The ecohydrology of coastal ghost forests

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Abstract

Sea level rise and storm surges affect coastal forests along low-lying shorelines. Salinization and flooding kill trees and favor the encroachment of salt-tolerant marsh vegetation. The hydrology of this ecological transition is complex and requires a multidisciplinary approach. Sea level rise (press) and storms (pulses) act on different timescales, affecting the forest vegetation in different ways. Salinization can occur both by vertical infiltration during flooding or from the aquifer driven by tides and sea level rise. Here we detail the ecohydrological processes acting in the critical zone of retreating coastal forests. An increase in sea level has a three-pronged effect on flooding and salinization: it raises the maximum elevation of storm surges, shifts the freshwater-saltwater interface inland, and elevates the water table, leading to surface flooding from below.

Trees can modify their root systems and local soil hydrology to better withstand salinization. Hydrological stress from intermittent storm surges inhibits tree growth, as evidenced by tree-ring analysis. Tree rings also reveal a lag between the time when tree growth significantly slows and when the tree ultimately dies. Tree dieback reduces transpiration, retaining more water in the soil and creating conditions more favorable for flooding. Sedimentation from storm waters combined to organic matter decomposition can change the landscape, affecting flooding and runoff. Our results indicate that only a multi-disciplinary approach can fully capture the ecohydrology of retreating forests in a period of accelerated sea level rise.

1. Introduction

Low lying coastal areas are extremely vulnerable to sea level rise (SLR) and storm surges (Kearney et al. 2019, Kirwan and Gedan, 2019; Schieder and Kirwan 2019). Increasing sea levels push the interface between fresh and salt groundwater inland, affecting coastal forests and agricultural fields (Fagherazzi et al. 2019a). Soil salinization kills trees and crops and favors the expansion of salt marshes inland (Williams et al., 1999a). Ghost forests, composed of dead trees, starkly punctuate the coastline, serving as poignant symbols of climate change (Kirwan and Gedan, 2019). The impact of SLR is amplified along gentle shorelines, such as those found in the Mid-Atlantic region of the United States. Here the retreat of forests and agricultural lands occurs at fast rates with devastating consequences for ecosystems and communities (Fagherazzi et al. 2019b, Molino et al. 2022). Though less widely studied, storm surge events, occurring on short temporal scales, can have greater impact on coastal groundwaters and the ecosystems they support. The impact of storm surges on groundwater has been studied with field measurements and hydrological models (Cantelon et al. 2022). Coupled groundwater-surface water 2D models have been used to explore the influence of different soil characteristics (Yang et al. 2018) and topographic connectivity (Yu et al. 2016) on salinization due to storm surge events and on the recovery time (time to reach the pre-storm conditions, i.e. the value on the day prior to the storm). Terry and Falkland (2010) estimated a recovery time of 1 year in a coastal aquifer affected by a category 5 cyclone, while a similar event was felt in a low-permeability surficial aquifer up to 8 years (Xiao et al. 2019). Saltwater intrusion due to the supertyphoon Haiyan persisted in a sandy aquifer in the Philippines for 2 years (Cardenas et al. 2015).

In coastal vegetated areas, storm surge flooding and salinization can kill salt intolerant or moderately tolerant vegetation species (Woods et al. 2020; Pezeshki 1992; Munns and Tester, 2010; Middleton and David, 2022). Saltwater infiltration affects the active root zone, which typically occupies the upper decimeters of the soil (Mou et al., 1995; Xu et al., 2016; Parker & Lear, 1996). Coastal forests, in particular, have very shallow water tables, and the waterlogged or saturated soils with low oxygen levels inhibit the establishment of deep root systems (Coutts & Philipson, 1978). Consequently, root development is largely confined to the upper, aerobic soil layers (Boggie, 1972; Lieffers & Rothwell, 1987). In retreating coastal forests, roots are often distributed asymmetrically, growing preferentially toward upland freshwater sources (Messerschmidt et al., 2021).

When salinity thresholds are exceeded for extended periods, trees and crops progressively die, encouraging the establishment of more salt-tolerant vegetation species (Tully et al. 2019).

In this paper we present a review of the eco-hydrological processes that control the migration of ghost forests inland. The review is based on the preliminary results of a large-scale project funded by the US National Science Foundation. In this project, an interdisciplinary team has been collecting extensive field data in ghost forests along the Delmarva peninsula, USA. The review is based on field data and simple conceptual models that will inform sophisticated ecohydrological models of forest–groundwater interactions (e.g. Rodriguez-Iturbe, 2000, Rodríguez-Iturbe and Porporato 2007, D'Odorico et al. 2010).

In Figure 1 we report the main processes and interactions covered in this overview. Storm surges and sea level rise flood tree roots, increasing ground water and soil salinity in a complex manner (Section 2). In particular, storm surges homogenize the forest hydrology, killing trees and reducing biodiversity (Section 3). Soil properties can either mitigate or exacerbate the salinization process during storm surges (Section 4). While trees can initially adapt to saturated and saline soils by altering their root zones (Section 5), prolonged exposure eventually results in damage or death. Major salinization events are recorded in tree rings (Section 6). Tree dieback and the decomposition of belowground organic material can lower forest elevation, which in turn increases vulnerability to storm surge flooding (Section 7). However, storm surges may also deposit sediment that raises forest elevation.

