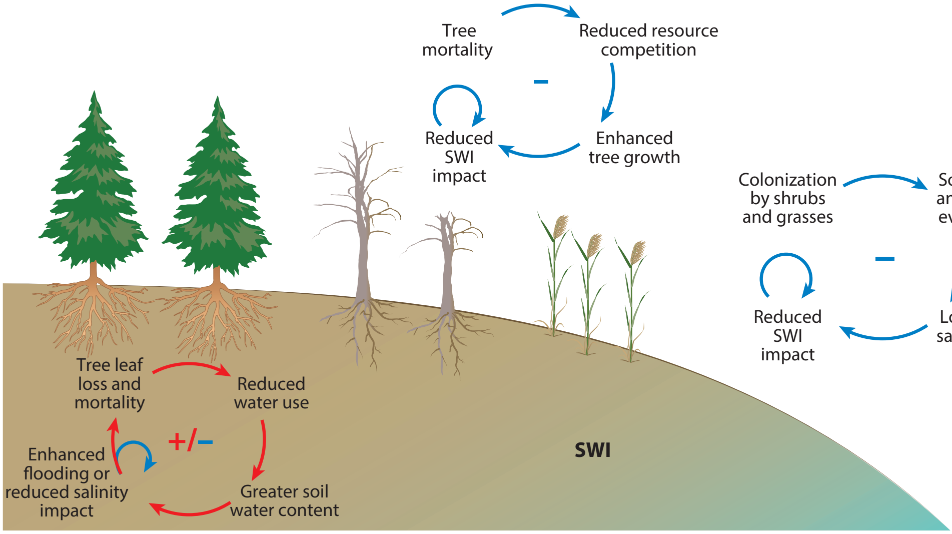


Figure 7

Summary of the biotic feedbacks that influence SWI and its impact on coastal forests. (*Top*) Tree mortality results in reduced resource competition (light, nutrients, and water), which leads to enhanced growth of surviving trees in a stabilizing (−) feedback. Tree mortality also leads to colonization by understory shrubs and grasses, which shade the soil, reduce evaporation, and may reduce salinity, resulting in a stabilizing feedback. (*Bottom*) Tree leaf loss and mortality lead to reduced water use, which simultaneously increases soil water content and reduces salinity. This feedback can result in enhanced tree mortality (amplifying feedback) or reduced tree mortality (stabilizing feedback) depending on the relative sensitivity of the vegetation to hypoxia and salinity. Abbreviation: SWI, saltwater intrusion.

4.2. Uncertain or Conditional Feedbacks

Biotic feedbacks that mitigate SWI and forest loss are inherently complex, and alternative pathways are possible. In particular, the net effects of reduced tree water use are still poorly understood and species dependent. As trees become stressed and use less water, soils generally become more water saturated. Saturated soils create hypoxia in the root zone, a stress that amplifies salinity impacts in trees (Conner et al. 2007, Pezeshki et al. 1990, Poulter et al. 2008). Greenhouse studies suggest that individual tree water use may decline by approximately 10% per 1 PSU of salinity increase. However, field studies find that reductions vary between species (7–38% declines per 1 PSU) (Duberstein et al. 2020), and the majority of these observations come from the same forest type and geographic region (**Figure 8**). While reduced transpiration favors reduced salinity (i.e., negative feedback), co-occurring increases in soil saturation could amplify vegetation change (i.e., positive feedback).

For most tree species, our knowledge of salinity and inundation tolerances is lacking or based on early life history stages and pot experiments rather than mature individuals in the field. Rooting depth and resource foraging strategies differ by species. For example, *J. virginiana* preferentially forages upslope, toward freshwater sources, which likely helps the species persist in saltwater-affected areas but also makes these individuals unstable and more prone to windthrow (Messerschmidt et al. 2021). Deeply rooted species also likely regulate the depth to the water table and therefore influence neighboring plants (Aschehoug & Callaway 2014). Thus, species-dependent rooting strategies may help individual species survive SWI but make them more vulnerable to other stresses (e.g., hypoxia and windthrow) that would accelerate forest retreat.

