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An Integrative Salt Marsh Conceptual Framework for Global Comparisons

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CURRENT EVIDENCE

An integrative salt marsh conceptual framework for global comparisons

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Scientific Significance Statement

Salt marshes are transitional ecosystems that link land and sea. They occur globally and take on a variety of forms, differing in structure and function. Despite these differences, salt marshes are often discussed as a singular ecosystem type, compared to a select few well-studied locations, and currently lack a unifying conceptual framework. We propose an integrative conceptual framework to assist salt marsh scientists in developing suitable questions, making accurate comparisons, and pushing for more comprehensive assessments of salt marshes at multiple spatial scales. We present this new framework in a series of illustrative examples and discuss considerations when undertaking comparisons. We anticipate this framework will encourage cross-disciplinary and global collaborations, ultimately improving our ability to understand the complex controls on salt marsh ecosystem functions by appropriately framing salt marsh science.

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Abstract

Salt marshes occur globally across climatic and coastal settings, providing key linkages between terrestrial and marine ecosystems. However, salt marsh science lacks a unifying conceptual framework; consequently, historically well-studied locations have been used as normative benchmarks. To allow for more effective comparisons across the diversity of salt marshes, we developed an integrative salt marsh conceptual framework. We review ecosystem-relevant drivers from global to local spatial scales, integrate these multi-scale settings into a framework, and provide guidance on applying the framework using specific variables on 11 global examples. Overall, this framework allows for appropriate comparison of study sites by accounting for global, coastal, inter-, and intra-system spatial settings unique to each salt marsh. We anticipate that incorporating this framework into salt marsh science will provide a mechanism to critically evaluate research questions and a foundation for effective quantitative studies that deepen our understanding of salt marsh function across spatial scales.

Salt marsh ecosystems exist at the interface between terrestrial and marine habitats (Levin et al. 2001), serve as an important conduit for the flow of energy and nutrients (Teal 1962), and provide numerous ecosystem services (Barbier et al. 2011; Friess et al. 2020). Salt marshes occur in approximately half of all countries worldwide, covering latitudes from 78.2°N (Svalbard, Norway) to 54.8°S (Isla de los Estados, Argentina) (Mcowen et al. 2017), and can be found on suitable coastlines of all continents except Antarctica. Global salt marsh area is conservatively estimated at $\sim 55,000$ km^2 based on available spatial data from 43 countries that are assumed to represent the major salt marsh areas of the world (Davidson and Finlayson 2018, 2019). Salt marsh structure, function, and associated services are controlled by a variety of relatively well-studied drivers and stressors (e.g., salinity, inundation, temperature, freshwater/sediment availability, plant communities), and the spatiotemporal evolution of these bio-geomorphic landforms are affected by feedbacks between these drivers (Chapman 1938; Adams 1963; Clarke and Hannon 1967, 1969; Adam 1993; Fagherazzi et al. 2013). Despite occurring in diverse settings globally, salt marshes are often treated as a singular ecosystem type with some dominant regions serving as normative for comparative ecology.

While decades of salt marsh research has been conducted globally, studies performed in relatively few locations (e.g., Western Atlantic salt marshes of the United States, North-Western European salt marshes) are often contextualized as being comparable to other salt marsh studies undertaken elsewhere. Thus, a few well-studied and well-funded locations are often disproportionately cited in the literature. As a result of this generalization, studies addressing the key drivers and stressors of salt marsh ecosystems (Chapman 1938; Clarke and Hannon 1967, 1969; Bertness and Ellison 1987) rarely frame these drivers explicitly with respect to the nested spatial scales at which they are measured (e.g., geographic area, climate, coastal setting, or site differences), hampering the ability to accurately compare findings within or between studies. Discussions of cross comparisons within and between systems have taken place for decades (e.g., Ragotzkie 1959); however, previous data limitations often required extrapolation or inference from those few well-studied systems. Global salt marsh science is now more data rich, increasingly comprehensive, and contains better spatial coverage than ever before, but comparisons constrained to those valuable, yet limited, well-studied locations remain common (Kimball et al. 2021). To remedy this practice and to foster consideration of spatial scale when undertaking comparisons, a unifying conceptual framework to characterize connections in salt marsh science is needed (Ziegler et al. 2021*a*).

Typologies and conceptual frameworks are a common feature of the natural sciences that can characterize systems at multiple spatial scales and settings (e.g., climatic, coastal, ecological), provide context for data collection and analyses, and allow for suitable comparisons across study locations. Many ecosystems have a history of typology/framework development and coastal ecosystems are no exception (Mangroves—Lugo and Snedaker 1974, Thom 1984, Woodroffe 1992, Twilley et al. 1999; Corals—reviewed by Andréfouët 2011; Estuaries—Davidson et al. 1991, Elliott and McLusky 2002; Mudflats—Dyer 1998; Seagrass meadows—Buia et al. 2004, Mazarrasa et al. 2021; Coastal wetlands—Sievers et al. 2021). Salt marshes, however, lack a unifying global conceptual framework that explicitly considers spatial scale, despite scientists and practitioners heavily utilizing typologies focused on floristic composition (Chapman 1974; Adam 1993). In order to make meaningful comparisons across and within locations and to understand the mechanisms driving salt marsh function, there is a need to develop an integrated conceptual framework that can describe individual studies and prescribe appropriate comparisons, identify gaps, and elucidate collaborative opportunities (Ziegler et al. 2021*a*). As salt marshes are increasingly incorporated in nature-based solutions for climate mitigation and adaptation (Temmerman et al. 2013; Taillardat et al. 2020; Waltham et al. 2021), there is a pressing need for appropriate and reliable comparisons at all spatial scales.

We present an integrated conceptual framework (Fig. 1; Section Salt marsh conceptual framework) to aid researchers and practitioners in making appropriate comparisons, rebuffing the use of archetypal studies focused on a single region or type of salt marsh as normative and representative of all salt marshes. We focus on spatial components and the key ecosystem-relevant drivers that control processes at each spatial setting in this framework (Fig. 1), and recognize anthropogenic influence, biogeography, and landscape evolution as cross-scale components that should also be considered (Section Cross-scale considerations; Fagherazzi 2013). Using the spatial setting, drivers, and considerations, we provide explicit variables necessary to effectively apply this framework in real-world settings (Section Applying the framework). The framework application guidance uses a series of examples to showcase the diversity of salt marshes (Section Framework utility). We discuss how the conceptual framework can be used as a catalyst to inform quantitative comparative studies that advance salt marsh science (Sections Framework application and Future directions). We define salt marshes here as coastal wetlands influenced by tides, maintaining an oceanic influence, with soil salinity > 2 psu, and containing some level of herbaceous and/or succulent vegetation (*sensu lato* Adam 1993).

Salt marsh conceptual framework

Global setting

Diversity of salt marshes

Due to their global distribution, salt marshes experience a variety of climatic conditions. Temperature extremes and variation in precipitation magnitude/seasonality impact salt marsh ecosystem function at the largest spatial scales (Fig. 2). Global spatial datasets and climatic gradient studies are typically representative of temperate regions with extensive salt marsh coverage, while salt marshes in polar, tropical, and arid climates are often underrepresented.

Drivers—Temperature

Variation in temperature across latitudes influences key salt marsh ecosystem functions. Temperature impacts primary production, which ranges from 250 to 700 g m^{-2} yr^{-1} in sub-arctic and cold temperate regions (Smith et al. 1980; Glooschenko and Harper 1982) to 2200 g m^{-2} yr^{-1} in warm temperate regions of North America (Stagg et al. 2017; Feagin et al. 2020). Temperature directly and indirectly limits salt marsh distribution at both low and high latitudes (e.g., Idaszkin and Bortolus 2010). In a study comparing 143 salt marshes across southern and northern hemispheres, latitude (i.e., temperature, light, and growing season length) was an important parameter influencing carbon accumulation rate (Ouyang and Lee 2014), although this was not the case in the southern hemisphere where carbon stocks are generally lower despite optimal temperature (Rogers et al. 2019). Temperature also increases microbial activity (Mozdzer et al. 2014), increases decomposition (Kirwan et al. 2014), and decreases organic matter stabilization (Mueller et al. 2018). Other temperature-related consequences of the climatic gradient include soil salinity range—particularly at upland edges, in pannes/pans, salt-flats, or sabkhas, and areas with limited flushing—and resulting in impacts to nutrient cycles (Poffenbarger et al. 2011; Schutte et al. 2020), adjacent habitat type (e.g., grassland, forest, salt pannes—Adam 2002), and physical disturbance type (e.g., drought, tropical cyclones/hurricanes/typhoons, ice scour—Redfield 1972; Cahoon 2006).