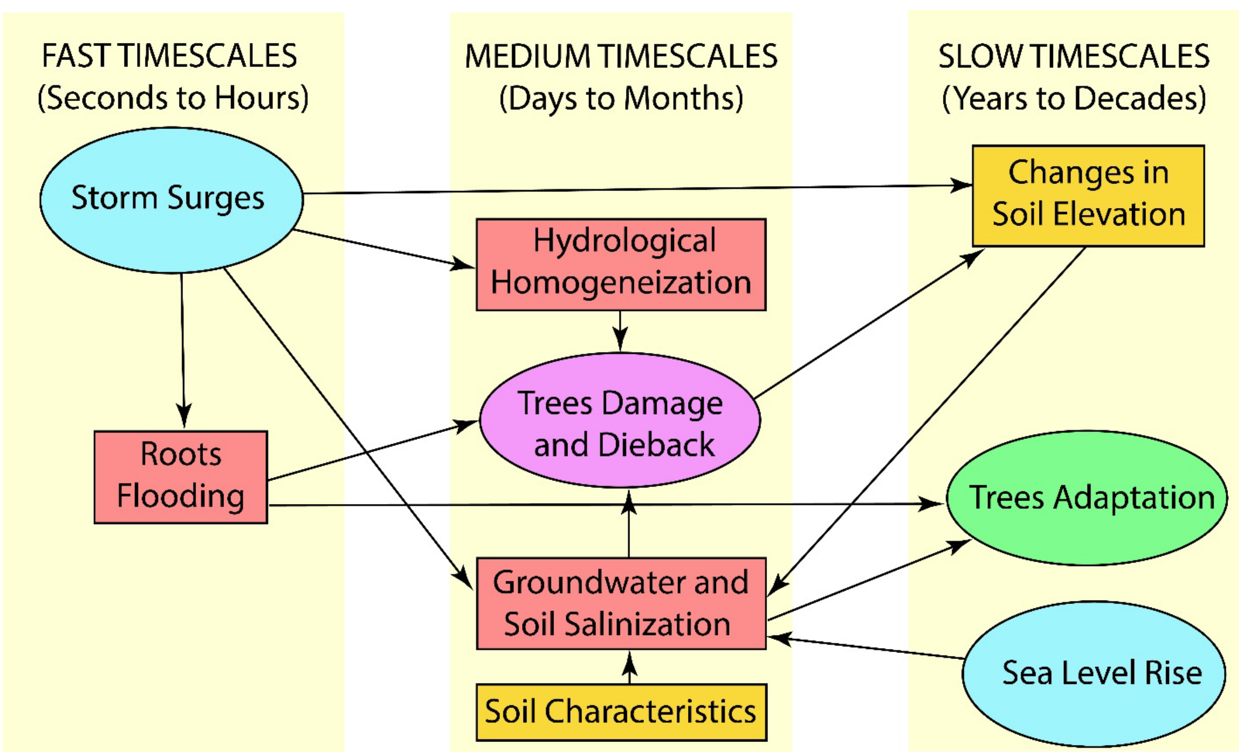

***Figure 1**: Processes affecting the ecohydrology of coastal ghost forests and related timescales.*

2. Hydrological processes causing forest ecosystem stress

The primary causes of marsh migration into forested uplands are increases in salinity and saturation of the root zone. These conditions stress upland trees and shrubs and support growth of saltmarsh vegetation. The drivers of these changes stem primarily from climate change, which upsets the balance of hydrologic forces – the ocean level on the seaside and the water table on the land side – and it is this balance that determines the salinity distribution in soils and groundwater. On the seaside, a rise in mean sea level increases the high tide mark, creating a new zone of regular saltwater inundation where marsh vegetation thrives (Figure 2, Zone A). Similarly, episodic extreme high tides and storm surges can propagate further inland, flooding freshwater ecosystems with saltwater (Figure 2, Zone B). The floodwaters infiltrate the soil, salinizing the root zone and shallow groundwater (Figure 2, Process 1 & Figure 3B) (Xiao et al., 2018). This process also causes saturated conditions during flooding (Figure 2, Process 2 & Figure 3A), and increases both soil moisture and the water table elevation for a period of time (Figure 3A and 3C). Evapotranspiration during the recovery period will accelerate pore drainage but can also cause evapoconcentration of salts (Yu et al., 2021), resulting in higher root zone salinities and potential formation of salt precipitates, which can subsequently dissolve during rainfall events (Geng & Boufadel, 2017), creating a secondary salt stress event. Along the Delmarva peninsula we saw shallow root zone salinization from both king tides and storm surges (Figure 3). During both events, we measured a rise in soil moisture and soil conductivity, as well as water table elevation (Figure 3A-C). The groundwater conductivity did not spike during these events (Figure 3D), indicating that the saltwater infiltrated vertically from the surface (Figure 2, Processes 1 and 2) and did not rise upward from movement of the subsurface interface and saturation from below (Figure 2, Processes 3 and 4). This dynamic may not occur in all coastal locations or during every flooding event. In steep coastal landscapes, the extent of flooding can be limited. Under very wet conditions, such as during storms with heavy precipitation, the infiltration of saltwater may be reduced due to already saturated soil.

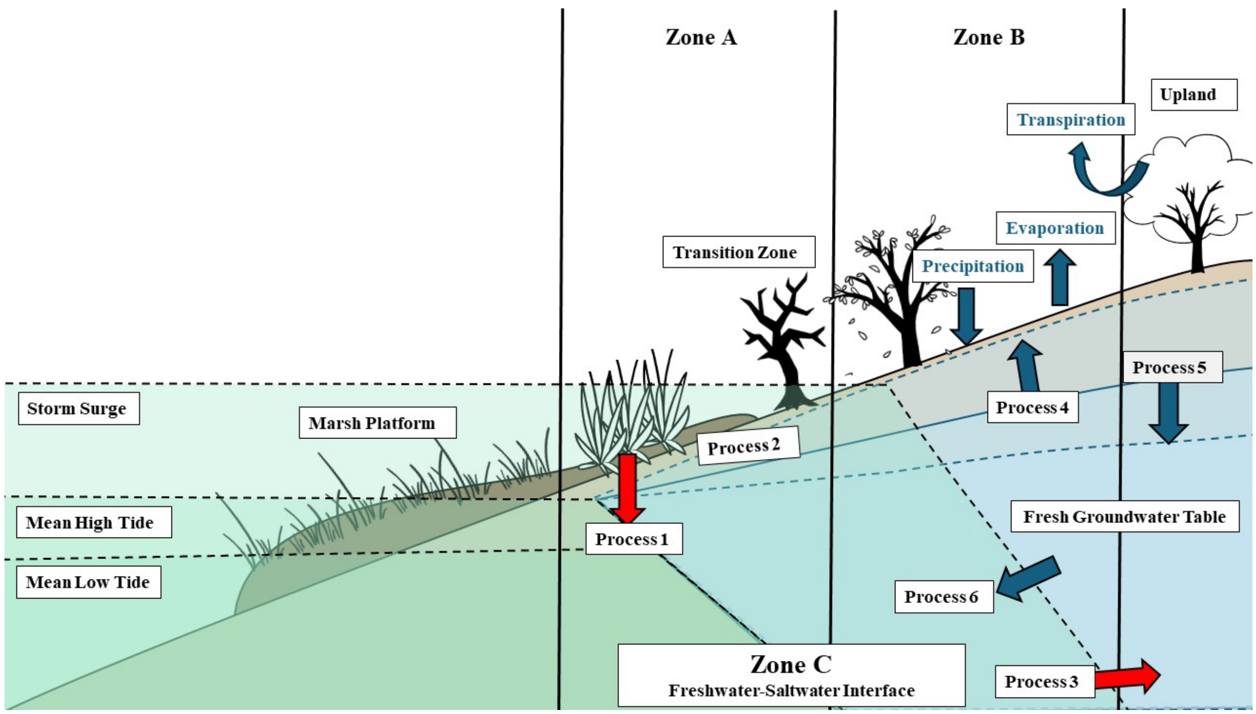

Figure 2: *Hydrological processes at the upland-marsh transition. Sea-level rise increases the level of mean and high tides, pushing the transition between saltmarsh and upland inland (Zone A). Increases in sea level and storm intensity also push periodic storm surges further inland into freshwater ecosystems (Zone B), salinizing (Process 1) and saturating (Process 2) soil and groundwater with saline surface water from above. Increases in mean sea level cause the deep freshwater-saltwater interface to move inland (Process 3) and the water table elevation to rise (Process 4), potentially causing surface flooding from below. Increases in net evapotranspiration and water extraction can cause the groundwater table elevation to fall*

(Process 5). After periods of heavy precipitation, the influx of fresh groundwater from the upland increases, pushing the freshwater-saltwater interface seaward (Process 6). The vertical dimension is deliberately exaggerated in the figure for clarity.

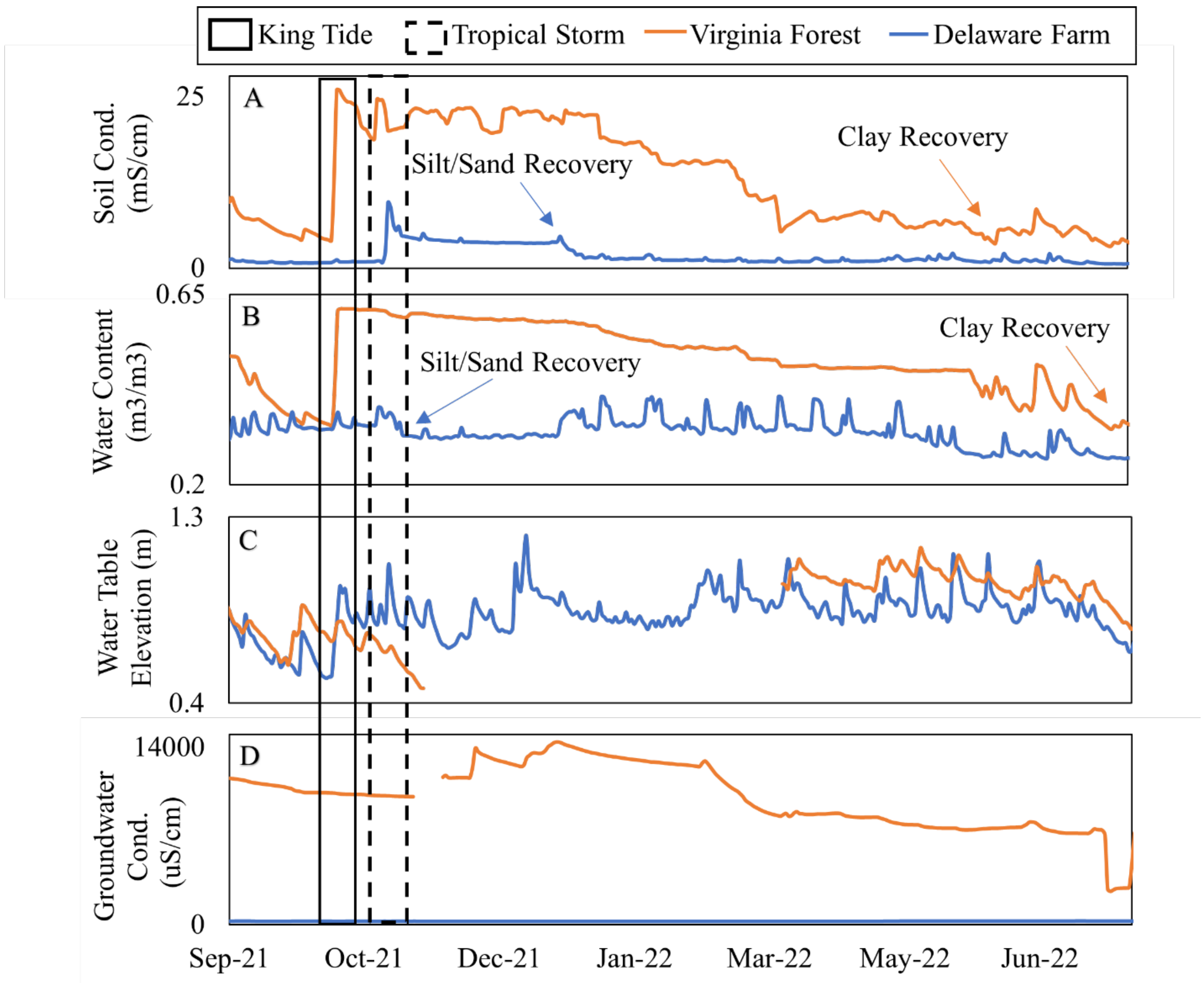

***Figure 3**: A: Volumetric soil water content, B: Soil conductivity, C: Water table elevation, and D: Groundwater Conductivity in a Virginia forest and a Delaware agricultural site during a king tide and tropical storm in 2021.*

