












The hidden influence of terrestrial groundwater on salt marsh function and resilience

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Salt marshes are hotspots of nutrient processing and carbon sequestration. So far, studies addressing spatiotemporal variability in and drivers of salt marsh biogeochemical function, carbon storage and resilience have focused on ocean-driven surface hydrologic influences, neglecting effects of terrestrial hydrology through subsurface connections. Here we evaluate drivers of salt marsh redox potential, a proxy for biogeochemical state, through wavelet analyses and information theory using data from seven marshes. The results point to terrestrial groundwater level as a dominant control on redox variability across all sites. Because redox is a key driver of biogeochemical processes, and specifically oxidation of organic matter that sequesters carbon and maintains marsh elevation, these terrestrial influences are critical to understanding marsh function and evolution. The newly identified links between onshore groundwater levels and marsh redox conditions shift the traditional paradigm and suggest that terrestrial hydrology is a primary control on salt marsh carbon sequestration potential and resilience.

Salt marshes are biogeochemical hotspots with disproportionately high rates of nutrient and carbon cycling, making them a globally important ecosystem for carbon sequestration, alkalinity export and nutrient attenuation^{1,2}. Previous research has identified the systematic flooding by tides as a central modulator of salt marsh biogeochemical cycling and ecosystem function³. Similarly, assessments of salt marsh responses to climate change focus primarily on the effects of sea-level rise (SLR) and surface hydrodynamics on marsh resilience—the ability

to accrete in pace with sea level^{4,5}. Few studies have considered the role of terrestrial hydrology on salt marsh biogeochemical processes and climate change responses, despite documented marsh connectivity to terrestrial aquifers via their upland and subsurface boundaries⁶ and the influence of upland precipitation on the hydraulic gradients that interact with tidal processes⁷. Given the vulnerability of terrestrial aquifers to water level changes induced by climate change (for example, drought and extreme precipitation) and anthropogenic influences

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(for example, aquifer extraction)⁸, this knowledge gap brings about uncertainties in future salt marsh health and ecosystem services.

Redox potential (Eh) is an integrated measure of electron transfer reactions that serves as a proxy for the biogeochemical state of salt marsh sediments, which provides important insights into ecosystem function and indicates oxic–anoxic transitions, dominant biogeochemical reactions (for example, aerobic respiration, methanogenesis, sulfate reduction and denitrification) and the spatiotemporal variability in marsh sediment biogeochemical conditions^{9,10}. The redox state and its drivers are particularly important to understand in coastal wetland environments, as they have a direct influence on carbon cycling and resilience to climate change^{11–13}. Specifically, salt marsh resilience and carbon sequestration capacity are facilitated, in part, by organic matter accretion. The characteristically low Eh in the marsh sediment resulting from limited oxygen penetration due to saturated conditions slows organic matter decomposition and enables salt marshes to both persist in the face of SLR and store large quantities of atmospherically derived carbon. This low Eh is maintained by shallow marsh groundwater levels (MGWLs) and frequent surface water inundation^{14,15}. However, this means that any changes to land, ocean or atmospheric conditions that increase Eh will enhance organic matter oxidation, thereby reducing carbon sequestration capacity and the marsh's ability to keep pace with SLR. So far, studies on marsh water level fluctuations¹⁶ that control redox conditions and the resulting biogeochemical cycling^{17–19} have focused on tidal inundation, with few studies considering submarsh aquifer interactions^{6,20}. No study has identified subsurface connections to upland aquifers as an influence on marsh water levels that are critical to maintaining reducing conditions, nor the physical advection of biogeochemically unique groundwater into the marsh platform.

Coastal wetlands, composed of peat-rich sediments, are relatively young ecosystems (<4,000 years old)²¹ and are often underlain by shallow aquifers composed of sand or glaciofluvial deposits with interbedded clay lenses that can create localized semi-confined conditions²². The present understanding of coastal aquifer influences on salt marsh function focuses primarily on marsh hydrology and ecology at the marsh–upland boundary. Upland–marsh hydraulic head gradients drive vertical groundwater discharge to marsh sediment from the underlying aquifer across the marsh^{6,23} and have been shown to influence porewater salinity and the dominant vegetation at the marsh–upland edge²⁴. Grande et al.¹⁴ showed that terrestrial groundwater levels (TGWLs) also mediate marsh soil saturation and the magnitude of soil drainage during low tide¹⁴. However, the extent to which upland aquifers influence marsh hydrology, and the influence of hydrologic connectivity on marsh biogeochemistry and redox conditions, has not yet been considered.

In contrast to coastal wetlands, the role of aquifer conditions on terrestrial wetland hydrology and biogeochemistry is well established. Terrestrial wetlands are discharge zones for groundwater, and groundwater is often that ecosystem's primary water source²⁵. Due to this tightly coupled groundwater–wetland connectivity, changes in local aquifer conditions, such as groundwater withdrawal and drought, have been shown to drive wetland degradation and loss²⁶. Groundwater contributions have also been shown to affect terrestrial wetland biogeochemical processes directly through solute delivery and indirectly through the regulation of water table elevation²⁷. Thus, links between terrestrial groundwater and wetland biogeochemical cycling in coastal environments warrant investigation.

Here, we use wavelet and mutual information (MI) analyses at salt marsh sites on the Atlantic, Gulf and Pacific coasts of the United States to show that upland groundwater levels are a dominant control on low and high marsh Eh. Wavelet analyses enable assessment of the periodicity of a time series such as detecting seasonal or annual trends, and MI analyses enable evaluation of the mutual dependence between two variables (that is, how tightly coupled are two variables?). Our results identify terrestrial groundwater as a strong driver of salt marsh Eh,

challenging the paradigm of ocean processes as the central modulator of salt marsh ecosystem function and resilience. Findings from this study are critical for more informed projections of salt marsh biogeochemical changes with global climate change and highlight the need to consider terrestrial aquifer conditions and their future evolution when assessing salt marsh function now and into the future. Further, our results suggest that systematic groundwater depletion²⁸ in coastal areas not only threatens water supply through seawater intrusion²⁹ but also threatens the function and survival of coastal marshes.