Drivers—Precipitation

Precipitation, and its influence on groundwater recharge, at the global setting (for additional discussion at the coastal setting *see* Sections Drivers—Tides and Drivers—Riverine input),
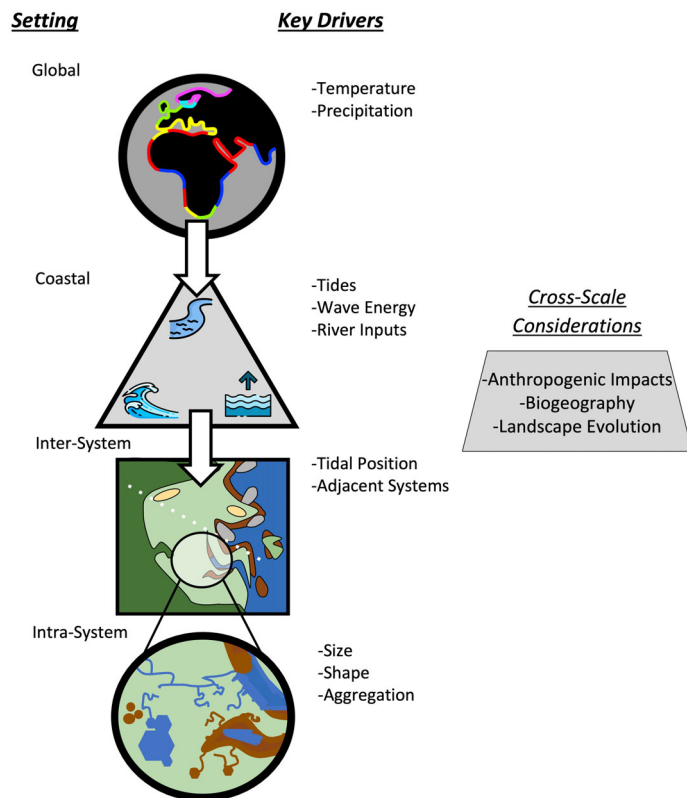

Fig. 1. Conceptual diagram of integrated framework to characterize salt marshes at multiple hierarchical spatial settings (global, coastal, inter-system, and intra-system), key drivers at each level, and cross-scale considerations for all levels. *See* Figs. 2–5 and Sections Global setting, Coastal setting, Inter-system setting, and Intra-system setting for greater detail at each level and Section Applying the framework for additional discussion regarding needed cross-scale considerations. Coastal setting internal graphics from flaticon.com.

The figure labels (left "Setting" column): Global, Coastal, Inter-System, Intra-System. The "Key Drivers" column: -Temperature, -Precipitation; -Tides, -Wave Energy, -River Inputs; -Tidal Position, -Adjacent Systems; -Size, -Shape, -Aggregation. Cross-Scale Considerations: -Anthropogenic Impacts, -Biogeography, -Landscape Evolution.
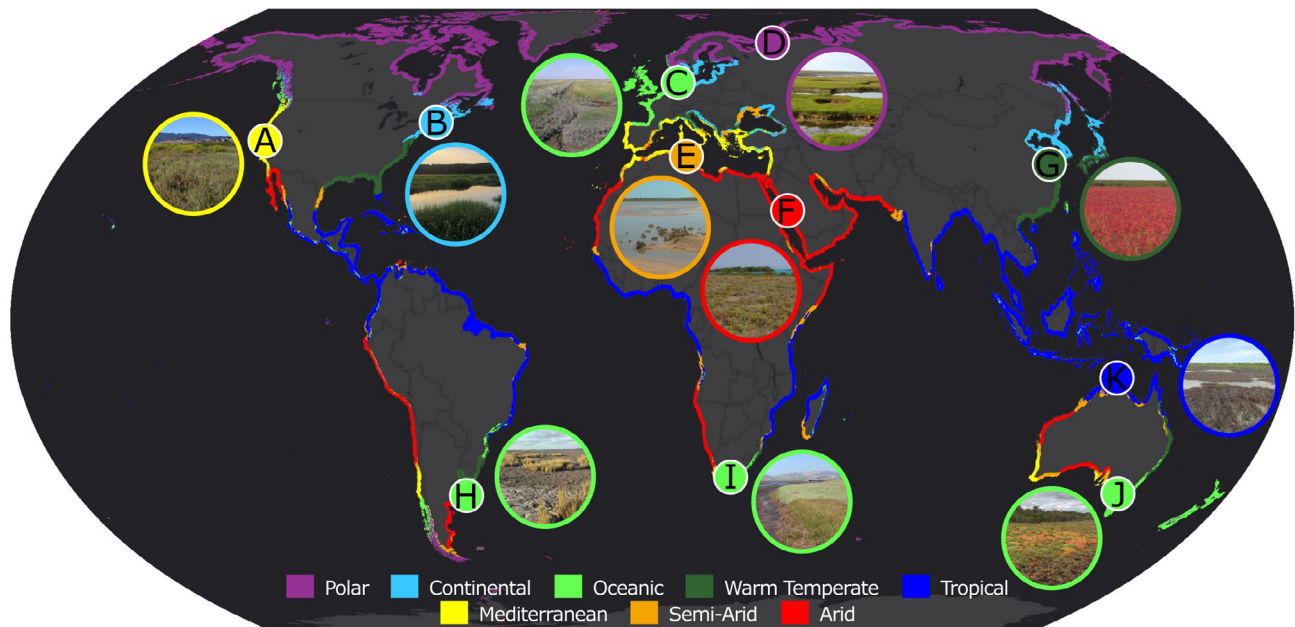
Fig. 2. Global coastlines with modified Köppen-Geiger climate map from Beck et al. (2018) as color bands. *See* Supporting Information Table S1 for climate type groupings. Equal Earth projection. A–K insets show case study systems: (**A**) San Francisco Bay-Delta, United States; (**B**) Plum Island Estuary, United States; (**C**) Wadden Sea Coast, Germany; (**D**) Indiga River Estuary, Russia; (**E**) Ras Lamsa, Tunisia; (**F**) Alkarar Lagoon, Saudi Arabia; (**G**) Yancheng Coast, China; (**H**) Mar Chiquita Coastal Lagoon, Argentina; (**I**) Groot Brak Estuary, South Africa; (**J**) Westernport Bay, Australia; and (**K**) West Alligator River Estuary, Australia. Photo credit: A—AD Manfree, B—DS Johnson; H—LJ Reyna Gandini, I—JB Adams; all other photos provided by authors.

is a predictor of salt marsh traits and functions (Moles et al. 2014). Global net primary ecosystem production has been correlated with precipitation in vegetated habitats that are grass-, shrub-, or tree-dominated (Del Grosso et al. 2008). Similarly, rainfall influences ecosystem structure and function in salt marshes across regional precipitation gradients (Isacch et al. 2006; Noto and Shurin 2017; Adams 2020; Hu et al. 2021). Rainfall thresholds shift salt marsh-mangrove ecotones in tropical tidal wetlands (Saintilan 2009), have been proposed as a driver of landward expansion of mangrove into salt marsh (Eslami-Andargoli et al. 2009), and are linked to salt marsh zonation and community composition in some arid and semi-arid regions (Osland et al. 2014; Gabler et al. 2017; Fariña et al. 2018). Across several climate settings, including tropical monsoonal and Mediterranean, salt marshes experience seasonal precipitation regimes with distinct wet and dry seasons that can drive ecosystem function, vegetation patterns, and habitat use by fauna in marshes and surrounding creeks (e.g., Jin et al. 2007; Braga et al. 2009). Salt marshes also occur on extremely arid coastlines, where they are dominated by succulents within a mix of bacterial and algal mats and sand/mudflats (Kassas and Zahran 1967; Mahmoud et al. 1982). The extreme salinity stress in these arid salt marshes leads to functional relationships that remain understudied (Bornman et al. 2004; Feher et al. 2017), yet are critical to achieving a global understanding of salt marsh function.