While the surface salinization and flooding pathway is relatively easy to see and track, there is also a subsurface pathway that is less apparent and responds to different mechanisms and timescales of change. In the saturated zone, the location of the interface between fresh and saline groundwater (Figure 2, Zone C) reflects an equilibrium between sea level and water table elevation. A rise in mean sea level that is not balanced by an equal rise in the water table will cause saline groundwater to move inland (Figure 2, Process 3). For a given recharge rate, as sea level rises, the water table also rises and generally keeps pace with SLR. The extent to which this rise occurs, however, depends in large part on the topographic gradient in the upland, since a rise in the water table above land surface will result in rejected recharge (i.e. overland flow toward the marsh fed by groundwater see Michael et al., 2013). A drop in the mean water table elevation, due to drought (Drexler and Ewel, 2001) or groundwater pumping (Houben and Post, 2017) for example, will produce the same salinization effect. These two processes – SLR and water table decline – similarly increase subsurface salinity, yet they have opposite effects on root zone saturation. SLR and increases in rainfall will raise the water table and induce root zone saturation (Figure 2, Process 4), whereas a mean water table decline deepens the unsaturated zone and tends to reduce incidence of root zone saturation (Figure 2, Process 5). If the influx of fresh groundwater from the upland increases, such as during periods of heavy rainfall, the freshwater-saltwater interface shifts seaward (Figure 2 Process 6).

Whether ecosystem stress leads to vegetation mortality depends on the magnitude of the stressor and its frequency and duration. The primary controls on the maximum salinity are the salinity of the adjacent tidal surface waters, the availability of freshwater for dilution, and the potential for evapoconcentration. Each of these may vary over time as a result of climatic and anthropogenic change. Flooding waters during storms will likely become more saline with SLR, rainfall patterns and intensity may change, and evapotranspiration will increase marginally with temperature rise and substantially with ecosystem change. For example, tree dieback reduces transpiration, while the encroachment of shrubs and grasses could increase it. Additionally, a reduction in canopy cover would lead to higher evaporation rates in the top layers of soil.

The controls on stressor frequency and duration are perhaps more complicated. As sea level rises, the frequency of both salinization and saturation events will increase at a given position along the marsh-upland transition, because a given tidal amplitude or surge height will have a higher elevation and reach further inland. In addition, the frequency and intensity of surges have increased (Xiao & Tang, 2019), indicating that not only is the base surface water elevation rising, but the amplitude and frequency of these surges are also increasing. These processes lead to more frequent occurrences of both salinization and land surface saturation (Figure 2, Processes 1 and 2). Root zone saturation events from below (Figure 2, Process 4) are anticipated to rise in both frequency and duration as sea levels continue to increase. Furthermore, some coastal regions may experience higher average rainfall or more frequent extreme rainfall events.

These processes occur episodically, with fast hydrologic events sufficient to trigger stress. In contrast, the subsurface salinization mechanism requires longer timescales due to the slower movement of the freshwater-saltwater interface (Figure 2, Process 3). This shift depends on sustained changes in the land-sea hydraulic gradient, as the interface moves at the rate of advective groundwater flow. At our field sites, when the hydraulic gradient is negative, there is reversed flow and landward movement of the groundwater freshwater-saltwater interface (Figure 2 Zone C, Process 3). Figure 4 indicates the reversal of the hydraulic gradient during August-December 2022 and the increase in groundwater conductivity as well as the reversal back to normal flow in December 2022 and subsequent groundwater conductivity recovery. Vegetation can partly adapt to these salinization events. Plants can transport fresh water to saline areas via roots through hydraulic redistribution. During droughts, loblolly pine stands (*Pinus taeda*) are able to maintain high water potential in the upper soil layers by redistributing water through this mechanism (Domec et al., 2010). Hydraulic redistribution can thus help sustain transpiration and photosynthesis during dry periods. However, in saline soils, the accumulation of ions in the root xylem sap and leaf apoplast can inhibit hydraulic redistribution (Bazihizina et al., 2017).

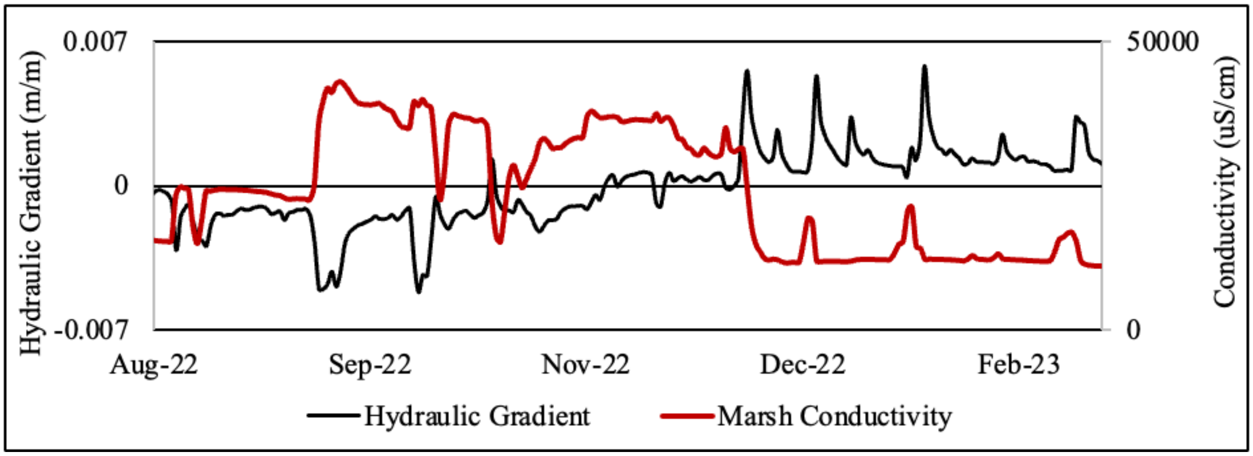

Figure 4*: Hydraulic gradient and conductivity of groundwater below the marsh at a Virginia farm site.*

The duration of stressor events is dependent on the duration of episodic events: duration of the high tides, storm-driven surge, and seasonal changes in the hydraulic gradient, for example. But this is only part of the story, as stressor duration also depends on the length of time needed to reset the salinity and moisture distributions – the time to flush saltwater out of the root zone, to drain the unsaturated zone, or to drop the water table. These timescales can be orders of magnitude longer than those of episodic events and may be influenced by factors beyond hydrology. For example, soil hydraulic properties are critical, as clayey soils tend to flush salt more slowly and take longer to drain than sandy soils (Taylor & Kruger, 2019). At a Delaware farm site, the soil conductivity takes about 3 months to recover following a surge, and soil moisture only one week to recover (Figure 3A & B). At a Virginia forested site, the soil conductivity takes 6 months to recover following a surge, and soil moisture can take up to 10 months to recover (Figure3A & B). This is due to much higher average surface sediment permeability at the Delaware site compared to the Virginia site, which allows for faster flushing and recovery times following a surge.

Vegetation response to salinization can also contribute to soil salinity recovery. High soil salinization following a storm surge reduces the photosynthetic activity of vegetation, which in turn lowers transpiration rates (Woods et al., 2020; Antonellini & Mollema, 2010). Reduced transpiration prevents further salt concentration and facilitates salt dilution by precipitation.

3. Coastal forest homogenization and biodiversity loss due to storm surge events

Many studies have focused on the hydrological, ecological and geomorphological consequences of hurricanes, characterized by large storm surges (Fernandes et al. 2018; Middleton 2016; Gardner et al. 2002; Fagherazzi et al. 2019a; Paudel and Battaglia 2021, Ury et al. 2021; Seyfried et al 2023). Recently, more attention has been paid on the effects of frequent and moderate storm events on coastal areas (Beebe et al. 2022; Wilson et al. 2015; Wilson et al. 2011; Nordio et al. 2023; Richardson et al. 2024).