Results and discussion

Terrestrial groundwater influences marsh Eh

We conducted a comprehensive data-driven analysis at two sites where continuous Eh, TGWL, MGWL and meteorological data are available: St Jones National Estuarine Research Reserve (NERR) in Dover, Delaware, and Elkhorn Slough NERR in Monterey Bay, California. Wavelet analyses were conducted using redox data from sites in the low and high marsh at St Jones and low, mid and high marsh at Elkhorn Slough to derive the dominant Eh oscillation frequencies. Site locations span from near the tidal channel (low marsh) to the upland edge (high marsh). MI was then used to quantify key factors causing temporal variability in Eh. Factors investigated included hourly TGWL, MGWL, precipitation, relative humidity, air temperature and total photosynthetically active radiation (PAR). We then expanded the MI analysis to five other coastal wetlands with Eh and water level data to explore commonality in responses to hydrologic drivers. Owing to data availability, only MI between Eh and TGWL and MGWL was assessed at the additional sites.

Both St Jones and Elkhorn Slough have low Eh in the marsh sediment, particularly below 10 cm, indicating widespread anoxic conditions, with considerable spatial and temporal variability in Eh across marsh positions and depths (for example, Fig. 1a,b and Supplementary Figs. 1–4). Based on the Morlet wavelet of marsh sediment Eh, many, but not all, depths and sites showed dominant powers at tidal (12 h) and daily (24 h) periods, suggesting a relationship between tidal water inundation of the salt marsh and Eh measurements (Fig. 1c–f). The dominance of 24 h periods on marsh sediment Eh could be the result of solar radiation and evapotranspiration. The intense spatiotemporal variability makes it difficult to identify consistent trends across all sites and depths, and the lack of multiannual data prevents assessment of the importance of lower frequency (that is, seasonal) periods. However, several monitoring points showed seasonality in the dominant powers. Many depths showed higher and/or more tidally and daily significant variability during drier periods (June to November) than wetter periods (December to May), coinciding with seasonality in TGWL (for example, Fig. 1e). For example, the Mediterranean climate at Elkhorn Slough drives large seasonal variability in the TGWL with high water table elevation from December to May and lower TGWL from June through November (Fig. 1a). The power in the wavelet spectrum also followed this seasonal trend with significant variability in marsh Eh at 12 and 24 h from May to November (Fig. 1e). While seasonal fluctuations in the TGWL at St Jones are less pronounced, periods of higher TGWL coincide, in some locations, with periods when Eh is lower and/or less variable. However, similar to tidal and daily periods, there was variability in these perceived trends with depth and between sites, making it difficult to draw conclusions about Eh drivers.

Given the spatiotemporal variability in the frequency and timing of redox fluctuations, MI analyses were conducted to further quantify links between marsh sediment Eh and TGWL and macroclimate variables (Fig. 2). Universally across all sites and monitoring depths at both St Jones and Elkhorn Slough, the variable with the most shared information with Eh was TGWL, exceeding the MI between marsh sediment Eh and MGWL on both tidal and multiday frequencies (Fig. 2 and Supplementary Figs. 5–7). For example, at St Jones, the average MI between marsh Eh and TGWL across all sites and depths was 0.33 ± 0.12 (mean \pm standard deviation), whereas the average MI between marsh Eh and MGWL was 0.19 ± 0.09 . At Elkhorn Slough, the average MI of