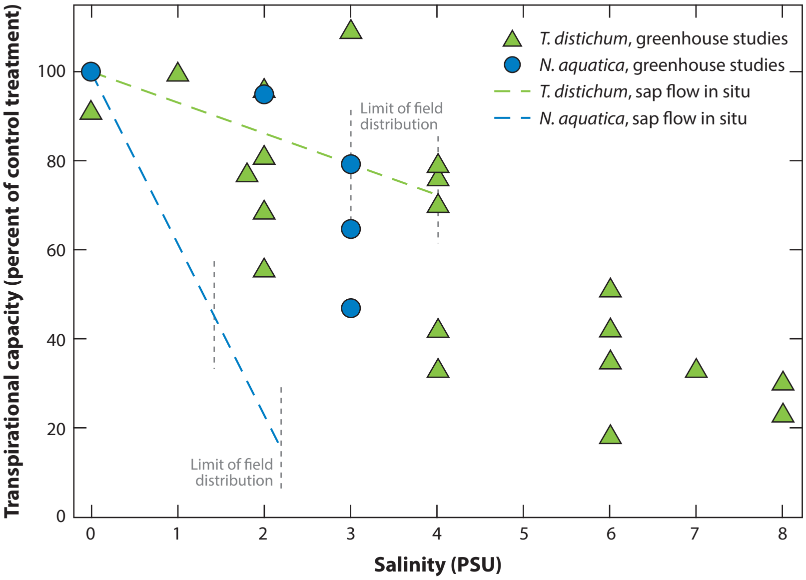


Figure 8

Reduction in tree water use (transpiration) in individuals grown in saline environments relative to controls grown in freshwater for two tree species common to forested tidal wetlands. Bald cypress (*Taxodium distichum*) transpiration is indicated with triangles and a green regression line; water tupelo (*Nyssa aquatica*) transpiration is indicated with circles and a blue regression line. The effect of salinity on transpiration increases at higher salinities. Data were collected from the field and compiled from other studies by Duberstein et al. (2020); sap flow in situ measurements came from Strawberry Swamp, South Carolina, as reported by Duberstein et al. (2020). Figure adapted from Duberstein et al. (2020) with permission from Elsevier.

4.3. Net Impact

Though SWI has been linked to forest mortality on the US Atlantic coast (e.g., Krauss et al. 2009, Liu et al. 2017, Thomas et al. 2015), forest retreat in the mid-Atlantic is only approximately half of what would be expected from SLR (Chen & Kirwan 2024), and favorable growth responses have been associated with early stages of salinization (S. Hall et al. 2022, Noe et al. 2021). Biotic feedbacks triggered by SLR may increase forest resiliency through advantageous responses to light availability, and the system may experience positive or negative feedbacks related to reduced water use by trees in decline and altered rates of surface evaporation (**Figure 8**). These processes explain why basal area can decline while stem number does not, as juveniles of shade-limited species recruit (Conner et al. 2007, Noe et al. 2021). These processes may also explain why some forests appear to resist change (Field et al. 2016) or transpire more when exposed to low levels of salinity (Wang et al. 2020). Finally, the effects of trees and tree mortality on light and water availability are apt to be species specific and context dependent, which complicates efforts to predict their net effect. Given the range of forest types experiencing coastal forest retreat (Kirwan & Gedan 2019) and the importance of trees as ecosystem engineers, the magnitudes of the effects can be substantial and are likely important in understanding local dynamics of coastal tree lines.