In Nordio et al. (2023) we focused on the effects of frequent storms triggering moderate surges on the groundwater systems. The tropical storm Melissa occurred on October 11-14, 2019, and affected the North Atlantic coast of the USA from North Carolina to Massachusetts. During this event, coastal water levels reached between 1 and 1.5 m above predicted levels (National Oceanic and Atmospheric Administration). An event of the magnitude of tropical storm Melissa has a return period, or frequency, of about 1-2 years.

To determine the groundwater response to this storm we used groundwater level and conductivity data we collected in eleven stations plus data from nine USGS station stations along the Mid Atlantic coast of the United States (Nordio et al. 2023). Each station was characterized by different soil properties and ecosystems. Recovery time was computed from data collected at each station for a period of one week. We found that recovery time for groundwater conductivity was ten times greater than the recovery time for groundwater level. Furthermore, in a soil composed of 80% of clay the recovery time for conductivity reached 50 days.

The estimated recovery time from a medium-intensity storm surge is shorter than that after a hurricane (Cardenas et al., 2015; Vithanage et al., 2012). However, hurricanes are less frequent, which reduces the overall duration of salinization compared to that caused by moderate storms. Ratios between groundwater recovery time and return period for the Melissa storm were compared to similar ratios derived from the literature for other storms that affected coastal sites around the world (Figure 5). The ratio represents the average percent of days in a year during which the area is salinized, with conductivity well above average seasonal values. In the long-term, storms like Melissa produce lasting effects comparable to strong hurricanes of category 3 and 4. A recovery timescale of months for groundwater specific conductivity can be crucial for salt-intolerant vegetation, particularly if it occurs with a return period of only one/two years. For example, salinity levels of 8 ppt sustained over six months can cause a 40% mortality rate in loblolly pine (*P. taeda*) stands and a 20% mortality rate in pond pine (*P. serotina*) stands (Poulter et al., 2008). In a glasshouse experiment, 60% of *Baccharis halimifolia*, 60% of *Myrica cerifera*, and 20% of *Juniperus virginiana* plants died after 30 days of flooding with saline water (10 g/L). At lower salinity levels (2–5 g/L), stomatal conductance was significantly reduced (Tolliver et al., 1997).

Post-surge values for both groundwater levels and conductivities were significantly higher than the pre-storm surge values. The results also indicate a significantly smaller variance in the post-surge conductivity and groundwater levels. This similarity across the wells after Melissa suggests more homogeneous post-storm hydrological conditions. Hydrological variability is crucial for biodiversity at most scales of analysis (Konar et al. 2013). Therefore, this homogenizing phenomenon could drastically reduce biodiversity and affect ecosystem functioning (Konar et al., 2013). However, it is important to note that hydrological homogenization can be short-lived, with some sites eventually recovering to pre-storm conditions. When temporal variations in salinity are significant, the homogenization effect on biodiversity becomes less clear. At some coastal locations, sea level rise and frequent tropical storms have already started to change the environment with an irreversible impact on biodiversity (Allen and Lendemer, 2016; Burkett et al. 2008), changes that could consequently affect the socio-economics of coastal communities (Sylvain and Wall, 2011; Midgley 2012). In this scenario, along forested areas close to marshland, mature trees can defoliate or die (Fagherazzi et al. 2019a). Seedlings are more sensitive to specific conductivity increase while mature trees can show greater salt tolerance (Poulter et al. 2008; Kirwan et al. 2007). For instance, the groundwater specific conductivity levels measured during the Melissa storm surge in a forest in Virginia were between two and five times higher than the tolerated conductivity levels of *Pinus taeda*, the dominant tree species at the site (thresholds~8 mS/cm, Poulter et al 2008). These high salinity levels compounded with the flooding stress affect photosynthetic activity, stomatal conductance, and biomass production (Pezeshki 1992).

The storm surge homogenization process was also studied by clustering hydrological variables and comparing them to forest ecological patterns. Linear Discriminant Analysis (LDA) was conducted by grouping all the groundwater and soil moisture variables collected in each site in Virginia (Nordio and Fagherazzi, 2022a). During a storm surge event, the clusters identified by LDA, which represent hydrologically and ecologically distinct forested sites, collapsed, confirming the homogenizing effect of the surge. In Figure 6b we show an example of the hydrological zonation in normal spring conditions, while Figure 6a reports hydrological zonation after a storm surge in the same season.

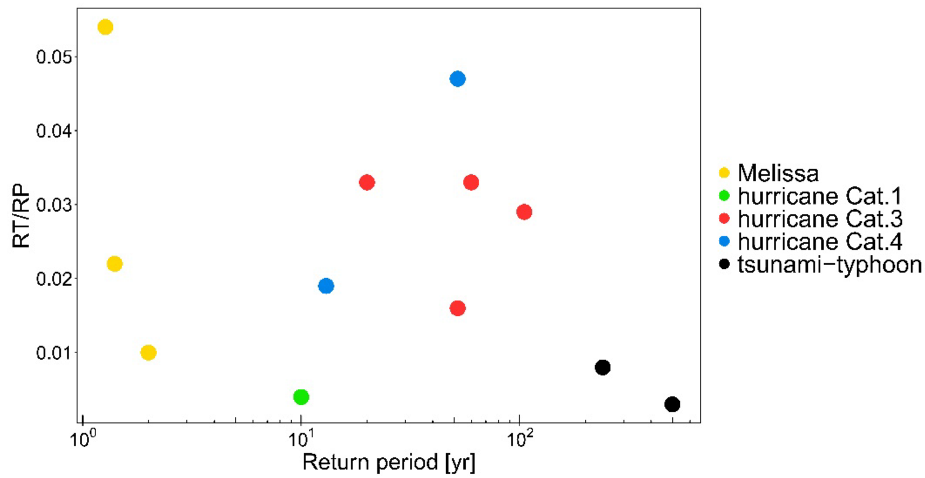

Figure 5*: Ratios between recovery time (RT) and return period (RP) for different storm events. Storms with a return period of 1-2 years can have the same effect of large and less frequent storms. Each Melissa point represents a different location where data were collected. The hurricane and tsunami-typhoon data were derived from the literature (modified after Nordio et al. 2023).*

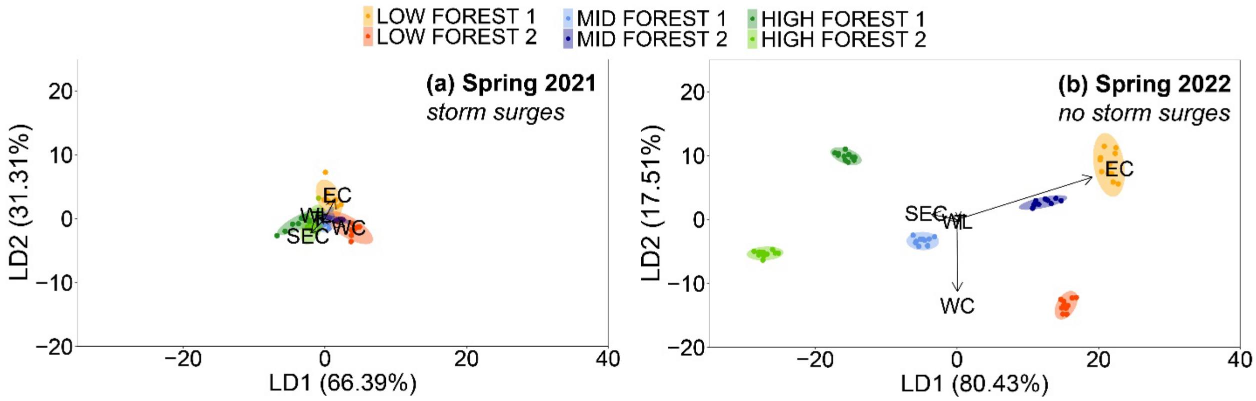

Figure 6: *Linear Discriminant Analysis of hydrological data in a coastal forest in Virginia. In Spring 2021 a storm surge flooded the forest. Arrows are proportional to the linear function loadings. The low forest sites are located near the salt marsh, while the high forest sites are situated upland. WL=groundwater level, EC= groundwater electrical conductivity, T=temperature, WC= soil water content, SEC=soil electrical conductivity (after Nordio et al. 2024).*

4. Effect of edaphic conditions on post-storm salinization

The ecohydrology of the root zone plays an essential role in coastal vegetated areas. Using the numerical model HYDRUS, we focused on the root zone dynamics during a storm surge event. HYDRUS 1D is a one-dimensional model that simulates water, heat and solute movement in a variably saturated medium (Šimůnek 2005). We estimated the impact of storm surge events on soils with different properties and different pre-storm conditions. In a sandy soil, salinization due to storm surges affects the entire unsaturated soil, contaminating the groundwater. In soils with a higher percentage of clay and silt salinization only partially involves the unsaturated root zone. The draining properties of a soil are important for the hydrological recovery to pre-storm conditions. However, in sandy areas, saltwater infiltration can easily reach the groundwater, salinizing critical water supplies (Barlow and Reichard, 2009).