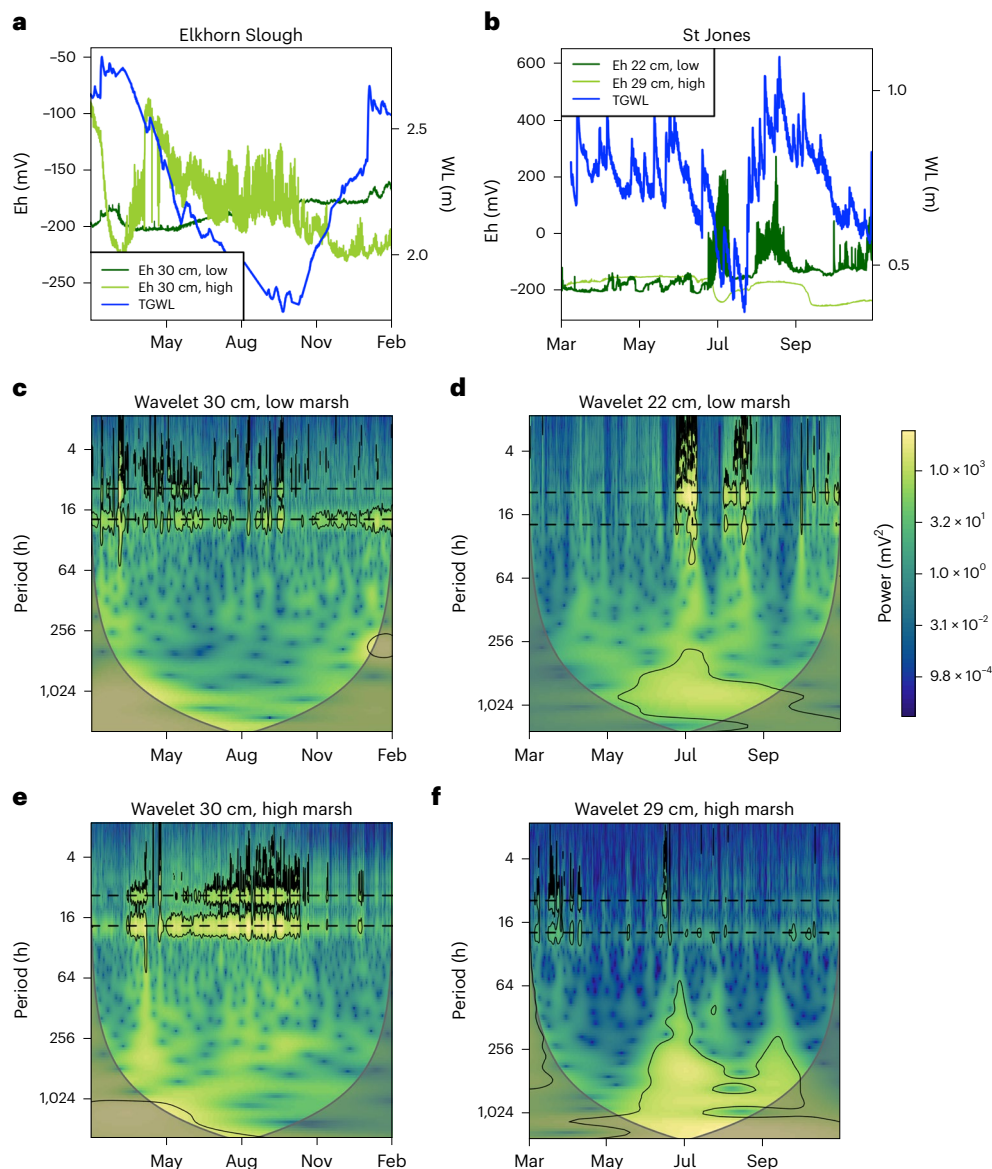


Fig. 1 | Time series and continuous wavelet spectrum for Elkhorn Slough and St Jones. **a, b**, Time series of Eh, TGWL and MGWL at two intramarsh sites (high and low marsh) at Elkhorn Slough (**a**) and St Jones (**b**). WL, water level. **c–f**, Continuous wavelet spectrum for the same Eh time series at each site. At Elkhorn Slough, the Eh at 30 cm in the low (**c**) and high (**e**) marsh is included. Included for St Jones is the wavelet spectrum for the Eh at 29 cm at the high marsh

site (**f**) and 22 cm at the low marsh site (**d**). In the wavelet spectrum, the grey-shaded regions represent the cone of influence. The colour bar represents the strength of power in the wavelet spectrum. The black polygons demarcate the time and periods of statistical significance (within 95% significance level). The dashed black lines indicate the 12 h and 24 h periods.

all sites and depths between marsh Eh and TGWL was 0.48 ± 0.09 , and 0.18 ± 0.08 between marsh Eh and MGWL. In addition, the MI of Eh with the TGWL was higher for all frequencies in the wavelet decomposition analysis (tidal and multiday) than the MI with the MGWL (Supplementary Fig. 7). This contradicts the present conceptual understanding that MGWL, mediated by tides, is the dominant control on marsh Eh, and instead identified TGWL as the variable most closely linked with marsh sediment Eh. At both St Jones and Elkhorn Slough, TGWL was followed by the MGWL, air temperature, relative humidity, total PAR and precipitation with respect to MI shared. Precipitation had the least shared MI with the subsurface Eh. However, uncertainty analyses show that relative humidity, total PAR and precipitation do not have a significant relationship with Eh at any of the sites and marsh positions (Supplementary Text 2 and Supplementary Fig. 6).

In the coastal zone, the TGWL regulates the land–sea hydraulic gradient in the marsh-connected aquifer, mediating vertical pressure

gradients and groundwater advection into the marsh from the underlying aquifer. When the upland–marsh hydraulic gradient is large, vertical groundwater discharge to the marsh sediment is greater and can sustain elevated MGWL even at low tide. These elevated water tables limit oxygen penetration into the sediment and minimize infiltration of oxygen- and solute-rich surface water, resulting in lower and less variable Eh. Groundwater also carries organic matter and electron acceptors, and thus, its advection into the marsh sediment can additionally alter sediment Eh. Conversely, when the marsh–upland terrestrial gradient falls, advection of this biogeochemically unique groundwater is reduced and marsh drainage and evaporative losses occur³⁰, enabling subsurface air penetration and tidally driven surface water recharge that increases Eh. Thus, terrestrial aquifers influence sediment Eh indirectly through the modulation of surface water infiltration and air–sediment penetration and directly through the characteristics of the vertically discharging groundwater (Fig. 3). Although this relationship

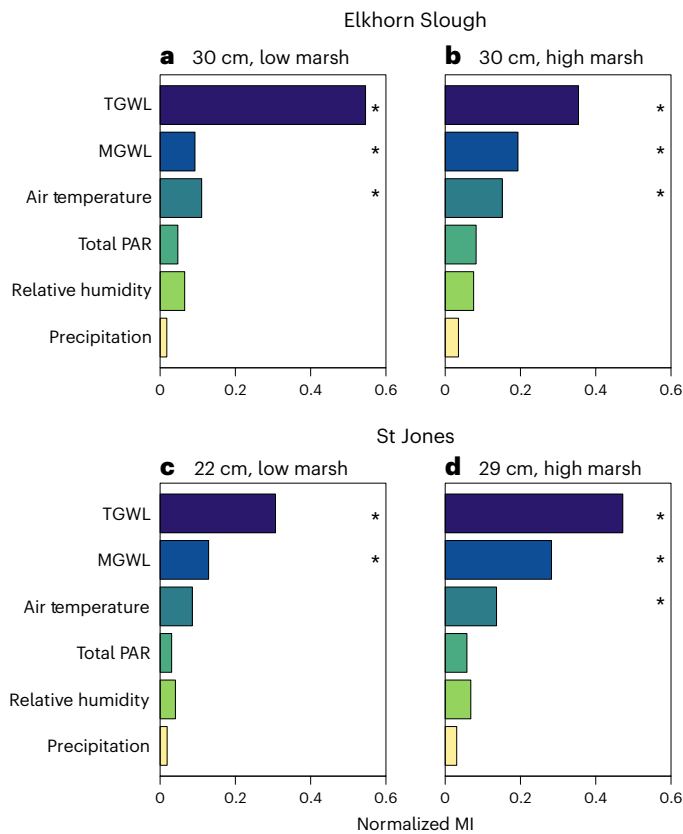


Fig. 2 | MI between Eh time series and other hydroclimatic parameters used to explore the temporal variability of Eh at Elkhorn Slough and St Jones. a,b, At Elkhorn Slough, MI is shown from the low marsh (a) and high marsh (b) at a depth of 30 cm. **c,d,** At St Jones, MI is shown for the low marsh at 22 cm deep (c) and high marsh at 29 cm deep (d). The stars highlight the significant MI between Eh and the parameters shown in the figure. The MI values are normalized by the entropy of each individual signal.

is most pronounced at Elkhorn Slough owing to large seasonal fluctuations in TGWL, our results suggest that a similar direct and indirect modulation of marsh Eh is also occurring at St Jones.