Coastal setting

Diversity of salt marshes

Salt marshes exist in a relatively narrow geomorphological setting between terrestrial and marine systems (Adam 1993), where they can coexist with several other habitat types (e.g., mangrove, salt flat, oyster reefs, microbial mats, etc.) and may form complex habitat mosaics (*see* Section Drivers—Adjacent systems). The interplay between marine (waves and tides) and fluvial (sediment and freshwater flow) processes defines the variety of coastal settings where salt marshes occur (Dalrymple et al. 1992). Suitable conditions may occur on open coasts where wave energy is low, or within estuaries where geomorphological features dampen wave energy. The convergence of these processes creates distinct coastal features that can be classified along a continuum of *tide-*, *river-*, and *wave-*dominated systems (Fig. 3; Boyd et al. 1992; Dalrymple et al. 1992; Rogers et al. 2017; CAFF 2019). Regardless of coastal forcing, salt marsh sediments range from primarily minerogenic to organogenic/biogenic (Turner et al. 2002). Minerogenic salt marshes are found in regions with adequate sediment supply from either terrestrial or marine sources. In contrast, organogenic/biogenic salt marshes mainly form through the input of organic matter and may develop peat deposits where conditions are favorable and plant distribution, occurrence, and productivity are sufficient. On a given portion of coastline or within an estuary, the influence of tides, riverine inputs, and waves vary in their contribution
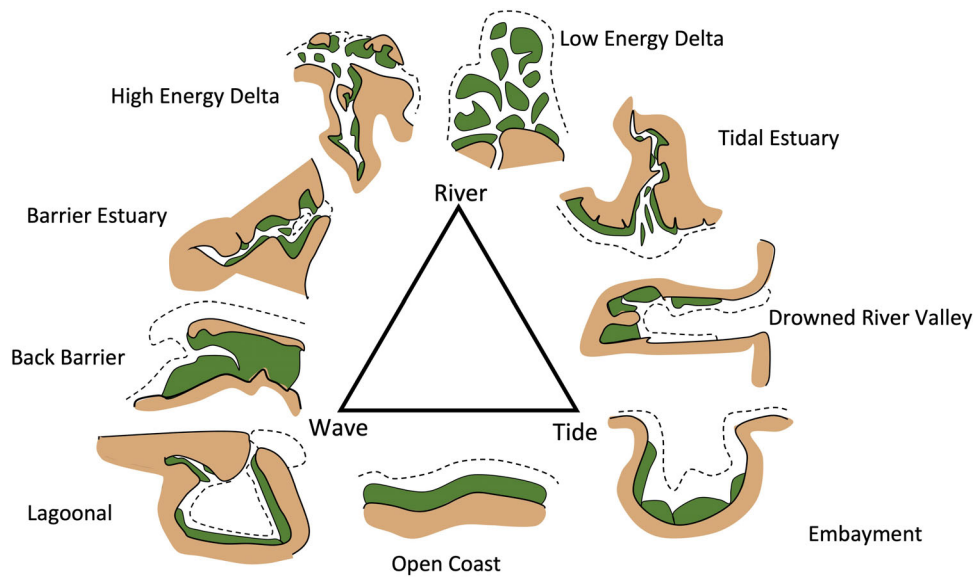
Fig. 3. Coastal settings continuum, where salt marshes are present based on dominant forcing. Dotted line indicates intertidal extent, green areas indicate salt marsh, and brown areas are adjacent upland ecosystem (adapted from Rogers et al. 2017 and Dalrymple et al. 1992).

resulting in a continuum of possible coastal settings (Fig. 3), with distinct impacts on salt marsh functions such as elevation maintenance, floral and faunal assemblages, and nutrient cycling.

Drivers—Tides

Tides are one of the main driving factors shaping and structuring salt marshes and the nutrient/energy linkages within them. All coastal systems have some level of tidal influence with tidal ranges from < 1 m (e.g., Mediterranean Basin) to > 10 m (e.g., Bay of Fundy). Discrete ranges are typically defined as microtidal (< 2 m), mesotidal (2–4 m), and macrotidal (> 4 m) (*sensu lato* Davies 1964). As salt marshes are restricted to areas with some level of tidal inundation and salinity, they occur from low intertidal channels to supratidal zones that only experience seasonal inundation or flooding during extreme events (Purer 1942; Veldkornet et al. 2015; Adams 2020). Salt marsh position depends on location, landscape evolution, and species specific tolerances (Veldkornet et al. 2015; Anderson et al. 2022). In the context of sea-level rise and substrate subsidence/auto-compaction, maintaining this intertidal position depends on an interplay of tidal inundation, *in situ* vegetation, and sediment supply, as sediment-laden tidal waters can deposit mineral and organic material on salt marsh surfaces, increasing surface elevation over time (Morris et al. 2002; Nolte et al. 2013). The dominance of biogenic vs. minerogenic accretionary processes will be critical for the response of salt marshes to human-induced sea-level rise. Where sea level has been rising for the past few millennia or sediment inputs are low salt marshes may be more biogenic (Redfield and Rubin 1962; Fagherazzi et al. 2012; Rogers et al. 2019). In contrast, where sea level has been stable or

falling for the past few millennia or where mineral sediment supply is high, then salt marshes are likely to be increasingly minerogenic (Allen 2000; Rogers et al. 2019; Lacy et al. 2020).

Drivers—Riverine input

River-dominated coastal settings, and their salt marshes, are characterized by high levels of freshwater inputs and are often accompanied by substantial alluvial suspended sediment loads (Cooper 1993). Larger catchments or watersheds have greater run-off, and this influences fluvial inputs and net (suspended and bedload) sediment loads that can be delivered to estuaries and the open coast. Deltas typically arise where rivers draining large catchments discharge into coastal areas (e.g., Mississippi River Delta) and exhibit high suspended sediment loads (Dalrymple et al. 1992); these greater sediment loads can offset the effects of sea-level rise, providing that modifications within catchments do not significantly alter hydrology and sediment supply (e.g., dams and diversions). Where fluvial inputs are low, supply of terrigenous sediment is also likely to be low and will limit the capacity of salt marshes to respond to sea-level rise by accumulating mineral sediments (Kirwan et al. 2016). Riverine inputs also regulate water circulation and salinity regimes (Dalrymple et al. 1992), and interactions with geomorphology influence fresh and saltwater mixing and stratification. Estuaries have been classified on the basis of circulation and salinity (e.g., salt wedge estuaries, fjords, moderately-highly stratified, vertically mixed) (Pritchard 1952), and the degree of mixing influences salinity of the substrate. Interactions between the ecophysiological tolerance of salt marsh biota and salinity regimes have important controls on species distributions and ultimately the development of zonation patterns and species mosaics

(Pennings and Callaway 1992; Silvestri et al. 2005). As riverine inputs are modulated by precipitation occurring within catchments, substrate salinity and sediment supply may exhibit similar patterns of seasonality or pulses associated with storms (Findlay 2009).

Drivers—Wave energy

Wave-dominated coastal settings are characterized by marine processes with high near-shore energy driving the formation of beaches and barriers that can buffer wave energy and afford protection for salt marshes behind barrier islands or within wave-dominated estuaries (Cooper 2001). Salt marshes are more expansive in areas that have low gradients and low energy, as these conditions promote sediment deposition and establishment. Salt marshes within wave-dominated estuaries can become intermittently disconnected from the marine environment when fluvial flows are relatively weak compared to wave energy, and marine sediment deposition causes the inlet to close (McSweeney et al. 2017; van Niekerk et al. 2020). These closures can lead to increased variability of environmental conditions important in structuring salt marsh function in wave-dominated estuaries (e.g., Riddin and Adams 2012; Clark and O'Connor 2019) and, along with sediment availability, influences accretion rates (Thorne et al. 2021). Inlet or entrance state and closure patterns are therefore critical controls on salt marsh distribution within wave-dominated estuaries.