In clay soils, characterized by low hydraulic conductivity, salinization only involves the first layers of the root zone. Although recovery takes longer than in sandy soils, roots are partially affected. In deep layers, the salinity does not increase. As a consequence, the soil column is stratified in terms of soil salinity and this stratification can be exacerbated by evaporation, transpiration and rainfall events (Liu et al. 2018; Guo et al. 2015; Geng and Boufadel, 2015).

The significance of storm surge characteristics and initial soil conditions on the increase in soil salinity was evaluated by considering various scenarios involving storm surge height (SSp), flooding duration (SSt), salt concentration in the flooding water (SSC), as well as initial soil water content (WCi) and soil salt concentration (Ci0). In soil characterized by higher percentage of sand such as sandy clay loam soil (SCL), the salt-concentration increase (ΔC) is controlled by surge salinity (Figure 7a). In soils consisting of silt and clay, pre-storm edaphic conditions become more important (Figure 7b-c). The initial water content and salinity of the soil are particularly important in coastal areas characterized by clay and silt. In these types of soils, salt concentration reached during a storm surge are extremely dangerous for salt intolerant vegetation survival.

Studies that focus on the role of initial conditions on the impact of extreme events are few, particularly in vegetated coastal areas. Our results highlight the significance of pre-storm conditions on coastal flooding, concentrating on the vertical saltwater infiltration and its consequences for local ecosystems. Moreover, higher soil water content likely limits the saltwater infiltration during storm surge flooding in low-lying areas. Here, the unsaturated zone is often thin over the year and saltwater infiltration is reduced, encouraging runoff and ponded conditions. Higher soil salinity values reached in fine soils when initial hydrological conditions are lower are exacerbated by the post-storm recovery process. Due to their low permeability, fine soils slow the saltwater dilution after the surge, undermining the survival of the salt intolerant vegetation.

Field data on water content and conductivity increases due to storm surge events, collected in a Virginia forest (Nordio and Fagherazzi, 2022a), confirm the results of the numerical model (Figure 8). In soil comprised of 80% clay the conductivity (proxy for salinity) is negatively correlated to water contents (Figure 8). Therefore, if the soil is already saturated with freshwater before the storm surge, less saline water can infiltrate, reducing salinization in the root zone.

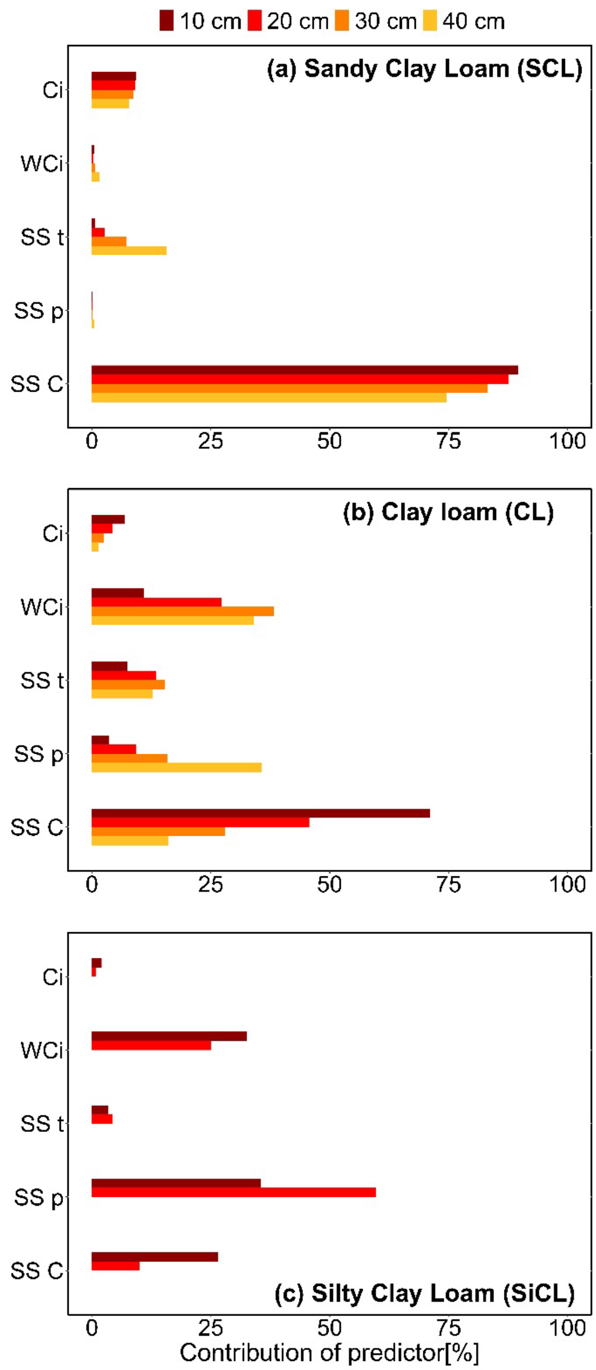

***Figure** 7: Contribution of pre-storm edaphic conditions and surge characteristics to soil salinity increase. SSp is storm surge height, SSt is storm surge flooding time, SSC is salt concentration in the surge water, WCi is water content in the soil the day before the storm, and Ci is salt concentration in the soil water the day before the storm (after Nordio and Fagherazzi 2024).*

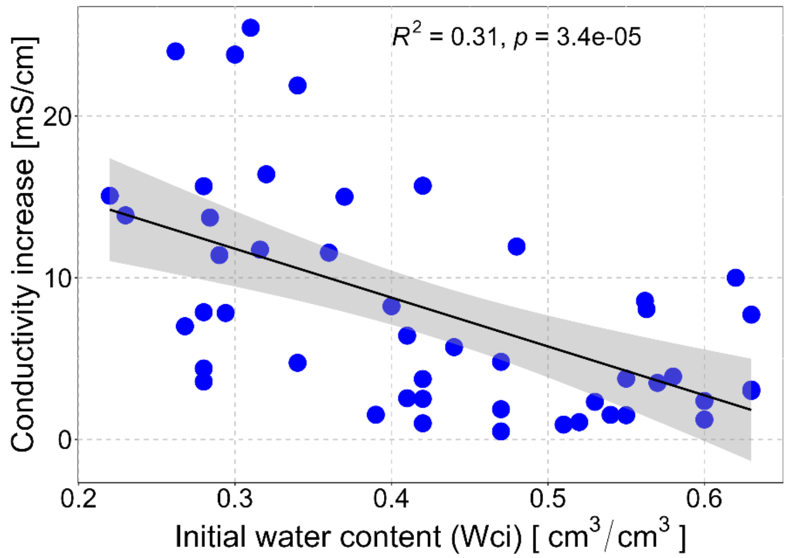

Figure 8*: Electrical conductivity increase driven by a storm surge in different sites of the Delmarva Peninsula as a function of initial water content (after Nordio and Fagherazzi 2024).*

5. Tree freshwater islands detected from geophysical data

Water content and salinity drastically affect subsoil electrical conductivity, making it possible to explore water table fluctuations and sea water transgressions along the coastline with geophysical methods. Among these, electrical resistivity tomography (ERT) has been widely applied in the unsaturated zone (Cassiani et al 2006) to monitor the effects of root system activities (e.g. Cassiani et al., 2015, Wadas et al 2022, Boaga et al 2014). ERT needs electrodes and cables installation assuring galvanic contact with soil and may be limited by logistics in some humid marshes or thickly vegetated forest boundaries, restricting the use for large-scale exploration. An alternative for the assessment of ground electrical properties is offered by electromagnetic contact-less methods, such as the Frequency Domain Electro-Magnetometers (FDEM, McNeil 1980, Boaga et al 2018). Different investigation depths can be explored adopting either multi-frequency instruments or multi-coils probes. Thanks to inversion procedures it is possible to retrieve accurate subsoil electrical models (Deidda et al. 2014; Diaz De Alba and Rodriguez 2016).