The MI between MGWL and Eh is not the most dominant, yet our results support previous assessments that MGWL impacts marsh Eh (refs. 14,15), as it is the second-strongest relationship at most locations and across analysed frequencies (Fig. 2 and Supplementary Fig. 6). MGWL is mediated by water level variability in tidal channels that drive diurnal infiltration of oxygenated and solute-rich surface water and subsequent drainage of the marsh platform. The magnitude of low-tide drainage can influence marsh Eh through mediation of the oxic–anoxic transition zone. While MGWL is, in part, used to represent the dynamic surface water environment of coastal wetlands, it also shares information with the TGWL (Supplementary Table 1), highlighting the effect of TGWL on marsh conditions. However, the MI between TGWL and Eh is greater than both TGWL and MGWL and MGWL and Eh, suggesting that seasonality in upland hydrologic conditions, as well as the direct discharge of groundwater, plays a stronger overall role in influencing the redox state of coastal wetlands.

In addition to hydrological factors, meteorological factors, including air temperature, total PAR and relative humidity, had intermediate amounts of shared information with Eh, although only air temperature was significant (Fig. 2). Air temperature directly impacts evaporation and evapotranspiration, which have been shown to influence MGWL and soil saturation, particularly in the marsh interior³¹. Air temperature also influences sediment temperature across the marsh, probably impacting rates of biogeochemical reactions.

It is important to note that, while precipitation had the least shared information of all parameters investigated, this does not necessarily indicate that precipitation has the least influence on sediment Eh. Precipitation can be considered a random walk, such that the occurrence and intensity of precipitation at any given time can be seen as a series of random steps. Although evaluating relationships between precipitation and Eh could provide useful context on the role of climate as a potential additional driver of marsh Eh, this was beyond the scope of the current study; however, this is an important future research area. Results from this study show that local precipitation alone cannot be used to forecast Eh but highlight the potential use of TGWL to predict marsh sediment Eh and draw important inferences about related marsh health. It is also important to acknowledge that, while MI can be useful in identifying drivers in spatially and temporally variable time series, it is difficult to isolate interrelated drivers. For example, TGWL varies seasonally in line with integrated macroclimate drivers across the entire drainage basin influencing a given marsh, and thus, more research is needed to identify the relative influence and direction of influence of TGWL alone.

Groundwater’s widespread importance in coastal wetland Eh

To assess the broader applicability of the strong marsh–upland relationships identified here, we conducted MI analyses on five additional sites where time series data of TGWL, MGWL and marsh Eh were available.

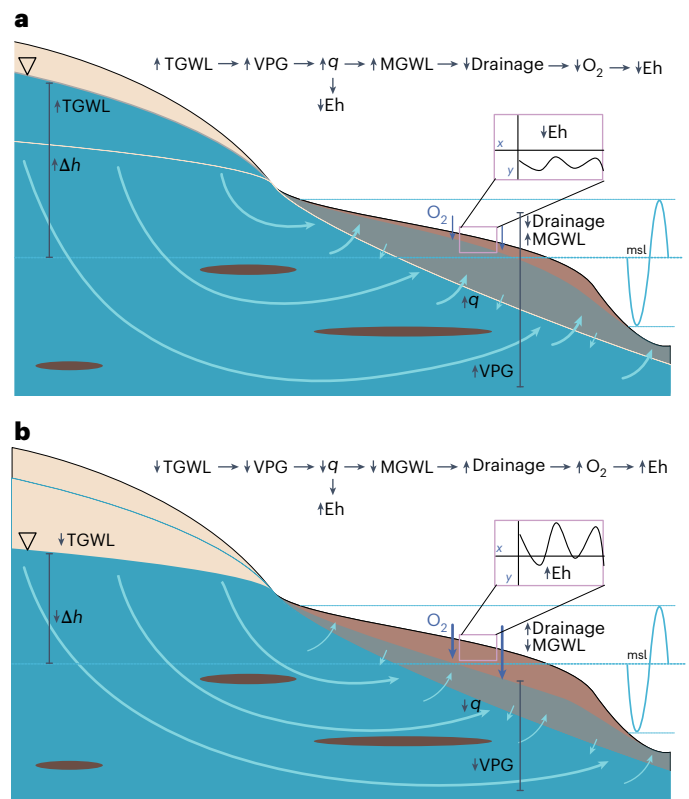


Fig. 3 | Conceptual diagrams of terrestrial groundwater impacts on salt marsh hydrology and Eh. a,b, Diagrams showing periods of high (a) and low (b) TGWL (downwards facing triangle). The light-brown zone is the terrestrial aquifer and the dark-brown zone is the marsh sediment. The shaded blue area over the marsh sediment shows the average marsh groundwater table, with lower average water tables in the dry season than in the wet season. The dashed light-blue lines are mean sea level (msl), high tide and low tide. The solid blue arrows indicate the direction (arrow) and magnitude (line size) of groundwater flow with unique biogeochemical characteristics. VPG, vertical pressure gradients; h , head; q , groundwater flux. Insets: the greater and more variable Eh observed during periods of low TGWL compared with periods of high TGWL.