Inter-system setting

Diversity of salt marshes

The location of salt marshes in the coastal seascape/landscape, their relative position in the tidal frame, the inundation frequency and period, and the identity of adjacent habitats plays an important role in determining salt marsh ecosystem structure and function. We define inundation as the frequency, depth, and duration in which any portion of the area is covered by tidal waters (sensu Hughes et al. 2019) and tidal position as the relative location within and outside the tidal frame based on a local tidal datum (supratidal, high mean intertidal, mean intertidal, low mean intertidal, subtidal). While salt marshes experience some level of inundation by definition, their vertical distribution may differ depending on edaphic conditions, surrounding habitat types, evolutionary history, competition dynamics, and local species assemblages (see Saintilan 2009). Salt marsh ecosystems occupy portions of the tidal frame from low intertidal channels to intertidal salt marsh plains to supratidal zones that only experience seasonal inundation or flooding during extreme events (Purer 1942; Veldkornet et al. 2015; Adams 2020). Furthermore, adjacent habitats and their characteristics influence salt marsh ecosystem function (e.g., flow of nutrients—Lesser et al. 2021).

Drivers—Tidal position

"High marsh" and "low marsh" are definitions used in some salt marshes (Nixon 1980; Bertness 1991) as salt marshes are heavily influenced by the frequency, depth, and duration of inundation. However, differences in relative context, vertical position, and datum-defined salt marsh elevations are needed when making comparisons across coastal settings. For example, relatively "low" or "high" marsh may be at very different absolute elevations defined by a datum when comparing river and tide dominated systems, especially if they have species with different inundation tolerances. Comparing or generalizing conditions between high and low marsh across regions may be inappropriate unless the question or generalization under consideration explicitly accounts for these positional differences across sites. The balance between vegetated and unvegetated components is based on inundation, salinity, and disturbance stress as well as the specific tolerances of plant species present (Johnson and York 1915; Chapman 1940; Bertness 1991). The tidal position of salt marshes is an interaction between salt marsh elevation and tidal processes (Allen and Pye 1992). Vertical position may also be influenced by biotic and abiotic factors such as competition, top-down processes, microclimates, soil conditions, local hydrology, or other factors, and is therefore geographically variable (e.g., Alberti et al. 2010; He et al. 2017). The structure, density, and condition of vegetation, due to tidal position, are key drivers of salt marsh function (Kneib 1997). For example, vegetation height can have a positive impact on accretion rates (Boorman et al. 1998) and differences in salt marsh vegetation structure/productivity are important for carbon stocks (Yando et al. 2016). Changes in these vegetation features may have substantial impacts on the habitat quality of individual salt marsh patches for salt marsh fauna (Smee et al. 2017) and adjacent habitats in the coastal seascape and landscape (Boström et al. 2011).

Drivers—Adjacent systems

Within seascape and landscape mosaics, adjacent habitats can influence salt marsh structure and function (e.g., habitat provision—Rountree and Able 2007, energetic support for food webs—Harris et al. 2021, and food web function—Lesser et al. 2021). Adjoining intertidal habitats include, but are not limited to, unvegetated flats, mangroves, microbial mats, oyster/coral reefs, rocky reefs, seagrasses, and open water/ponds (Fig. 4; Supporting Information Fig. S1) (discussed in Adams 1963). Adjacent subtidal habitats may include mudflats, seagrasses, and reefs (corals, oysters, rocky, etc.), while adjacent supratidal habitats may include infrequently inundated mangroves, beaches/dunes, salt flats, sabkhas, unvegetated flats, microbial mats, freshwater wetlands, supratidal forests, and other terrestrial habitats (Fig. 4; Supporting Information Fig. S1). In some cases, adjacent supratidal habitats may not locally exist in areas that do not maintain adequate supratidal environments (e.g., salt marsh islands). The arrangement of habitats both within the intertidal zone and in adjacent systems can influence salt marshes and their distribution through connectivity, nutrients, food web dynamics, and population
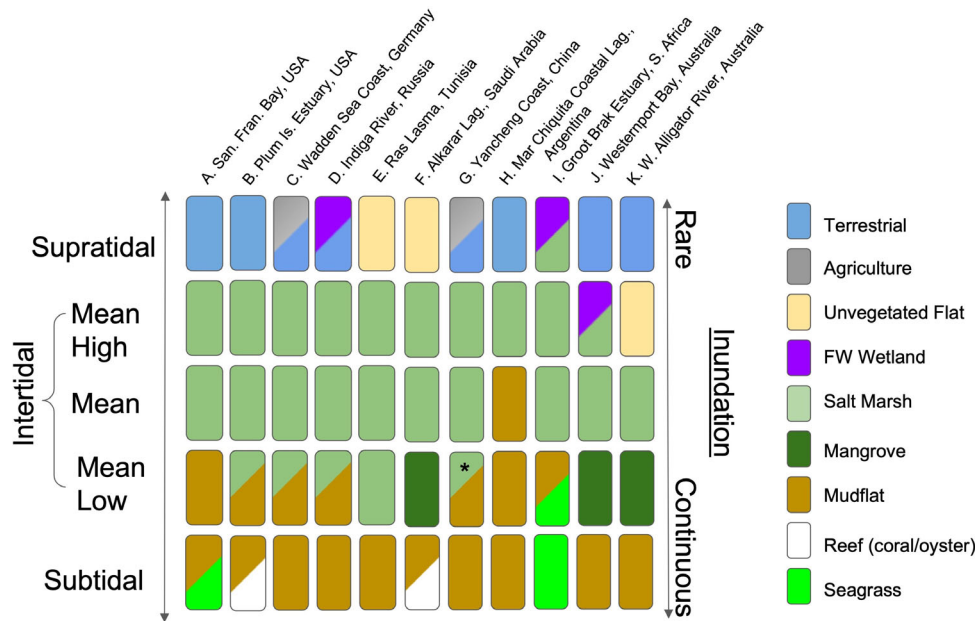
Fig. 4. Examples of salt marsh tidal position and adjacent ecosystem types. Inundation level is presented along a vertical gradient from rare to continuous. All locations are as in Fig. 2. *Invasive species are now dominant.

dynamics (Chapman 1940; Adams 1963; Able et al. 2012; Boström et al. 2018; James et al. 2021; Ziegler et al. 2021*b*,*c*). For example, along the land-sea interface, differences or changes in geomorphology and elevation can form berms, dikes, and levees within the salt marsh, altering water flow dynamics and sedimentation (Pedersen and Bartholdy 2007; Wegscheidl et al. 2015). In addition, humans have made extensive modifications to the landscape surrounding salt marshes impacting key processes (*see* Section Cross-scale considerations).

Intra-system setting

Diversity of salt marshes

Salt marshes are comprised of patches with different sizes, shapes, and arrangements (Boström et al. 2011). These patches can be formed by processes at multiple spatial scales that can differ within and between salt marshes. Open coast salt marshes can have simple semi-regular spacing of tidal creeks, while those that are enclosed can have more complex feather shapes (Van de Koppel et al. 2012). Smaller spatial scale processes such as establishment of expanding vegetation (Angelini and Silliman 2012), herbivory (McLaren and Jefferies 2004; Crotty et al. 2020), or erosion (Fanjul et al. 2015) can also influence salt marsh morphology.