In March 2023, we collected FDEM data at a site in the Delmarva Peninsula, Virginia (USA), to detect the increase of soil salinity in the transition zone between the forest border and the salt marshes. Saltwater intrusion and periodic flooding regulate the ecotone. From the inland areas to the coastal marshes, we collected data across a forest of loblolly pines (Pinus taeda) and a transition zone dominated by woody shrubs, including Juniperus virginiana, Iva frutescens, Baccharis halimifolia, and Myrica cerifera (Brinson et al., 1995; Fernandes et al., 2018), before reaching the marsh vegetation dominated by Spartina patens (Nordio and Fagherazzi, 2022b).

The data were acquired with a CMD-Explorer FDEM probe to map the electrical properties of the first meters of subsoil. In the marsh environment we focused on the root zone, adopting a CMD-MiniExplorer 6L probe (Table 1) for a more detailed imaging of the shallow subsoil. We filtered the raw FDEM data from outliers and then we inverted the datasets using the python-based code Emagpy (McLachlan et al 2021).

Model	Frequency (kHz)	Coils spacing (m)	Nominal Depth range (m)
CMD-Explorer	10	1.48-4.49 m	1.1 -6.7 m
CMD-MiniExplorer 6L	30	0.32-1.18 m	0.3 -2.1 m

Table 1 Specifications of FDEM probes CMD Explorer and CMD MiniExplorer 6L used in this study.

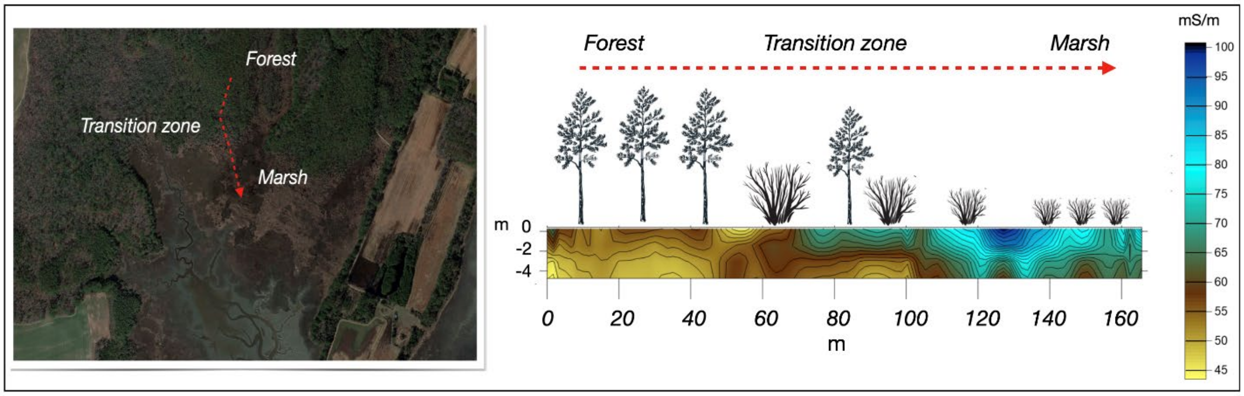

Figure 9 FDEM transect from the inland forests to the salt marshes and corresponding subsoil electrical conductivity in mS/m

Figure 9 shows the results of the inversion for the transect. Possible evidence of seawater transgression is indicated by the high conductivity values near the marsh in the FDEM transect. Here, conductivity may also be elevated due to evapotranspiration and subsequent salt concentration in the surface layers. Interestingly, conductivity decreases with depth, indicating that salinization is primarily caused by surface flooding rather than lateral intrusion. Lateral groundwater movement from upland areas could also contribute to the lower conductivity observed in the deeper aquifer layers.

Near the marsh, tree dieback makes light available to shrubs, with few sporadic trees still alive. Shrub zones are natural ecotones between marshes and uplands, and dieback and regrowth within these areas may be cyclical. Detailed FDEM measurements around isolated trees provide evidence that the root zone persists in less saline subsoil portions (Figure 10). The roots of these trees developed horizontally to avoid the saturated saltwater layer (see Figure 11a). Roots might also have dieback at depth because of salinization. Isolated trees appear to coincide with the presence of islands of fresh water in the otherwise very conductive salt marsh soil, as the 3D

FDEM inverted image indicates (Figure 11b). These tree roots appear to exploit natural relief or, intriguingly, alter the soil elevation around them to protect against soil salinization. Additionally, they may also facilitate the movement of precipitation freshwater to the root zone through stem flow. Recent research showed that roots were longer and more numerous in the direction of freshwater (Messerschmidt et al., 2021). These findings pose interesting perspectives on tree adaptation and future development of geophysical monitoring in these transition environments.

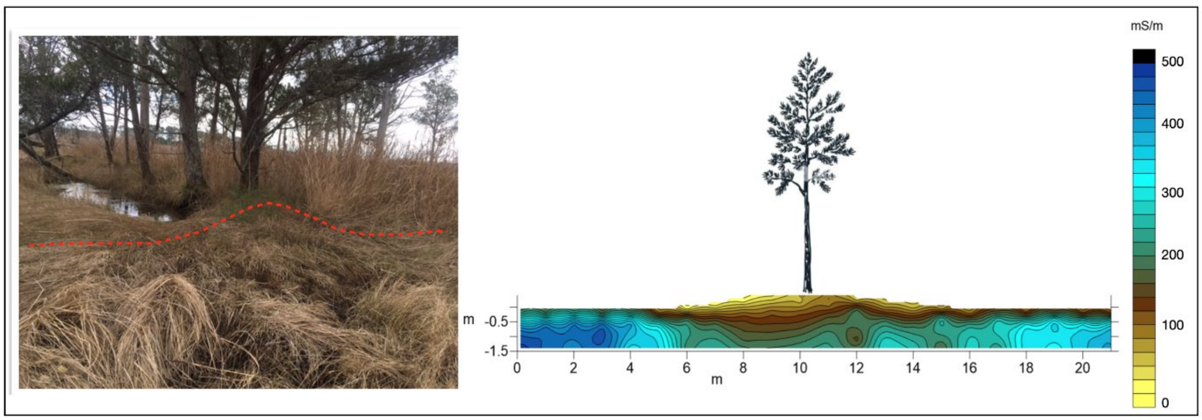

Figure 10. FDEM Transect across an isolated tree in a salt marsh area.

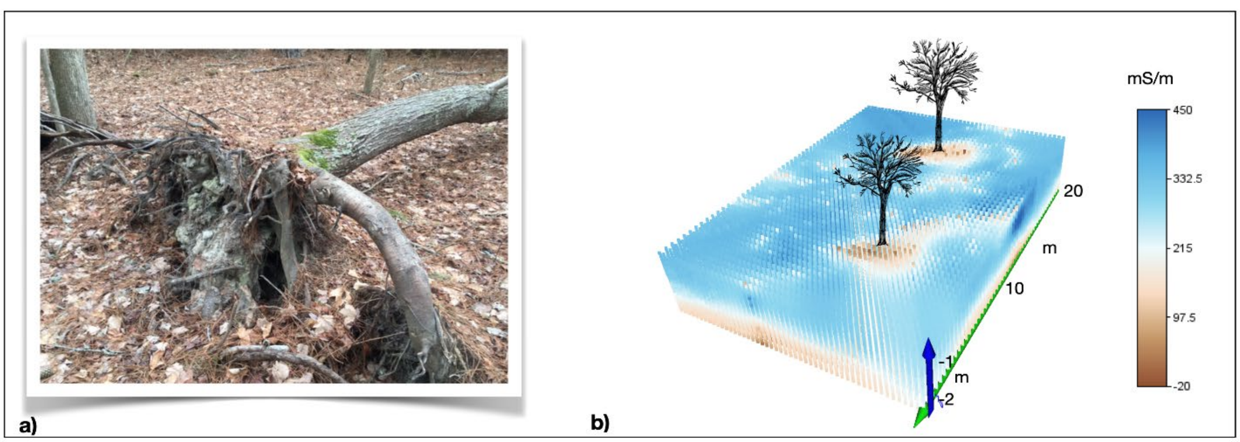

Figure 11. a) Roots of a dead tree in the Delmavra Peninsula marshes. b) FDEM 3d inverted results of a marshland plot; the brown low conductive zones correspond to the presence of 2 isolated trees.