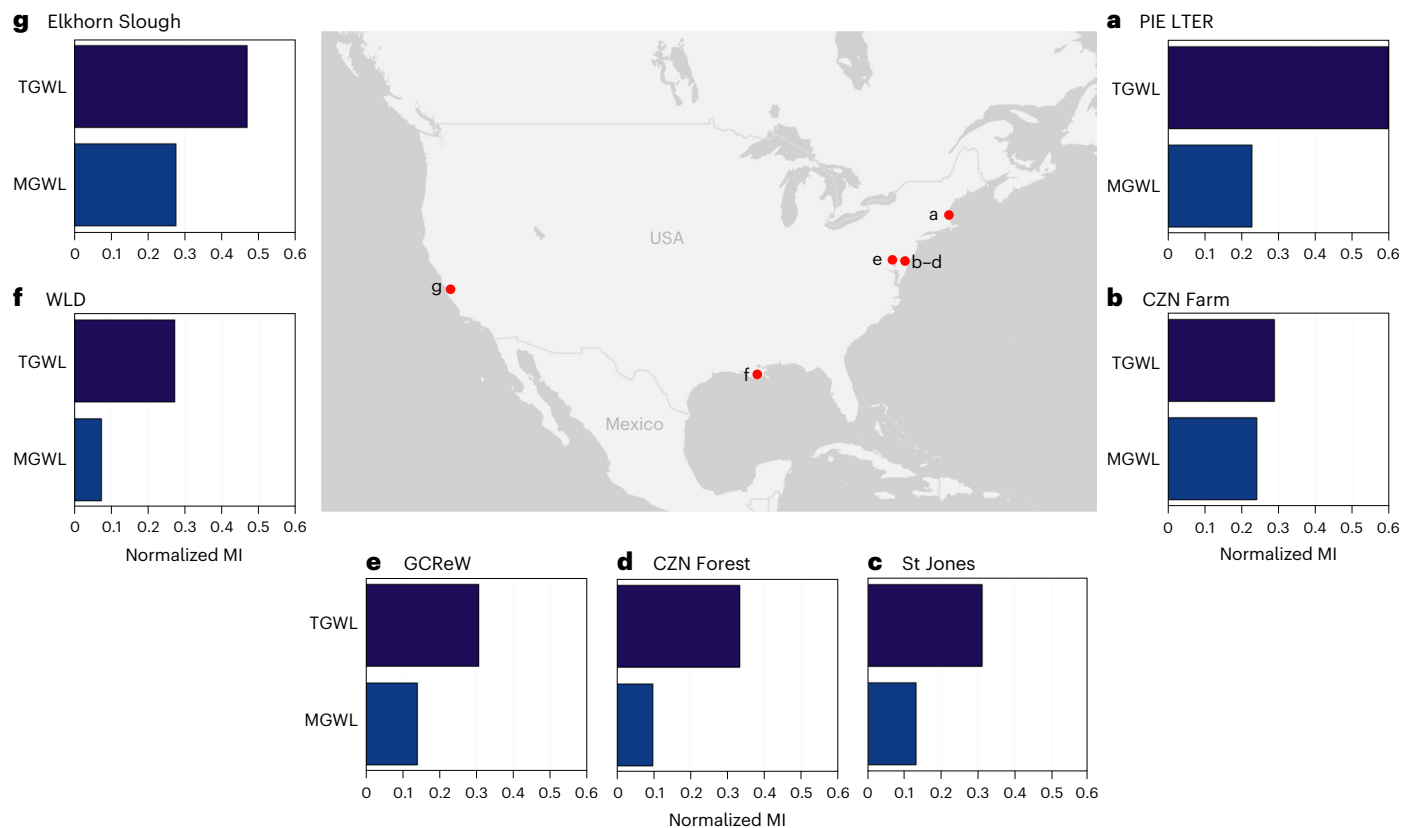


Fig. 4 | MI between Eh time series and TGWL and MGWL at seven sites. a–g, MI included for PIE LTER (depth 30 cm) (a), CZN Farm (120 cm) (b), St Jones (100 cm) (c), CZN Forest (120 cm) (d), GCRew (20 cm) (e), WLD (30 cm) (f) and Elkhorn Slough (50 cm) (g). The variations in MI of Eh with TGWL and Eh with MGWL were tested for statistical significance at each site using a two-sided *t*-test. *P* values for PIE, CZN Farm, St Jones, CZN Forest, GCRew, WLD and Elkhorn Slough were

<0.0001, 0.009, 0.001, 0.002, 0.03, <0.0001 and <0.0001, respectively. Thus, all the relationships between Eh and the parameters shown are statistically significant. The MI values are normalized by the entropy of each individual signal. Basemap from Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors and the GIS User Community.

Additional sites include Plum Island Estuary Long Term Ecological Research (PIE LTER) in Massachusetts, two Coastal Critical Zone Network sites in Delaware at a farm and forest (CZN Farm and Forest), the Department of Energy-supported research site at Wax Lake Delta (WLD) in Louisiana, and the Smithsonian's Global Change Research Wetland (GCRew) and adjacent upland forest in Maryland. These sites span Atlantic, Pacific and Gulf coasts and include a range of latitudes, geologic settings and terrestrial aquifer conditions. Meteorological data were not included in the MI analyses, as they were not available near all sites. Detailed descriptions of the sites and data sources for each site can be found in Methods and Supplementary Tables 2 and 3.

Unanimously across all sites and depths, the variable with the most shared information with marsh sediment Eh was TGWL (Fig. 4), further supporting the relationships uncovered at St Jones and Elkhorn Slough. At the CZN Forest, CZN Farm, WLD, PIE LTER and GCRew sites, the magnitude of shared information between marsh Eh and TGWL was 0.31 ± 0.04 , 0.26 ± 0.02 , 0.25 ± 0.02 , 0.49 ± 0.08 and 0.26 ± 0.03 , respectively, whereas the MI between marsh Eh and MGWL at the sites was 0.08 ± 0.01 , 0.22 ± 0.02 , 0.07 ± 0.01 , 0.2 ± 0.04 and 0.01 ± 0.03 , respectively. MI analyses highlight not only that marsh sediment Eh shares more information with TGWL than with MGWL, challenging the conventional paradigm, but also that this relationship is found at multiple sites that span hydrologic, climatic and geologic settings across the United States (Supplementary Table 3). The differences between sites further highlights the mechanistic links between coastal wetlands and adjacent aquifers. Of the seven sites, PIE LTER and Elkhorn Slough have the highest MI with TGWL. These sites are located outside the topographically low Coastal Plain and in regions with generally

steeper topographic slopes. Given that hydraulic gradients often follow topographic gradients, the increased MI may be driven by increased vertical hydraulic gradients and discharge to the coastal wetland (that is, increasing aquifer–marsh connectivity). Conversely, the WLD site has the lowest MI between redox and TGWL, potentially a result of its location in a low-lying delta in the Coastal Plain with probably lower vertical gradients and less variability in gradients between wetland and aquifer.