5. ANTHROPOGENIC FEEDBACKS

Hydrologic, geomorphic, and biotic feedbacks are all influenced by land management decisions that alter the trajectory of SWI into coastal ecosystems. Anthropogenic activities with potential to alter SWI into coastal forests include commercial planting of relatively salt-tolerant loblolly pines, grading and ditching, early timber harvests, and other silvicultural activities (McClure & Kedmenecz 2023). In residential and recreational areas, mowing lawns and grassy areas that are converting to salt marsh species may influence SWI (Anisfeld et al. 2017). Nevertheless, anthropogenic feedbacks are best illustrated by the response of agricultural land to SWI. Agriculture represents approximately 20% of total nonmarsh area (and 40% of uplands) vulnerable to future SWI in the continental United States (Osland et al. 2022) and at least in some locations is more vulnerable than forests (Gedan et al. 2020). High vulnerability and substantial economic implications have prompted wide-ranging interventions of variable effectiveness to reduce losses and extend the life spans of fields and farms (**Figure 1**). Farmers and landowners are responding to SWI on individual fields and farms, where they resist and adapt to SWI before ceasing managing lands all together (retreat) (**Figure 9**).

5.1. Stabilizing Feedbacks

Landowners resist SWI through a variety of strategies at the field level, many of which result in negative feedbacks that have short-term stabilizing impacts. Although relatively uncommon due to its high financial cost, some landowners choose to raise the elevation of farm fields either by dredging agricultural ditches and placing the spoils on the edges of farm fields or by importing soil (Tully et al. 2019a). Farmers also apply calcium in the form of gypsum to remediate soils with

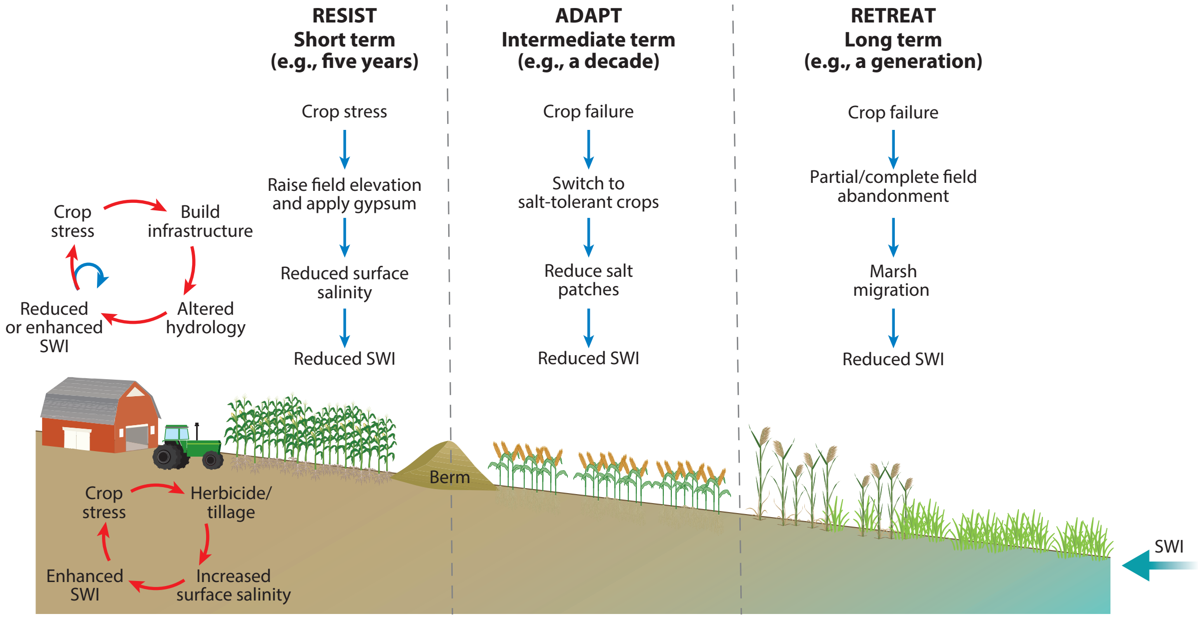


Figure 9

Anthropogenic feedbacks that influence SWI into farmland follow a resist, adapt, and retreat framework as fields become increasingly salinized. Red arrows indicate amplifying (+) feedbacks, and blue arrows indicate stabilizing (−) feedbacks. (*Left*) Field management to resist the impacts of SWI includes structural improvements (installing drainage tiles, ditches, and levees) that tend to reduce SWI but may inadvertently connect fields with saltwater sources and prevent drainage of freshwater. Raising field elevations and applying gypsum slow the impact of SWI. Other resistance strategies include herbicide and tillage, which tend to concentrate salts near the soil surface and lead to further crop stress. (*Middle*) Field management efforts to adapt to SWI include planting salt-tolerant crops that increase plant water use and may lessen the spread of SWI to locations further inland. (*Right*) Finally, fields are abandoned and may receive restoration measures to facilitate marsh encroachment. Abbreviation: SWI, saltwater intrusion.