6. Salinization effect on coastal forests

Salinization and flooding in coastal forests reduce trees water uptake thus affecting the hydrology of the ecosystem (Duberstein et al 2020; Krauss and Duberstein 2010). Hypoxia decreases the capacity of roots to acquire water (Pedersen et al., 2021; Dat et al 2006), while the elevated osmotic potential of saline water reduces the water flux through the roots (Boursiac et al 2005; McDowell et al 2022). Salinization also results in decreased hydraulic conductivity of trees (Stiller 2009; Zhang et al 2021). Primary mechanisms for conductivity decline may include osmotic stress (Munns and Tester 2008, Mendez-Alonzo et al 2016) or salt toxicity (Munns and Tester 2008, Zhang et al 2021), either of which can lead to carbon starvation (Matallana-Ramirez et al 2021), impaired hydraulic function (Zhang et al 2021), and cavitation within the xylem, triggering hydraulic failure (McDowell et al 2022; Tyree & Sperry, 1989). The ability of trees to reduce ground and surface water levels is non-trivial as forests play a role in the regulation of the hydrologic cycle by transferring ground water to the atmosphere through transpiration (Bonan 2008). The difference between precipitation and ecosystem-level evapotranspiration determines the excess water available for runoff, drainage, and recharge (Ward et al 2018). In plantation settings, trees have even been associated with reduced annual streamflow in nearby streams (Jackson et al 2005). In the *Pinus* genus, common in Mid-Atlantic coastal forests, water is transported through tracheid within the xylem of sap wood, with the majority of transport occurring in the outer most rings and rapidly declining radially towards the pith (Bodo and Arain 2021, Ewers and Oren 2000, Ruzol et al 2022). If trees respond to salt exposure with a reduction in wood tissue production, their ability to transfer ground water to the atmosphere may also be affected with ramifications to the system's hydrologic cycle.

For example, a reduction in transpiration would help maintain higher water levels in the soil, preventing the infiltration of additional saltwater during storm surges. While this reduction in transpiration could delay further forest salinization, it also favors soil water saturation, which may trigger hypoxia and more stress in the trees (McDowell et al 2022).

Tree cores can be used to determine the response of coastal forests to salinization (e.g. Kirwan et al., 2007; Fernandez et al., 2018; Hall et al. 2022). Here we report an analysis of tree cores in a Maryland coastal forest. Eighty-one Pinus taeda trees located within the transition zone between forest and salt marsh were cored in January 2020, and their years of germination were analyzed for a regeneration event study.

Germination dates indicate an establishment period from approximately 1925-1930 with subsequent regeneration events occurring in the early 1930s and 1960s. The last tree within our analysis germinated in 1978 (Figure 12). Interestingly, several regeneration events appear to occur immediately after major hurricanes in 1933 (Weightman 1933), 1938 (Roth 2006) and 1939 (Tannehill 1939). The average basal area increment (BAI) rose steadily between 1925 and 1976, then began to decline (Figure 12). Typically, BAI increases steadily, then levels off as the tree ages with a sigmoidal growth pattern (Weiner and Thomas 2001). However, some studies in *P. taeda* have shown a decline in BAI with age (Cheng et al 2014, Weiner and Thomas 2001). Here, the decline in BAI, combined with the simultaneous cessation of regeneration, indicates that tree decline began in the late 1970s. Several anomalies in the declining BAI trend occur post 1980. Significant, multi-year recoveries in BAI began in 1986 and 2012, each followed by 4 to 7 years of increased BAI before a subsequent decline. Both events followed multiple storms with significant precipitation over short periods of time. Hurricane Danny, Tropical Storm Henri and Hurricane Gloria in 1985. Hurricane Irene and Tropical Storm Lee in 2011, and hurricanes

Isaac and Sandy in 2012. The reversal in BAI trend following multiple high precipitation events could be explained by a flushing of salt contaminated soils. Other studies have also indicated increased tree growth in salt stressed systems following years with high fall precipitation (Hall et al 2022).

The maximum 4-year BAI occurred from 1989 to 1992, while the minimum 4-year BAI was recorded from 2005 to 2008, reflecting a 61% reduction in woody tissue production. This decline could lead to a substantial reduction in water uptake by the forest, potentially accelerating system inundation while possibly reducing salinization.

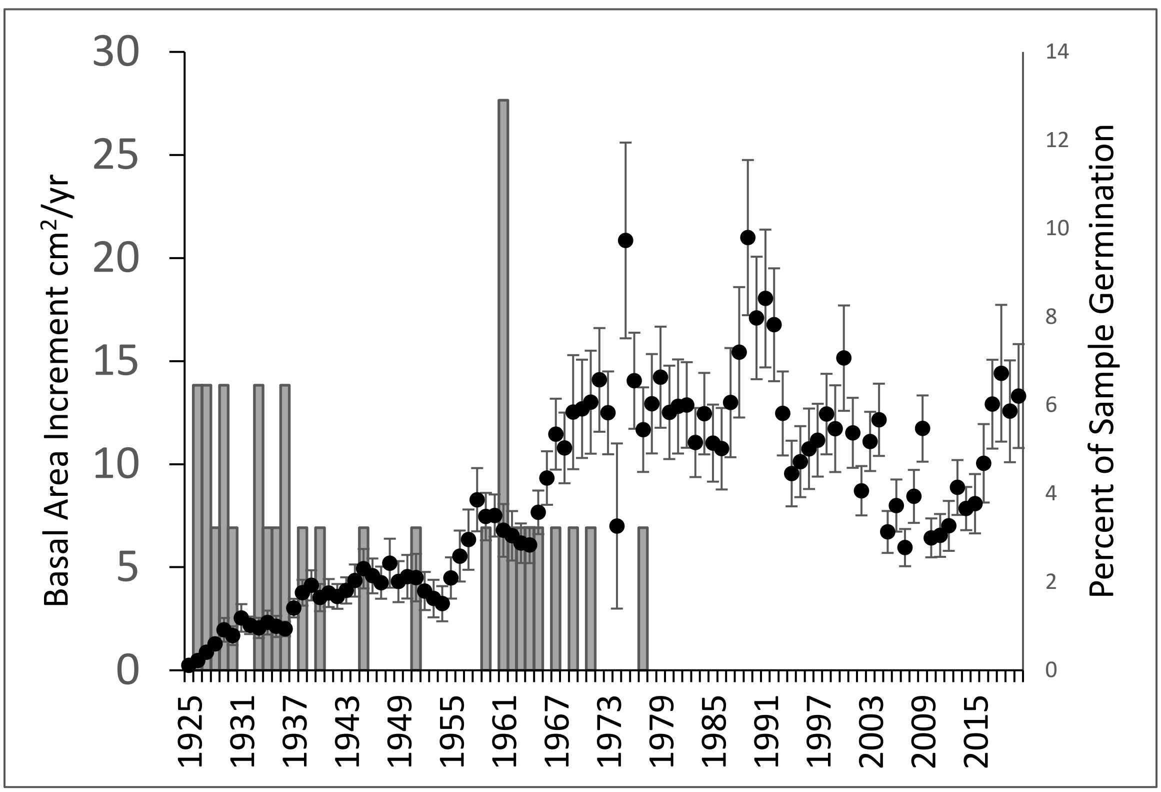

Figure 12: *Basal area increment from trees growing within the transition zone at Monie Bay, Maryland (black dots and bars representing standard error) with tree germination on the secondary axis (indicated with grey boxes).*

Tree rings analysis can therefore provide an excellent picture of the long-term effects of hydrological stressors on forests. The example provided herein indicate that trees do respond to major salinization events triggered by tropical storms, and also respond to heavy rainfall events that flush the salt in the soil.

6. Hydrological controls on accretion and subsidence at the marsh-forest boundary

Projections of sea-level driven marsh migration into retreating coastal forests assume a static topography, where the elevation of the soil surface remains constant through time (Kirwan at al. 2016, Schuerch et al. 2018, Osland et al. 2022; Molino et al 2022). However, geomorphic processes including accretion, subsidence, and erosion are well known to influence the elevation of other coastal environments during sea level rise (FitzGerald et al. 2008; Kirwan and Megonigal 2013; Potouroglou et al. 2017). Hydrology and elevation are thoroughly intertwined. Elevation and topographic slope directly affect groundwater discharge and inundation frequency (Yu et al. 2016, Michael et al. 2013), while indirectly controlling hydrology through plant species distribution and its effect on evapotranspiration (Field et al. 2016, Poulter, et al. 2009, Stagg et al 2020, Wendelberger and Richards 2017). In turn, hydrologic processes are a strong control of both ecologic and geomorphic processes at the marsh upland boundary (Langston et al. 2017, Miller et al. 2021, Williams et al. 1999b, Whelan et al. 2005). Therefore, it is important to understand the complex interactions between hydrology, geomorphology, and ecology. Elevation gain at the marsh forest boundary is possible during large storm events through deposition of sediment on the soil surface (Gardner et al. 1992, Whelan et al. 2009, Williams and Flanagan 2009), or through soil organic matter accumulation associated with transitional species such as *Phragmites australis* that produce large quantities of belowground biomass (Rooth et al.