The compelling interactions uncovered at all sites highlight the need for more studies on the connectivity between coastal aquifers and coastal wetland ecosystems such as salt marshes. The limited number of sites with relevant data emphasize the need for more widespread installation of coincident marsh and upland hydrological and biogeochemical monitoring, co-located with macroclimate data collection.

Terrestrial–marsh connectivity in a changing climate

Most studies in coastal wetlands have focused on the importance of tidal forcings on biogeochemical cycling, neglecting the role of hydrologically connected terrestrial watersheds. Our findings demonstrate that TGWL affects key drivers of biochemical processes by controlling Eh temporal variability across all marsh sites and monitoring depths. This observed link between terrestrial groundwater and coastal wetland dynamics identifies a new, potentially dominant driver of coastal wetland change. Specifically, terrestrial groundwater levels are dynamic and subject to variability due to climate change and anthropogenic influences⁸. Groundwater extraction for drinking water, irrigation and industry decreases groundwater levels if withdrawn at rates that exceed aquifer recharge. Urbanization and expansion of impervious

surfaces, as well as droughts, limit aquifer recharge, decreasing TGWL in some coastal aquifers. By contrast, SLR and changing precipitation patterns are driving an increase in coastal water table elevation in other coastal regions^{32,33}. Based on the strong links between TGWL and coastal wetland Eh exhibited here, aquifer changes will drive coastal wetland change through alteration of redox conditions and redox-sensitive biogeochemical processes such as methanogenesis. We expect lower TGWLs (for example, due to excessive groundwater extraction) to increase coastal wetland Eh (Fig. 1a,b), resulting in accelerated organic matter decomposition and weakened marsh resilience due to slowed vertical accretion. This will also reduce the carbon sequestration capacity of coastal wetlands, with implications for local and global carbon budgets. Conversely, an increase in the TGWL may increase coastal wetland carbon sequestration capacity and resilience by lowering the Eh and decreasing organic matter decomposition rates. So far, aquifers and the varying stressors they are subject to (for example, drought, increased precipitation and irrigation) have not been incorporated into coastal wetland climate change projections³⁴. Furthermore, management decisions and policies targeting coastal aquifers have centred on the sustainability of freshwater resources. Few focus on maintaining terrestrial ecosystem health (for example, groundwater-dependent ecosystems) and none, to our knowledge, consider effects on coastal wetlands. Results from this study provide additional motivation for sustainable management of coastal aquifers, as well-managed aquifers may increase the resilience of societally and economically beneficial coastal marsh environments.

Our results highlight the need to account for present and future aquifer conditions and the extent of upland–marsh hydraulic connectivity when considering salt marsh function. While data availability limited our analysis to US coastal wetlands, the sites included in this study cover diverse geologic settings and climates (Supplementary Table 3), and thus, the findings are broadly applicable to coastal wetlands and connected aquifers worldwide. More data are needed globally to better understand these marsh–upland links, their magnitude and directionality, and the influence of anthropogenic activity and climate change. Specifically, hydraulic head measurements in the marsh, submarsh aquifer and terrestrial unconfined aquifer paired with continuous Eh measurements in an array of locations would expand process-based understanding. Insights from this study were made possible by heavily instrumented experimental sites with high-frequency, continuous Eh and groundwater level measurements spanning coastal wetland-to-upland gradients. With more co-located measurements of coastal wetland and upland water levels and biogeochemical characteristics, we can begin to unravel the complex links between terrestrial aquifers and coastal wetland function and survival in the face of population growth and a changing climate.

Methods

Field sites and data collection

This study uses data from novel in situ redox probes that continuously record Eh at multiple depths, allowing long-term time series measurements of soil Eh, in line with the measurement frequency of meteorologic, hydrologic and oceanic parameters. Collecting continuous Eh data in conjunction with marsh and upland groundwater levels enables the utilization of times series analyses such as wavelet analyses to advance process-based understanding of spatiotemporal variability in and drivers of marsh biogeochemistry.

We use previously published TGWL, MGWL and marsh sediment Eh data to evaluate marsh–aquifer connectivity at two sites on the Atlantic and Pacific coasts of the United States. Sites include St Jones NERR and Elkhorn Slough NERR. More in-depth descriptions of Eh and water level data collection are discussed by Grande et al.¹⁴ and Guimond et al.¹⁵. In brief, redox probes are constructed of fibreglass-epoxy tubes with platinum electrodes that are connected to a datalogger (Campbell Scientific). Each redox probe was paired with a Ag/AgCl/KCl reference

electrode that was installed into the groundwater to compare the oxidation–reduction potential of the platinum electrodes to the reference electrode and provide a millivolt measurement. Water level data were collected from monitoring wells equipped with pressure sensors continuously monitoring the subsurface water level.