Drivers—Patch size

Salt marsh patch size effects have been studied at a limited number of sites, with larger patches often providing relative increase for some functions, but not all. In a degrading salt marsh, patches larger than 20 m^2 entrapped larger amounts of

shells around their edges, reducing patch erosion, and allowing plant regrowth, while patches smaller than 20 m^2 tended to collapse (Yan et al. 2021). Furthermore, a positive correlation between salt marsh patch size and accretion rates has been observed in some marshes (Sánchez et al. 2001) and larger sized patches have been shown to be more resistant to sea-level rise in some locations (Gittman et al. 2018). Similarly, recolonization of *Spartina alterniflora* salt marsh was more successful when remnant patches were larger than 20 m^2 (Angelini and Silliman 2012). Larger patches have also been shown to support a more complex food web (Martinson et al. 2012) and have greater densities of insects (patches of 20 vs. 1 ha; Raupp and Denno 1979). However, in some cases intermediate-sized patches ($\sim$ 1 ha) may better support nekton communities (Ziegler et al. 2021*b*). Despite these studies, additional work is needed on linking salt marsh patch size to ecosystem function.

Drivers—Patch shape

Patch shape influences the amount of edge vs. interior habitat, and ecological functions can be variable between patch edges and interiors in salt marshes (Peterson and Turner 1994; Kim et al. 2012; Ziegler et al. 2021*b*,*c*). Salt marsh platforms and the associated creek channel networks are formed by interactions between hydrology, geomorphology, and biological/ecological features (e.g., vegetation structure and density; burrows) (D'Alpaos et al. 2007). Channel networks exert strong control on hydrodynamics, sediment transport, and nutrient exchange

via tidal action; however, salt marsh vegetation regulates wave attenuation (Möller and Spencer 2002), reduces tidal energy, and promotes sediment deposition by trapping suspended particles (Temmerman et al. 2005; D'Alpaos et al. 2007). Environmental variability between the edge and interior of salt marsh patches can drive the spatial distribution of salt marsh vegetation species depending on patch size and the level of heterogeneity (Morzaria-Luna et al. 2004; Kim et al. 2012; Veldkornet et al. 2016). There is also evidence that the shape of patches can affect habitat provisioning to consumer species, with patch shape in salt marshes having species-specific impacts on the body size of commercially important fisheries species (James et al. 2021), body condition of juvenile fishes (Ziegler, unpublished data), hydrologic and dissolved oxygen regulation (Runca et al. 1996; Ravera 2000), and greater fish density and species richness associated with more circular patches (Green et al. 2012).

Drivers—Patch aggregation

Salt marsh patch aggregation describes the distance of salt marsh patches relative to one another. The relative distance of salt marsh patches influences the movement of species between patches as well as dispersal and can result in differences in community structure (James et al. 2021). Fragmentation (Wilcove et al. 1986; Fahrig 2003) is common in salt marshes with high wave exposure (Couvillion et al. 2016) and occurs when the vegetated portion of the salt marsh is degraded and converted into shallow open water (i.e., sand or mudflats) (Shakeri et al. 2020) or salt pannes (Beheshti et al. 2022), increasing the ratio of edge length relative to interior area. Salt marsh fragmentation does not occur uniformly across a shoreline and can lead to areas of highly eroded escarpments adjacent to gradual sloping shorelines, thus potentially influencing the functionality and accessibility of the edge for various coastal species (Meyer and Posey 2019; Keller et al. 2019).

Framework application

Applying the framework

The purpose of the conceptual framework is to explicitly differentiate the underlying choices scientists make when deciding to compare study sites, and therefore lay the foundation for future comparative work. This framework can be applied across disparate locations using readily available data on variables that are used to measure the key drivers presented in Section Salt marsh conceptual framework. While variables at each spatial setting occur along continuous gradients, we suggest using a limited number of categories in most cases to reduce the complexity of applying the framework. These categories may be subtle and discretion should be used in their application. Once the overall settings of study sites are assessed based on measured or derived variables and specific

comparative questions and functions are refined, a more evidence-based comparison can be attempted (e.g., treating key environmental variables as continuous axes, testing for the utility of simple categories across spatial scales, developing predictive models for specific functions of interest) using the conceptual framework presented here (Fig. 6).

Global setting

We recommend users first characterize the temperature and precipitation regimes of their study sites. We suggest identifying one of the eight suggested Köppen-Geiger climate types (Supporting Information Table S1) by either quantifying local climate data or assigning climate type using available spatial products (e.g., Beck et al. 2018) to provide a reasonable compromise between specificity and applicability (Fig. 6).

Coastal setting

We recommend using water monitoring data such as riverine or tidal gauges to measure key variables of tidal energy, fluvial discharge, and wave energy. Users can identify coastal geomorphological type by either quantifying each forcing using local data (Heap et al. 2001) or assigning type using dominant landforms as a proxy (Dalrymple et al. 1992; van Niekerk et al. 2020). We suggest nine coastal geomorphological types that represent broad differences, acknowledging that tidal, river, and wave forcings exist along a continuum.

Inter-system setting

We recommend using positional data to identify relative position and dominant community type of all habitats across the coastal continuum (inter-, sub-, and supra-tidal), to provide a thorough understanding of the coastal seascape (Fig. 4; Supporting Information Fig. S1). Users can determine such a tidal datum-based positional framework by quantifying elevation using tools such as real-time kinematic GPS and linking to local hydrological data (which may also be measured using *in situ* water level loggers), coupled with site-level habitat maps. In the absence of local hydrology and elevation data, habitat types can be used as an approximation for tidal position, leveraging local expert knowledge. For example, commonly found salt marsh species with high flooding tolerances can help define frequently inundated areas (e.g., *S. alterniflora*, *Porterasia coarctata*), while species commonly found at upland transitions that prefer infrequent inundation can help define upland edge (e.g., *Cressa truxillensis*, *Disphyma crassifolium*, *Iva frutescens*, *Juncus kraussii*, *Spartina densiflora*).

Intra-system setting

We recommend users measure local spatial data, including both salt marsh amount and fragmentation (Fig. 5). Users can quantify these variables with habitat maps from remotely sensed imagery and geographic information systems. For salt

marsh amount, we suggest quantifying the extent of salt marsh around each study site by orders of magnitude (i.e., 10s vs. 1000s m^2). For salt marsh fragmentation, we suggest a continuous vs. fragmented classification, understanding that these classes represent end-members of continuous variables. Because of its importance in seascape and landscape ecology, there are many different metrics and indices developed to represent fragmentation (e.g., aggregation index; He et al. 2000) that can be applied to salt marshes (Wang et al. 2014) and measured using remotely sensed data products and openly available tools (e.g., *FRAGSTATS*—McGarigal et al. 2012; R package *landscapemetrics*—Hesselbarth et al. 2019). If remotely sensed resources are not available, users can also assign relative size and fragmentation using field measurements such as marsh edge length and estimated area.
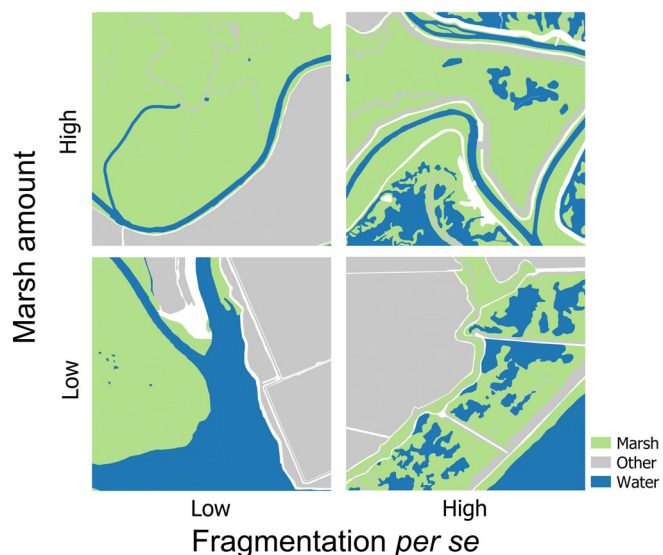

Fig. 5. Areas of salt marsh (green), water (blue), and other terrestrial features (gray) with varying relative (high and low) amounts and fragmentation of salt marsh. Each square represents a 1.5 × 1.5 km area. Each row or column represents the same amount of salt marsh (*y*-axis) or fragmentation (*x*-axis). Fragmentation was quantified with the aggregation index (He et al. 2000). Aggregation index is a spatial pattern metric between 0 and 100 that represents how clumped cover types (e.g., marsh) are to one another. Higher aggregation index values represent more aggregation, while lower values indicate that similar habitats are more separated (i.e., fragmented). High marsh amount (top row) ~ 140 ha, low marsh amount (bottom row) ~ 65 ha. Low fragmentation (left column) aggregation index ~ 97, high fragmentation (right column) aggregation index ~ 92. High fragmentation had smaller average patch size (low marsh amount: low fragmentation = 11.7 ha, high fragmentation = 5.1 ha; high marsh amount: low fragmentation = 13.5 ha, high fragmentation = 1.7 ha) and higher perimeter to area ratio (i.e., more complex shape, low marsh amount: low fragmentation = 0.14, high fragmentation = 0.31; high marsh amount: low fragmentation = 0.24, high fragmentation = 0.38). All areas shown are from the San Francisco Bay-Delta, USA. Water class represents all non-marsh intertidal and subtidal cover types; other class is all non-marsh supratidal cover types.