2003). Marsh soil may expand due to the growth of pore space with flood waters or shrink due to compaction during drying (Cahoon et al. 2011). Conversely, sea level rise may also lead to elevation loss. For example, salt exposure may change the soil pore size creating a possible mechanism for soil collapse (Chambers et al. 2019), and pulses of salt water can stimulate higher decomposition rates (Sirrianni et al. 2023; Weston et al. 2011). The death of adult trees and the collapse of their root structures can lead to subsidence, especially in organic rich soils (Middleton and David 2022, Miller et al. 2021, Cahoon et al. 2003). Thus, the elevation of the marsh-forest boundary is controlled by complex and potentially competing processes.

Even small changes in elevation can have significant ecological and hydrological impacts, as coastal hydrology and ecology are closely intertwined and highly sensitive to such variations (Fagherazzi et al 2019a, Kearney et al 2019). For example, a local reduction in soil elevation may create sloughs and hollows that retain ponded water, causing damage to forest vegetation (Pezeshki et al. 1990). Vegetation loss in these flooded zones would reduce both aboveground litter deposition and belowground organic matter production, further decreasing the relative elevation compared to nearby areas. The hydrological pathways of shallow floodwaters and rainfall are highly sensitive to microtopography (Courtwright and Findlay, 2011). As a result, changes in topography could influence flooding events and, consequently, vegetation cover.

To examine forest elevation changes, we installed rod surface elevation tables (RSETs) across a retreating coastal forest near Monie Bay, Maryland, USA. RSETs (Figure 13a) consist of a mechanical leveling device attached to a rod benchmark driven to refusal (Lynch et al. 2015). Three RSETs were installed in each of the high, mid, and low forest zones, representing a gradient of salt and inundation stress. The high forest is undisturbed, while the low forest borders the marsh and presents widespread tree dieback (ghost forest). The average elevations of the

RSETs are 1.00m, 0.81m, and 0.63m NAVD88 (NAVD88 approximates mean sea level in the region), respectively. These RSETs were paired with shallow pipes driven to ~30cm to measure shallow root zone processes and feldspar marker horizon layers to measure surface accretion. Based on previous work, we hypothesize that healthy forests will have nearly stable soil elevations, but that subsidence is likely in the low forest due to tree mortality and increased decomposition rates. Preliminary RSET results from Monie Bay suggest that elevations in the high forest are indeed stable (< -0.15 mm yr^{-1}). Unexpectedly, there was little change in elevation in the more salt affected mid (-0.5 mm yr^{-1}) and low (-1 mm yr^{-1}) forests, despite some temporal variability (Figure 13b). There was also no significant accretion above the feldspar marker horizon layers at any of the RSETs ($<$2mm at each location). This lack of accretion confirms there was no hidden subsidence in the RSET record that was offset by increased surficial deposition. The unexpected stability in measured soil elevations may indicate that elevation change only occurs during large events. Alternatively, increases in elevation from *Phragmites* belowground biomass may be offsetting decreases in elevation from tree mortality, resulting in measured net elevation change rates that are small. Subsidence rates that exceed 1cm yr^{-1} were documented in other types of coastal forests and suggest that subsidence could alter rates of marsh migration into uplands (Cahoon et al. 2003, Middleton and David 2022). Our measurements do not yet span the 5 years window recommended for establishing elevation change rate trends (Lynch et al. 2015).

The SET data also show an elevation fluctuation of about 7 mm between October 2021 and April 2023. This interannual variability in elevation is not fully explained but may be linked to long-term hydrological changes, such as yearly variations in groundwater table or soil moisture that impact edaphic conditions. Such fluctuations in elevation could influence microtopography, potentially altering flooding and infiltration patterns. The unexpected absence of subsidence in the preliminary RSET record, along with the presence of unexplained interannual oscillations, underscores the need for a deeper understanding of the factors controlling elevation change at the marsh-upland boundary and their potential effects on ecohydrology.

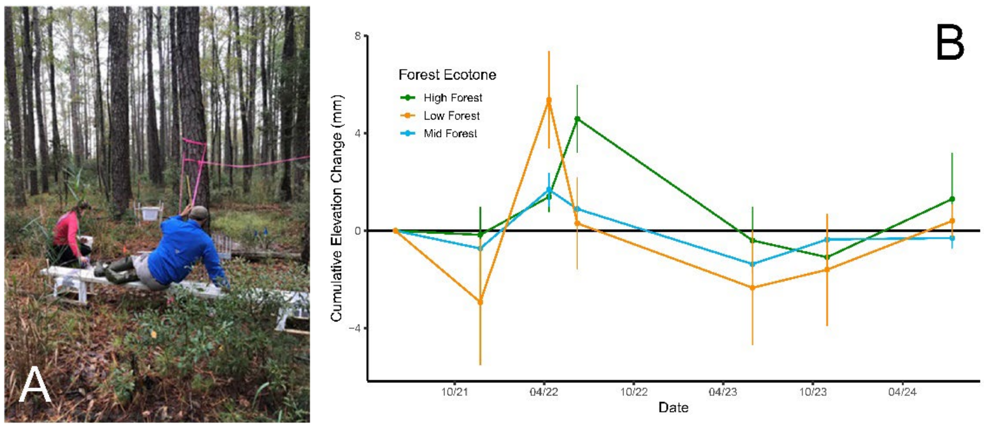

***Figure 13**: A) Measuring soil elevation with an RSET; B) Cumulative elevation change (mm) of the high, mid, and low forest at Monie Bay, MD. The high forest is undisturbed while the low forest is bordering the salt marsh. 2 years of monitoring is shown.*

Conclusions and future research directions for the ecohydrology of ghost forests

In this overview paper we showcase results of ecohydrological studies in ghost forests. Complex feedbacks between soil and groundwater hydrology, vegetation, and surface topography requires an interdisciplinary approach based on robust field data. As indicated in the examples presented herein, even limited data can inspire new, exciting hypotheses on the functioning of the salt marsh-forest ecotone and its hydrology. This field evidence and preliminary hypotheses can spur more sophisticated studies based on recent eco-hydrological advances (e.g. Porporato et al. 2002, Calabrese et al. 2017). The fast rate at which the salt marsh expands in the forest creates a perfect environment where to test theoretical ecohydrological models. The hydrology of ghost forests is complex, with groundwater salt intrusion, flooding by saline water, rainfall, and evapotranspiration all playing a pivotal role. The interplay between the gradual rise of sea levels over time and the sudden, intense impacts of storm flooding renders the system intriguing from a hydrological perspective.

The intermittent nature of rainfall and storm surges provides opportunities for applying new stochastic approaches developed in recent years (e.g. Kang et al. 2024, Del Jesus et al. 2015). Rapid variations in vegetation cover can strongly affect hydrology, by modulating water uptake and microclimate. Changes in vegetation are at the base of recent exciting results on ecohydrology (Rodríguez-Iturbe, and Porporato 2007, Huang et al. 2018, Huang et al. 2021). In ghost forests, these changes occur so rapidly that they allow for real-time measurements of key variables. The fast retreat of the forest and consequent expansion of the salt marsh allow for the use of space-for-time substitution, in which different locations of the forest can be used to represent different stages of the system. This enables a fast characterization of forest retreat at large spatial scales through surveys.

The interplay between hydrology, ecology, geomorphology, and biogeochemistry requires multidisciplinary teams conducting synchronous measurements. Vegetation response is complex, with tree dieback caused by different factors and occurring over long periods of time (Chen and Kirwan, 2024). For example, the distinct roles of salinization and flooding on tree stress are still unclear. Encroachment of new vegetation species is also complex and controlled by competition and facilitation mediated by hydrology (Jobe and Gedan 2021). Interdisciplinary collaboration is therefore warranted.

In the near future, there is a need to integrate conceptual models and field measurements in ghost forests with recent theoretical models of ecohydrology (e.g. Rodriguez-Iturbe 2000).

Additionally, there is a need to develop new theoretical frameworks based on the stochastic nature of storms that better represent the dynamics of the forest-marsh boundary.

Ghost forests are a stark reminder of sea level rise and the increasing frequency of storms. Both drivers are hallmark indicators of climate change. The ecohydrology of the forest-marsh boundary is therefore at the forefront of climate change studies, quantifying the effects of global warming on coastal ecosystems and communities.

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