St Jones is located along the St Jones River, adjacent to the Delaware Bay, in Dover, Delaware, within the Altantic Coastal Plain Province. The reserve includes approximately 2.8 km² of tidal wetlands (fresh and saltwater) with peat varying approximately 1–27 m in depth (–2 m in study region). The marsh sediment is underlain by sand and gravel deposits of the Columbian group formed through glacier advance and retreat³⁵. These sandy deposits form the unconfined aquifer, hydrologically connected to these extensive wetlands. This region experiences a temperate climate and annual average precipitation totals of 117 cm. Tides are semidiurnal with an average tidal range of 1.5 m. The St Jones salt marshes are dominated by saltmarsh cordgrass (*Spartina alterniflora*) and saltmarsh hay (*Spartina patens*). The NERR maintains a meteorological station at the reserve (NERR Monitoring Network: St Jones River), providing continuous measurement of air temperature, total PAR, relative humidity and precipitation for spectral analyses³⁶. Monitoring wells and redox probes were installed in the low marsh (diurnally inundated) and high marsh (periodically inundated). A detailed description of the sites and instrumentation is given by Guimond et al.¹⁵.

Elkhorn Slough NERR is located along an 11-km-long estuary in Monterey Bay, California, within the Pacific Border Province. The reserve includes 6.9 km² of tidal wetlands composed of peat, clays and sand. In the ‘back slough’, the study area, peat depths vary between 1 m and 6 m (–3 m along the study transect) and is underlain by fluvially derived sand and gravel. The area also comprises clay and silt layers that overlay muddy sand layers³⁷. The sandy deposits form the unconfined aquifer that contributes groundwater to the marsh system. In the uplands and surrounding hillslopes, the top three metres are composed of sands that overlay clay lenses that can form shallow purchased aquifers. The region is characterized by a Mediterranean climate with annual precipitation totalling 51 cm per year, most of which is received during the winter and spring. The estuary has a mixed semidiurnal tidal cycle of approximately 2.7 m, with changes in amplitude over the tidal lunar cycle. The salt marsh vegetation is dominated by pickleweed (*Sarcocornia pacifica*, also known as *Salicornia pacifica*). The meteorological data were retrieved from the NERR Monitoring Network (San Francisco NERR)³⁶. Observation piezometers and monitoring wells were installed across a 60 m experimental transect that spans from near the tidal channel into the adjacent hillslope. Redox probes were co-located with monitoring wells in the low, mid and high marsh positions. The experimental transect and the instrumentation has been described in detail in previous studies^{14,23,38}. The water level and Eh data are available since 2021 (refs. 38–40).

Spectral analyses

Redox reactions often show significant spatiotemporal variability⁴¹. Unlike traditional methods, such as correlations or principal component analyses, that cannot incorporate temporal changes, wavelet analyses help perform timescale analysis of water chemistry parameters⁴². Continuous wavelet transform can simultaneously decompose a time series into time and frequency domains, enabling the determination of discontinuities, seasonal trends and long-term patterns in the time series⁴³.

We use wavelet analysis to measure Eh patterns and identify dominant scales of variability across different salt marsh elevations at St Jones and Elkhorn Slough. Continuous wavelet transform is obtained by decomposing the data with a wavelet function and creating wavelet coefficients that designate the relationship between the wavelet function and the data (Supplementary Text 1 and Supplementary Fig. 8). We used the Morlet wavelet to derive the dominant frequencies from the

Eh time series data. The Morlet wavelet is suitable for feature extraction because it is well localized in space and time⁴⁴, and it has been used in similar datasets¹⁴.

We evaluated the timescales of variability in Eh and hydrological variables by decomposing the Eh time series into approximation coefficients related to tidal cycles and multiday frequencies. We used the maximum-overlap discrete wavelet transform⁴⁵ because of its capability of multiresolution analysis. At each scale, the maximum-overlap discrete wavelet transform applies a high-pass wavelet filter and a low-pass scaling filter of a specific length to the time series to respectively yield wavelet coefficients and scaling coefficients for every point in the time series. The time series can be decomposed into the detail added from successively coarser to finer scales and either summed or evaluated individually to analyse patterns at varying scales⁴⁶. In our analysis, we used the Least Symmetric 8 wavelet filter, as resulting wavelet coefficients are less correlated across timescales and retain less contamination from neighbouring scales compared with the traditional Haar wavelet while preserving a relatively low number of coefficients influenced by boundary conditions. We reconstructed the detail in the Eh time series for dyadic scales of 1 (2^1 , 2 h scale) to 12 (2^{12} , ~170 days). We studied the fourth detail component (2^4) to analyse the temporal effect of tidal and other multihour processes and the tenth detail component (2^{10}) to examine multiday relationships of hydrological drivers with Eh (Supplementary Text 1). While we desired higher detail components for the multiday or seasonal-scale analyses, the length of the dataset prevented the wavelet decomposition from extracting useful information beyond the values used (Supplementary Text 1 and Supplementary Fig. 8).

Mutual information analyses

The MI of two random variables quantifies how much information is obtained about one variable by observing the other variable. We used MI to quantify the key factors causing temporal variability in the Eh time series. The principal benefit of MI over other statistical approaches, such as correlation coefficients, is that MI is not limited to linear dependencies⁴⁷. MI is comprehensive and defines how different the joint distribution of two variables is from the product of their marginal distributions⁴⁸. In MI, the null hypothesis is that $MI(X; Y) = 0$ (that is, that the two signals, X and Y , are independent). To test the statistical significance of the analysis, we used an equal-variance t -test, valid for large samples from non-normal distributions. We can use it when both datasets have the same number of samples. We determined statistical significance at the 95% level using a Monte Carlo approach with random walks (Supplementary Text 2 and Supplementary Figs. 9–12) and applying the same sequence of calculation procedures as in the analysis. Additional tests on synthetic time series characterized the response of MI with interaction strength. We normalized the MI to scale the results between 0 (no MI) and 1 (perfect correlation) using the entropy of each individual signal. We used a two-sided Mann–Whitney U -test to determine if the variations in MI of Eh and the different parameters used in the analyses were significant. We used P values to assess the significance between parameters ($\alpha = 0.05$).