excessive sodium cations caused by SWI (Fowler et al. 2014, Weissman et al. 2021). Farmers may adapt to SWI by planting salt-tolerant crops that fit into a region-specific crop rotation or can be planted with existing equipment. For example, sorghum (*Sorghum bicolor*) has moderate tolerance to SWI in the mid-Atlantic region (de la Reguera et al. 2020), and salt-tolerant rice cultivars increase paddy yields in Bangladesh (Hossain et al. 2012, Rabbani et al. 2015). Maintaining above- and belowground biomass in crops supports water infiltration and transpiration (see Section 4), which can reduce the concentration of salts on the soil surface due to evaporation. Together, these resistance and adaptation strategies may extend the life spans of agricultural fields and have a short-term stabilizing effect on SWI.

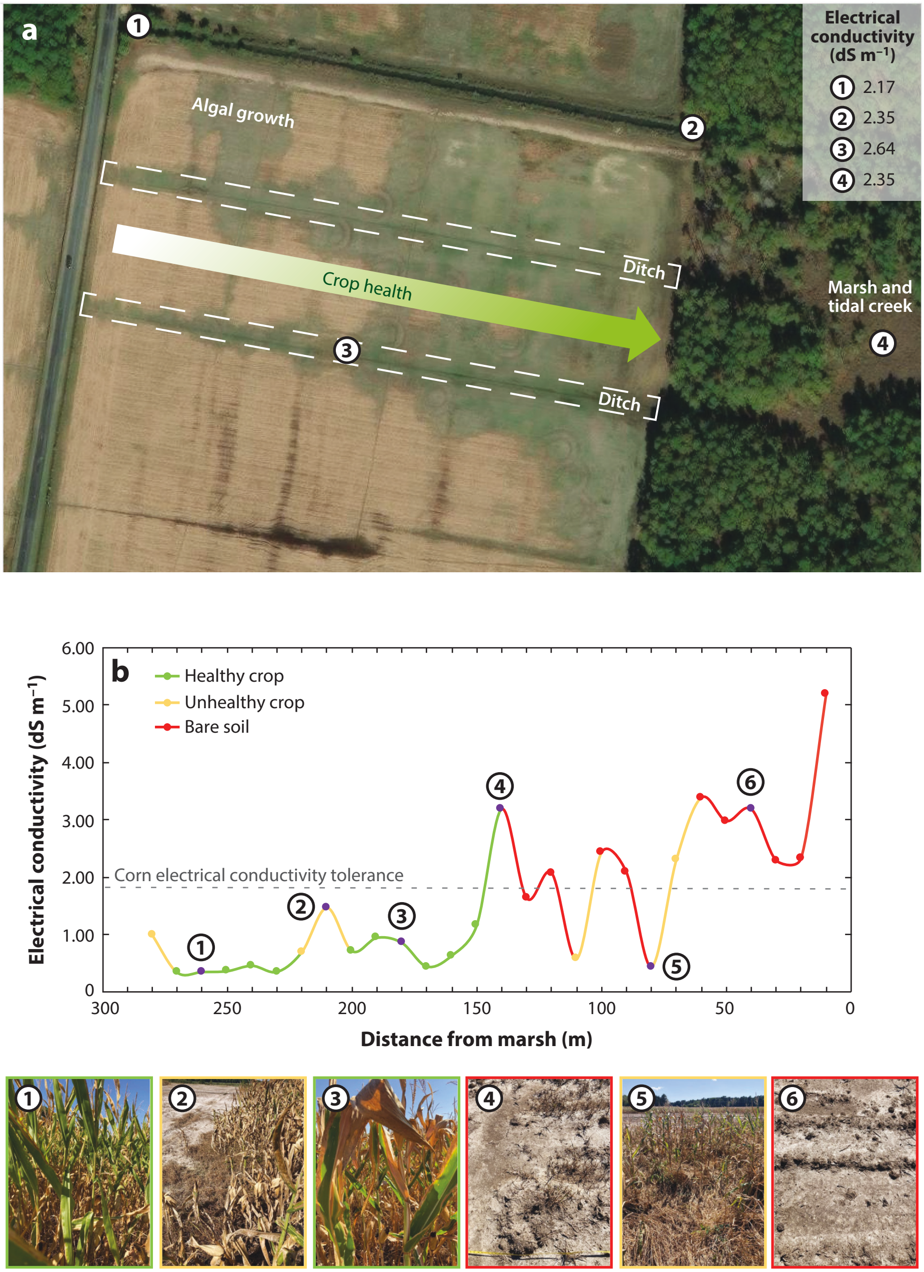
Perhaps counterintuitively, allowing marshes to migrate inland may limit the impacts of SWI on adjacent fields. Marsh vegetation limits wave height and energy (Möller et al. 2014), thereby limiting the aboveground extent of storm surge. Belowground, organic-rich soils associated with marshes act as a physical barrier to coastal saltwater infiltrating into fresh inland groundwater (Guimond & Michael 2021). In areas of northwest Europe, dikes are being purposefully set back to regain ecosystem services associated with marshes (Wolters et al. 2005). Though soil compaction associated with historical farming limits biodiversity in restored wetlands (Dale et al. 2019), marsh restoration is largely responsible for the maintenance of global tidal marsh area despite losses from SLR (Murray et al. 2022). Nevertheless, farmers are unlikely to turn over productive agricultural land as a preventative measure, opting instead to allow migration on already salt-impacted fields. Landowners tend to continue managing salt-damaged fields (**Figure 10*a***), even if only through regular mowing of naturally recruited species (e.g., agricultural weeds and native marsh species). Complete abandonment of agricultural fields is generally considered a last resort and may occur only when the land is too wet to support heavy machinery.