Cross-scale considerations
Anthropogenic influence

In placing locations in the framework, there are several additional factors that should be considered, as they can influence ecosystem function across multiple spatial scales. Perhaps most important is the influence of humans on landscapes at multiple settings. At the global setting, the impacts of anthropogenic climate change on drivers (temperature, precipitation, seasonality) need to be considered as these are dynamic and may differ in their rates of change (Colombano et al. 2021). Future climatic shifts may exceed site-specific ecological and physical thresholds, drastically impacting ecosystem function if key drivers at any spatial setting are changed from historical conditions. At the coastal setting, damming, diking, and hydrological modification of the watershed can greatly impact the ability of salt marshes to maintain their relative elevation if sediment and/or freshwater inputs have been modified compared to conditions when salt marshes formed (e.g., Watson and Byrne 2013). At the inter-system setting, the relative position of the salt marsh (i.e., hydrology) and the identity of adjacent systems and key linkages in the coastal seascape/landscape can be influenced by coastal development, diking, nearby dredging, and artificial breaching of inlets. Finally, at the intra-system level, salt marsh amount and configuration can be impacted by multiple human-related activities (e.g., ditching, ponding, dredging, grazing, hay-making, and bait-digging). Understanding human alteration of study sites at each spatial setting is crucial to understand what is influencing ecosystem functions of interest and to make valid comparisons across study sites.

Biogeography

A significant consideration when applying this conceptual framework is biogeography, with particular focus on the identity of species within the region of interest and their spatial distribution. The number of species in salt marshes is often limited due to high levels of abiotic stress, and regional species pools differ due to individual biogeographic histories. Two systems may be similar at all settings in our framework but may have different functionality due to differences in regional and site-specific species assemblages. For example, smooth cordgrass (*S. alterniflora*) (Bortolus et al. 2019) is a native salt marsh foundation species in eastern North America (Dayton 1972) that has exceptionally high inundation tolerance. Not all salt marshes have such a dominant plant species that can survive under such high levels of inundation (i.e., below mean sea level). Where introduced, *Spartina* species can become invasive and displace native salt marsh species or invade unvegetated mudflat, impacting trophic dynamics in invertebrates, habitat for associated marsh birds, sediment trapping, and nutrient cycling (Grosholz et al. 2009; Li et al. 2009) (*see* Figs. 4, 7 on the Yangcheng Coast, China). More generally, marshes dominated by graminoid species may show distinct patterns in carbon accumulation (Yando et al. 2016), sediment trapping (Lacy et al. 2020), and trophic web linkages (Schrama et al. 2017; Ziegler et al. 2019) compared to marshes dominated
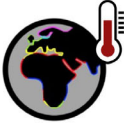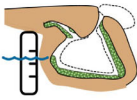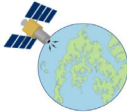
Setting	Key Drivers	Variables	Application
Global	Temperature regime · · · · · · · · · · · · · · · · · Precipitation regime	Climate data (temperature, precipitation)	Identify Köppen-Geiger climate type: Quantify climate using local data Assign climate using spatial products (Beck et al. 2018)
Coastal	Tidal forcing · · · · · · · · · · · · · · · · · Riverine input · · · · · · · · · · · · · · · · · Wave energy	Water data (tidal energy, fluvial discharge, wave energy)	Identify coastal geomorphology type: Quantify relative energy with local data (Heap et al. 2001 Appendix B) Assign geomorphology using dominant landform features (Boyd et al. 1992)
Inter-system	Tidal position · · · · · · · · · · · · · · · · · Adjacent systems	Position data (relative elevation, tidal datum, community type)	Identify positions of coastal ecosystems: Quantify identity and position using local data (Hughes et al. 2019) Assign identity and position using habitat maps (NatureServe)
Intra-system	Patch size · · · · · · · · · · · · · · · · · Patch shape · · · · · · · · · · · · · · · · · Patch aggregation	Local spatial data (salt marsh amount, fragmentation metrics)	Identify salt marsh spatial arrangement: Quantify characteristics using local imagery (McGarigal et al. 2012, Hesselbarth et al. 2019) Assign relative characteristics using ground-based measurements

Fig. 6. A how-to guide for placing sites and studies into the conceptual framework at each spatial setting. For additional guidance, *see* Section Applying the framework. Vector images courtesy of IAN Image Library.

by more succulent species. As an example, a species shift that could result from increased marsh salinity such as the replacement of a graminoid species (e.g., *Schoenoplectus* spp.) with simple architecture by a succulent plant with more complex architecture (e.g., *Sarcocornia* spp.), would change the deposition of sediment on the marsh surface by changing the frontal area of vegetation that interacts with a sediment-laden water column (reviewed in Cahoon et al. 2021). Furthermore, the presence of certain faunal species (e.g., bioturbators, herbivores) can establish and modulate particular biotic interactions that change the functioning of a salt marsh (e.g., Coverdale et al. 2014; Alberti et al. 2015; Wasson et al. 2019; Beheshti et al. 2022). These functional differences may be partially attributable to differences in plant structural architecture and functional traits, regardless of environmental setting. The identity of salt marsh plant and animal species is not explicitly captured in our framework, but is crucial to account for in comparative salt marsh science.

Landscape evolution

Landscape evolution provides additional context to salt marshes at all levels and needs to be considered. It is important to understand not only recent (decades—centuries), but also long-term (millennia) processes that still have a large impact on systems and their functioning. For example, Rogers et al. (2019) highlight the need to understand millennial-scale variation in sea levels to accurately account for wetland carbon storage. The stability of sea levels can be important for structuring, with more stable sea levels typically presenting with more high marsh area, and more dynamic areas dominated by a greater extent of low marsh when examined at longer time scales (Rogers et al. 2019).

Framework utility

Conceptual foundation

By making explicit the inherent spatial structuring of environmental gradients that influence ecosystem function, this framework can act as a conceptual foundation for salt marsh science. In doing so, the framework provides insight into which salt marshes may be appropriate for comparisons for specific spatial scales and functions, a feature that is especially important for estimating function at sites that are lacking robust datasets. For comparative studies, not directly accounting for the inherent spatial structure in environmental gradients can lead to high variability in measured ecosystem functional responses, making it more difficult to distinguish

Fig. 7. Example comparisons. Each panel showcases an image of the particular location, its global setting (color of ring on icon), coastal setting (icon of coastal landform), inter-patch setting (five color blocks from supratidal → subtidal as discussed in Section Inter-system setting and Fig. 4). A detailed table of all components is presented in Supporting Information Table S2. Photo credit for (A) San Francisco Bay-Delta, USA—Amber D. Manfree; (B) Plum Island Estuary, USA—David S. Johnson; (H) Mar Chiquita Coastal Lagoon, Argentina—Leandro J. Reyna Gandini; (I) Groot Brak Estuary, South Africa— Janine B. Adams; all other photos provided by authors.

environmental driver signal from noise. Accounting for variation at several spatial scales may lead to enhanced explanatory power for analyses. This framework requires users to refine their questions and to think more deeply about how they expect functional variability to be structured across spatial scales. These considerations will necessarily vary based on the research question and functional response under study.