For St Jones and Elkhorn Slough, MI analyses included hourly TGWL, MGWL and meteorological data including precipitation, relative humidity, air temperature and total PAR. Because MGWL integrates marsh- and ocean-driven surface hydrologic processes, the surface water level is not included in the MI analyses. Supporting analyses show little MI between surface water level and the marsh Eh (Supplementary Fig. 13). Relative humidity, air temperature and PAR were interpreted as proxies for evapotranspiration. The meteorological data for St Jones and Elkhorn Slough were downloaded from the NERR Monitoring Network³⁶. The Eh, TGWL and MGWL from St Jones were sourced from refs. 15, 49–51. At Elkhorn Slough, Eh, TGWL and MGWL data were sourced from refs. 38–40.

Five additional sites, where continuous Eh data were available, were also analysed by MI methodological approaches. MI analyses were

confined to assessments of MGWL and TGWL, excluding meteorological data as they were not available at every site. Additional sites include PIE LTER, two Coastal Critical Zone Network sites in Delaware at a farm and forest (CZN Farm and Forest), a Department of Energy-supported site in WLD in coastal Louisiana, and the Smithsonian's GCREW site in Maryland. The time period of analysis for all seven sites is included in Supplementary Table 2, and a synopsis of site descriptions is presented in Supplementary Table 3.

The PIE LTER site is located on the upper tidal Parker River in Newbury, Massachusetts, within the New England Province (Appalachian Highlands). The Parker River basin contains aquifers that consist of ice-contact deposits composed of sand and gravel and less productive, sandy glacial-outwash deposits. Both kinds of aquifer are buried beneath younger marine or swamp deposits⁵². The climate is temperate, and the region receives about 1.2 m of precipitation per year. Site vegetation is *Typha angustifolia*, and the average tidal range is about 3 m. Continuous Eh measurements were associated with the Ameriflux site US-Plo (42.7496, -70.9157), which is located in the high marsh. Measurements were conducted at four depths (5 cm, 10 cm, 15 cm and 30 cm) and in three replicate locations. Marsh water levels were recorded with a pressure transducer (Campbell Scientific, CS456). The marsh Eh and MGWL are available as Supplementary Data. The TGWL was sourced from the USGS National Water Dashboard, site Ma-niw 27 (42.7553722, -70.93948889) in Newbury, Massachusetts.

The CZN Farm site is located in Dover, Delaware, and the CZN Forest site is located in Milford, Delaware, with the same geologic, climatic and ecological characteristics as St Jones (see above). The tides are semidiurnal with a average tidal range of 0.8 m. Redox probes were deployed in the low marsh, following the same approach as Guimond et al.¹⁵. Monitoring wells were installed in the upland and low marsh at both sites and equipped with conductivity, temperature and depth loggers (Solinst, M3001 Levelogger 5). Redox probes were co-located with the marsh monitoring well. The data and additional details are published on HydroShare by Pratt et al.^{53,54}.

GCREW, located in Edgewater, Maryland, within the Atlantic Coastal Plain Province, is part of Kirkpatrick Marsh, a microtidal brackish high marsh on the western shore of the Chesapeake Bay with highly organic soils. These peat soils are 4–5 m deep and underlain by marine clay and sand deposits comprising the unconfined aquifer. This site experiences a temperate climate with average annual precipitation of 949 mm and semidiurnal tides with an average tidal range of 0.40 m. Eh and MGWL data were collected from GCREW's SMARTX experiment⁵⁵ in the high marsh. Eh data were collected using 18 replicate platinum-ringed probes every 30 min from 2022 to 2023. Measurements were made at 5 and 20 cm below the soil surface. MGWL data were collected every 15 min using an In-Situ AquaTROLL 200. TGWL was collected from the adjacent Terrestrial Ecosystem Manipulation to Probe the Effects of Storm Treatments (TEMPEST) experiment⁵⁶. The groundwater level was measured using an In-Situ Aqua Troll 600 multiparameter sonde deployed in groundwater wells in the centre of the control plot, which does not receive flood manipulation treatments⁵⁷. The plot is an upland deciduous forest with a soil profile composed of organic-matter-rich sandy loam (top 0.3 m), silty clay soil from 0.3 to 1.6 m, and silty sands below that⁵⁷. The data are available at ref. 58.

WLD is a prograding, freshwater delta located in the Atchafalaya Basin of coastal Louisiana with the Coastal Plain Province. Under the marsh sediment lies a shallow aquifer (<2 m) composed of sandy sediments deposited on consolidated mud bedrock^{59,60}. The region experiences a humid subtropical climate with average precipitation of ~150 cm per year. Delta vegetation includes *Salix* spp., *Colocasia* spp. and *Nymphaeaceae* spp. The water level on the deltaic islands is influenced by semidiurnal microtidal cycles of ~30 to 40 cm, seasonal discharge through the Wax Lake Outlet, wind patterns that push marine water inland, and biogeomorphic effects on channel–floodplain connectivity⁶¹. Redox probes were installed at four positions

along an elevation transect on the proximal end of Mike Island that extended from the supratidal/high intertidal zone to the low intertidal/subtidal zone (-0.5 m elevation difference) with sensor depths at 10 cm, 20 cm, 30 cm and 40 cm below the ground surface, following a similar approach to Guimond et al.¹⁵. Water depth relative to the ground surface was monitored at two locations: at the infrequently inundated supratidal–intertidal boundary directly upslope of the redox transect (TGWL) and next to a redox probe in the persistently saturated subtidal zone (MGWL). Both groundwater and Eh data are available as Supplementary Data.

Data availability

All data are available in public repositories or included as supplementary data as indicated in the text.

Code availability

The codes to replicate the analysis are available via Zenodo at <https://doi.org/10.5281/zenodo.10855140> (ref. 62).

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Author contributions

J.A.G., E.G. and B.A. conceived the study idea and design. J.A.G., E.G., H.A.M., D.P., E.H., G.L.N., N.D.W., I.F., P.R. and M.J.B. contributed data. E.G. conducted the analyses. J.A.G., E.G. and B.A. analysed the results. J.A.G. wrote the paper with important input from E.G. and B.A. E.G. wrote the Supplementary Information text. All co-authors provided edits and feedback on the paper text and figures.

Competing interests

The authors declare no competing interests.

Additional information

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