5.2. Amplifying Feedbacks

Standard agricultural practices may inadvertently enhance the spread of SWI across a farm field, leading to positive feedbacks that accelerate ecosystem change (**Figure 10**). Most growers in conventional grain production systems spray broad-spectrum postemergent herbicides to manage weeds (e.g., glyphosate), which can kill salt-tolerant native plants. SWI on the edges of agricultural fields, often appearing as a white patch visible from aerial imagery (Mondal et al. 2023) (**Figure 1*b***), is exacerbated by spraying of herbicides across the entire field. Herbicide kills encroaching salt-tolerant marsh species, resulting in increased evaporation and bare agricultural soils with salinities that are even higher than those in adjacent tidal creeks and salt marsh (**Figure 10*b***). Similar hydrologic impacts may be caused by soil compaction, which leads to lower elevations, reduced infiltration of freshwater, and dampened hydrologic fluctuations (Van Putte et al. 2020). Tillage (i.e., deep ripping) has been suggested as a strategy to ameliorate saline soils (Pratley & Kirkegaard 2019, Riddell et al. 1988). Yet emerging research suggests that salinity can increase with depth in some locations, so that tillage would increase the pace of crop damage by bringing saltier soils up to the surface. Soil salinization may also cause farmers and land managers to increase irrigation with fresh groundwater to flush the salts from the root zone. Increased groundwater pumping would in turn reduce the elevation of the water table locally, causing both vertical and lateral (surface and subsurface) SWI (Hingst et al. 2023).