We illustrate the framework's utility as a conceptual foundation by comparing a series of example salt marshes from around the world: (A) San Francisco Bay-Delta, United States; (B) Plum Island Estuary, United States; (C) Wadden Sea Coast, Germany; (D) Indiga River Estuary, Russia; (E) Ras Lamsa, Tunisia; (F) Alkarar Lagoon, Saudi Arabia; (G) Yancheng Coast, China; (H) Mar Chiquita Coastal Lagoon, Argentina; (I) Groot

Brak Estuary, South Africa; (J) Westernport Bay, Australia; and (K) West Alligator River Estuary, Australia (Figs. 2, 4, 7; Supporting Information Table S2). We use a simplified iconography to show multiple framework settings for each location. A full description of each location and how we placed them in the framework, along with images (Fig. 7), can be found in Fig. 6 and Supporting Information Table S2, with the exception of intra-system setting which may be highly variable within each location (e.g., San Francisco Bay, Fig. 5). For each setting, we used the suggested application pathway (Fig. 6) using a combination of existing literature, local data, and the expertise of authors who have worked in each site to make evaluations, following guidance in Section Applying the framework and Fig. 6.

Making appropriate comparisons

Our framework supports making appropriate comparisons by bringing the specific multi-scale settings of each study location to the forefront. Applying this framework requires researchers to evaluate the suitability of other studies beyond the fact that similar functions are measured, instead ensuring that settings across a variety of spatial scales are similar as required by the research question. For example, if researchers are studying what drives sedimentation rates in salt marshes of the San Francisco Bay-Delta, USA (Fig. 7A), what other salt marshes should they be compared to? Researchers may first try to compare measured rates to systems located nearby, including mostly lagoonal estuaries along the outer California coast (Heady et al. 2014). Another option would be to compare results to well-studied systems with long-term data like Chesapeake Bay, USA or Plum Island Estuary, USA (Fig. 7B), which are in different climate regions and are dominated by different functional types of vegetation (succulent in California, USA [Vasey et al. 2012], graminoid along Atlantic coast, USA [Johnson and York 1915]). A comparison to a well-studied site is not necessarily inappropriate in all cases depending on the question being asked, but the question and comparison need to be evaluated critically. For example, if the goal is to understand what drives sedimentation patterns in salt marshes in Mediterranean areas then other Mediterranean or even semi-arid and arid areas, like Ras Lamsa, Tunisia (Fig. 7E) or Alkarar Lagoon, Saudi Arabia (Fig. 7F), should be considered for comparison. Similarly, if a tidally-driven salt marsh in a more arid climate does not have sedimentation rate data available, considering where sites are placed in the conceptual framework can assist in predicting that sites with a similar climate and coastal setting are more appropriate comparisons than data-rich study sites regardless of their setting. With limited resources, being able to accurately estimate function at locations without robust data is paramount. Of course, researchers know that making appropriate comparisons is important to tease out the patterns in complex ecological data, and make tough decisions on what other data to compare and contrast in their products; the current framework is a tool to magnify and clarify that desire. The importance of specific settings in the framework

necessarily depends on the functional response being measured. For example, sedimentation rate may vary strongly with coastal setting (Amoudry and Souza 2011), while faunal habitat use may depend much more on local patch size and configuration (Raupp and Denno 1979; Martinson et al. 2012; Ziegler et al. 2021b).

The framework also assists researchers asking questions that purposely vary in spatial setting, as in latitudinal gradient work (e.g., Pennings and Bertness 1999; Pennings and Silliman 2005; Canepuccia et al. 2018; Mueller et al. 2018; Peer et al. 2018; Liu et al. 2020). For example, if researchers are exploring how fish habitat usage of salt marsh patches (size and configuration) varies across a latitudinal gradient, how can the conceptual framework help choose appropriate study sites? In this case, the global setting and climate is varied to answer the question, but controlling for the other settings in the framework will help provide clarity in what the researchers would like to address, and contrasting that ideal to what the researchers are actually addressing given the availability of study sites. Using the 11 example salt marshes in Fig. 6, which are admittedly more global in distribution than typical latitudinal studies along a specific coast, a study design could include West Alligator River, Australia (Fig. 7K) at the lowest latitudes; Yangcheng Coast, China (Fig. 7G), Plum Island Estuary, USA (Fig. 7B), and Wadden Sea Coast, Germany (Fig. 7C) across the middle latitudes; and Indiga River, Russia (Fig. 7D) at the highest latitudes. These sites avoid the driest climates, controlling for precipitation broadly. The sites do vary in coastal setting (open coast, back barrier, and tidal estuary) so finding less river-influenced coastal settings at high and low latitudes could improve the design by reducing variability at the coastal spatial scale. However, inter-system setting is quite similar across sites with mudflats in the subtidal, extensive marshes throughout the intertidal, and terrestrial systems in the supratidal. If the researchers determine from previous knowledge that coastal setting is less important to constrain than inter-system setting given site access, this may be an appropriate design. In selecting specific locations, controlling for intra-system setting across all sites or varying it systematically as a variable of interest will be critical (James et al. 2021).

Enhancing quantitative analyses

This framework can act as a necessary primary step that supports quantitative analyses for specific functions. While the framework uses simple categories for each spatial setting to assist readers, we acknowledge the continuous nature of the key drivers of salt marshes at every setting. By starting with a framework that is simple to apply and categorical in nature, researchers can take the next step in testing the utility of these categorical bins for their function of interest, including threshold detection along continuous driver axes, cross-scale effect size for multiple drivers, multivariate model

development, and if categories of settings are even appropriate.

As an example, soil carbon storage is a commonly measured metric globally. Many estimates have provided regional, national, or sometimes even global averages (e.g., Kauffman et al. 2020). Often, variability in these large soil core databases is not well-explained by the tested factors, instead being reasonably approximated by single estimates (e.g., Holmquist et al. 2018). This is partially due to lack of relevant spatial data (Uhran et al. 2021). However, small-scale studies can clearly show strong differences in carbon storage at intra- and intersystem settings along environmental gradients (Simpson et al. 2017; Jones et al. 2018; Raw et al. 2019, 2020; Ward et al. 2021; Human et al. 2022; Owers et al. 2022), and coastal setting can also play a strong role via control on sediment accretion processes (Gorham et al. 2021). Our framework can inform the quantitative analyses of these datasets in this case by explicitly testing for the influence of nested spatial settings on the variability in soil carbon. For example, using all 11 salt marshes, we could investigate the oceanic climate sites to control for global setting (Wadden Sea Coast, Germany; Mar Chiquita Coastal Lagoon, Argentina; Groot Brak Estuary, South Africa; Westernport Bay, Australia). We could then test if coastal setting (between regions) or inter/intra-system setting (within regions) contains more variability in soil carbon density. By accounting for potential variability at small scales that is typically ignored in larger meta-analytic approaches, it is possible that stronger signals will emerge from the data. Regardless, there is strong evidence that coastal setting can be a strong driver of coastal ecosystem function, as shown by the work of Gorham et al. (2021) and Rovai et al. (2018).

Using the conceptual framework could also help partition variability into *a priori* spatially-referenced settings, which may improve the ability to determine the importance of environmental drivers (and which scales they operate on) compared to current meta-analytic approaches. These meta-analyses provide a necessary baseline for the field and highlight current gaps in understanding, both of which are crucial (e.g., Holmquist et al. 2018; Uhran et al. 2021 for soil carbon). However, to move towards prediction at regional and site scales, variability must be more highly compartmented and constrained. For soil carbon, perhaps an analysis with a threshold of precipitation/water vapor deficit, categories of coastal setting, a threshold of porewater salinity, and categories of marsh fragmentation would provide enhanced explanatory power over current approaches. In this way, the conceptual framework outlined here supports the scaffolding of a more quantitative analysis, making that analysis and subsequent predictive modeling more efficient and tractable. The need to test this framework with specific functions is not only a portion of its design, but also an imperative follow-up. Lower levels of the framework in particular have not been sufficiently constrained in comparative work; we suggest more robust consideration of smaller-scale settings (tidal position,

configuration) may reduce confounding variation and increase explanatory power. As these analyses necessarily vary across scales and for individual functions, we have not attempted their full incorporation here. However, we expect and hope that this conceptual foundation will spur this type of analysis, which is crucial to advancing understanding and allowing prediction given changing conditions.