5.3. Uncertain or Conditional Feedbacks

Structural interventions to counteract a rising water table include ditching (**Figure 10*a***) and small earthen levees (**Figure 1*b***). Drainage ditches may enhance salinization during storms and high-tide events by increasing sea-to-land hydraulic connectivity (Bhattachan et al. 2018, Giambastiani et al. 2007, Poulter et al. 2008). For example, ditches designed to drain water off an agricultural field now deliver saltwater to the field, as evidenced by salinities in ditches that are equivalent to those in an adjacent tidal creek (**Figure 10*a***). Ditches also enhance vertical infiltration of saltwater due to expansion of the unsaturated zone and reduced soil moisture. Ditches that are not maintained may begin to function as small-scale topographic depressions



(*Caption appears on following page*)

Figure 10 (*Figure appears on preceding page*)

A salinized agricultural field illustrating a potential anthropogenic feedback where ditching increases the spatial extent of SWI. (*a*) Ditches and drains connect the field to the adjacent marsh and tidal creek. Although ditches were originally constructed to increase drainage of water off the field, they now deliver saltwater to the field. The electrical conductivity—a proxy for salinity—of the water in the ditches (①–③) is equivalent to that of the tidal creek (④). Green algal growth on the field reflects soils that remain wet. (*b*) Electrical conductivity in soils and crop stress increase toward the marsh and tidal creek. The soil conductivity transect in panel *b* corresponds to the colored crop health gradient in panel *a*, and the numbers correspond to the photographs at the bottom. Crop failure occurs where the conductivity in the soils exceeds 1.8 dS m^{-1} (∼0.9 ppt). Note that conductivity in bare soils is higher than that in tidal creeks, which likely reflects the concentration of salts from evaporation. Abbreviation: SWI, saltwater intrusion.

(Fisher et al. 1996), allowing more saltwater to pond on the surface and infiltrate into the aquifer (Yu et al. 2016). Ditches may also be accompanied by earthen berms made from the material excavated to create the ditch (**Figure 1*b***). These berms are often less than 1 m in height (E.A. Hall et al. 2022) and are intended to reduce exposure of productive uplands to regular tidal inundation. However, berms trap rainwater draining from uplands and saline water from overtopping events, leading to high variability in salinity levels and the formation of marshes landward of the levee (Santoro et al. 2023) (**Figure 1*b***). Exposure of previously anaerobic soils in diked and drained wetlands can enhance decomposition and subsidence (Millard et al. 2013), leading to the formation of ponds (Smith et al. 2017) if the berms are breached or overtopped. The costs of maintaining privately owned berms have increased over time, making them less economically viable as a method to limit SWI (Smith et al. 2017). As a result, many berms along the mid-Atlantic have fallen into disrepair, decreasing in height and forming breaches that enhance SWI (E.A. Hall et al. 2022, Smith et al. 2017). Therefore, structural features such as ditches and berms can either amplify or mediate the impacts of SWI on coastal farmland.

5.4. Net Impact

Anthropogenic feedbacks on SWI may occur through typical farming practices or in localized responses to different stages of crop stress, changing across the landscape as well as within a single field or farm. We hypothesize that on short timescales (e.g., five years), farmers may be able to resist SWI by making structural changes, raising the surface elevation of the field, and applying gypsum (**Figure 9**). Resistance strategies may become less economically viable through time as yields decline. Adaptation strategies extend the productive life of the field over intermediate timescales (e.g., a decade) but may require landowners to switch to salt-tolerant crops of lower value. Once a field becomes too wet for farm equipment and the resistance and adaptation strategies have been exhausted, farmers may retreat (e.g., abandon the field). Thus, feedbacks may switch from positive (e.g., herbicide application) during the resistance stage to negative (alternative crops and field abandonment) during the adaptation and retreat stages (**Figure 9**). This framework is simplistic because characteristics of abandoned fields depend on previous management (Gedan & Fernández-Pascual 2019), especially as it relates to soil compaction (Dale et al. 2019), and decisions made at the field scale can propagate up to the landscape scale (i.e., ditching and impoundments deflect water to neighboring fields). Thus, decision-making in the coastal zone reflects a heterogeneous patchwork of strategies that are used to manage farmland in various states of stress, each with different impacts on SWI.

6. SUMMARY AND PRIORITIES FOR FUTURE RESEARCH

This review identifies several feedbacks that could influence SWI and its impact on coastal ecosystems. Prominent negative feedbacks that help reduce the impacts of SWI include reduced saltwater infiltration with a rising water table, vegetation shifts that reduce both evapotranspiration of freshwater and competition among surviving trees, and increases in soil elevation through organic matter accumulation. Some farmland management activities, such as shifting to salt-tolerant crops and adding soil to increase field elevation, result in feedbacks that resemble those operating in natural ecosystems. Yet many of these stabilizing feedbacks are potentially offset by positive feedbacks that include increased soil saturation, land subsidence, and anthropogenic structures that prevent water from draining from salinized agricultural fields. These proposed feedbacks include interactions among hydrologic, geomorphic, biotic, and anthropogenic processes and stand in contrast to assumptions of a passive terrestrial landscape.

Despite a number of proposed feedbacks regulating SWI into coastal ecosystems, it remains unknown whether the net impact of these feedbacks will be to mitigate or amplify vegetation change. There are some indications that negative feedbacks may dominate positive feedbacks and help stabilize ecosystems in early stages of SWI. Rates of coastal forest retreat are approximately half the rate expected from SLR propagating across static topography (Chen & Kirwan 2024). Growth rates of individual trees are often maximized in locations experiencing limited SWI, where tree mortality has alleviated competition for resources such as light, water, and nutrients among surviving trees (S. Hall et al. 2022, Noe et al. 2021). Finally, efforts to prolong the life spans of agricultural production (Tully et al. 2019a) suggest at least the perception that the impacts of SWI can be slowed.

Large-scale vegetation shifts, characterized by the migration of marshes into terrestrial forests and agricultural fields, indicate that there are limits to the ability of negative feedbacks to maintain current ecosystem extents (Fagherazzi et al. 2019, Kirwan & Gedan 2019). In some cases, these vegetation shifts may be accompanied by feedbacks that initially minimize but later amplify the impacts of SWI, particularly in later stages of salinity stress. A rising water table limits salt infiltration into soils during high-water events (**Figure 3**) but eventually leads to hypoxic soils and tree mortality. While initial tree mortality may increase growth rates of surviving trees (**Figure 7**), large-scale tree mortality may induce root-zone collapse that promotes land subsidence (**Figure 5**). Finally, canals and ditch-bank systems designed to mediate SWI into agricultural fields can become sources of saltwater that accelerate the stress and eventual mortality of crops (**Figure 10**). That the direction of feedback depends on the severity of stress suggests the potential for tipping points, with implications for both natural ecosystem succession and coastal management.

Most of the feedbacks proposed in this review are new, untested, and unquantified. The feedbacks also reflect a bias toward research conducted in the US Atlantic and Gulf of Mexico coasts, where rapid SLR drives SWI into a gently sloping, largely rural, coastal plain. We therefore suggest future research that addresses the following questions:

1. What are the magnitude and net direction of individual feedbacks that regulate SWI into coastal landscapes?
2. Under what conditions and management scenarios does the net impact of these feedbacks switch from stabilizing to amplifying?
3. How do feedbacks that influence SWI apply to locations beyond the US Atlantic coast, and how sensitive are they to particular species, climate regions, and geomorphic settings?

SWI into coastal landscapes simultaneously affects natural ecosystems and the vitality of coastal communities. Quantifying these poorly understood feedbacks represents an important step in developing landscape models that can predict the fate of ecosystems (e.g., Osland et al. 2022) and Earth system models that can predict associated fluxes of nutrients and sediments (Ward et al. 2020). Our review provides a framework to predict when and where rates of ecosystem change will be the fastest (i.e., shifts from negative to positive feedbacks). But understanding feedbacks may also lead to improvements in managing coastal landscapes, where the public benefits of SWI (e.g., nutrient assimilation associated with wetland expansion) are frequently at odds with private losses (e.g., reduced crop production) (Fagherazzi et al. 2019). Toward these efforts, our review provides a framework to determine when and where land management is best suited to altering ecosystem trajectories. In particular, knowledge of these feedbacks may inform strategies to manage coasts in ways that slow the most detrimental impacts of SWI while facilitating healthy ecosystems.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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