Future directions

We foresee this framework reducing the prevalence of biased comparisons and improving representation of the spatial settings inherent to salt marsh ecosystems. We highlight that many of the field's best-studied salt marshes represent only a small portion of the functional space that these ecosystems can encompass and selecting appropriate comparisons can help disentangle multiple causal factors of salt marsh function. While important for advancing our understanding of salt marsh science in certain ecologically and economically important areas, the continued narrow focus on well-studied salt marshes diminishes capacity to effectively understand and describe how salt marshes function globally and what interventions might address conservation and restoration needs. This evaluation of settings across spatial scales minimizes the impulse to use well-studied salt marshes as normative benchmarks; even the best-studied salt marsh may not be a good comparison if it is systematically different at a crucial level in the framework for the question and function of interest. Therefore, we propose that data-rich locations only serve as references where appropriate. By appropriately accounting for the diversity of salt marshes globally, the patterns and processes that influence these ecosystems will become apparent.

Our conceptual framework allows for appropriate comparisons, questions, and inferences across the wide diversity of salt marsh ecosystems. We propose that this framework serve as a basis for clearly communicating the environmental setting and spatial scale of analysis that salt marsh studies are conducted and compared. While the subtle differences achieved through the application of this framework may not be pertinent to some studies, it will be critical to others. The utility of this framework for all salt marshes should be tested to determine possible combinations of categories, their prevalence, and knowledge gaps, as well as to understand the difference in the structure, function, and services of salt marsh typologies. Comparative studies in salt marshes are needed to provide critical data for planners, policymakers, and scientists to restore, conserve, and integrate salt marshes into the broader coastal seascape/landscape, particularly in light of projected future climate change impacts. We anticipate that this framework will serve as a step towards incorporating salt marsh macro- and meso-ecology into powerful approaches for understanding how salt marshes across the globe function today and into the future, while promoting collaborative efforts.

References

Able, K. W., D. N. Vivian, G. Petruzzelli, and S. M. Hagan. 2012. Connectivity among salt marsh subhabitats: Residency and movements of the mummichog (*Fundulus heteroclitus*). Estuaries Coasts **35**: 743–753. doi:10.1007/s12237-011-9471-x

Adam, P. 1993. *Saltmarsh ecology*. Cambridge Univ. Press. doi:10.1017/CBO9780511565328

Adam, P. 2002. Saltmarshes in a time of change. Environ. Conserv. **29**: 39–61. doi:10.1017/S0376892902000048

Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology **44**: 445–456. doi:10.2307/1932523

Adams, J. B. 2020. Salt marsh at the tip of Africa: Patterns, processes and changes in response to climate change. Estuar. Coast. Shelf Sci. **237**: 106650. doi:10.1016/j.ecss.2020.106650

Alberti, J., A. M. Casariego, P. Daleo, E. Fanjul, B. R. Silliman, M. Bertness, and O. Iribarne. 2010. Abiotic stress mediates top-down and bottom-up control in a southwestern Atlantic salt marsh. Oecologia **163**: 181–191. doi:10.1007/s00442-009-1504-9

Alberti, J., P. Daleo, E. Fanjul, M. Escapa, F. Botto, and O. Iribarne. 2015. Can a single species challenge paradigms of salt marsh functioning? Estuaries Coasts **38**: 1178–1188. doi:10.1007/s12237-014-9836-z

Allen, J. R. L., and K. Pye. 1992. *Saltmarshes: Morphodynamics, conservation and engineering significance*. Cambridge Univ. Press.

Allen, J. 2000. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. Quaternary Science Reviews **19**(12): 1155–1231. doi:10.1016/s0277-3791(99)00034-7

Amoudry, L. O., and A. J. Souza. 2011. Deterministic coastal morphological and sediment transport modeling: A review and discussion. Rev. Geophys. **49**: RG2002. doi:10.1029/2010RG000341

Anderson, C. P., G. A. Carter, and M. C. Waldron. 2022. Precise elevation thresholds associated with salt marsh–upland ecotones along the Mississippi Gulf Coast. Ann. Am. Assoc. Geogr. **112**: 1850–1865. doi:10.1080/24694452.2022.2047593

Andréfouët, S. 2011. Reef typology, p. 906–910. *In* D. Hopley [ed.], *Encyclopedia of modern coral reefs: Structure, form and process*. Springer. doi:10.1007/978-90-481-2639-2_270

Angelini, C., and B. R. Silliman. 2012. Patch size-dependent community recovery after massive disturbance. Ecology **93**: 101–110. doi:10.1890/11-0557.1

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. **81**: 169–193. doi:10.1890/10-1510.1

Beck, H. E., N. E. Zimmermann, T. R. McVicar, N. Vergopolan, A. Berg, and E. F. Wood. 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data **5**: 180214. doi:10.1038/sdata.2018.214

Beheshti, K., C. Endris, P. Goodwin, A. Pavlak, and K. Wasson. 2022. Burrowing crabs and physical factors hasten marsh recovery at panne edges. PloS One **17**: e0249330. doi:10.1371/journal.pone.0249330

Bertness, M. D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. Ecology **72**: 138–148. doi:10.2307/1938909

Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England marsh plant community. Ecol. Monogr. **57**: 129–147. doi:10.2307/1942621

Boorman, L. A., A. Garbutt, and D. Barratt. 1998. The role of vegetation in determining patterns of the accretion of salt marsh sediment. Geol. Soc. Lond. Spec. Publ. **139**: 389–399. doi:10.1144/gsl.sp.1998.139.01.29

Bornman, T. G., J. B. Adams, and C. Bezuidenhout. 2004. Adaptations of salt marsh to semi-arid environments and management implications for the Orange river mouth: Anthropogenic effects on arid systems. Trans. R. Soc. S. Afr. **59**: 125–131. doi:10.1080/00359190409519173

Bortolus, A., and others. 2019. Supporting *Spartina*: Interdisciplinary perspective shows *Spartina* as a distinct solid genus. Ecology **100**: e02863. doi:10.1002/ecy.2863

Boström, C., S. J. Pittman, C. Simenstad, and R. T. Kneib. 2011. Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. Mar. Ecol. Prog. Ser. **427**: 191–217. doi:10.3354/meps09051

Boström, C., S. J. Pittman, and C. A. Simenstad. 2018. Ecological consequences of seagrass and salt-marsh seascape patterning on marine fauna, p. 121–151. *In* S. J. Pittman [ed.], *Seascape ecology*. Wiley.

Boyd, R., R. Dalrymple, and B. A. Zaitlin. 1992. Classification of clastic coastal depositional environments. Sediment. Geol. **80**: 139–150. doi:10.1016/0037-0738(92)90037-R

Braga, C. F., C. R. Beasley, and V. J. Isaac. 2009. Effects of plant cover on the macrofauna of Spartina marshes in northern Brazil. Braz. Arch. Biol. Technol. **52**: 1409–1420. doi:10.1590/S1516-89132009000600013

Buia, M. C., M. C. Gambi, and M. Dappiano. 2004. Seagrass systems. Biol. Mar. Mediterr. **10**: 133–183.

CAFF. 2019. *Arctic coastal biodiversity monitoring plan*. Conservation of Arctic Flora and Fauna International Secretariat.

Cahoon, D. R. 2006. A review of major storm impacts on coastal wetland elevations. Estuaries Coasts **29**: 889–898. doi:10.1007/BF02798648

Cahoon, D. R., K. L. McKee, and J. T. Morris. 2021. How plants influence resilience of salt marsh and mangrove wetlands to sea-level rise. Estuaries Coasts **44**: 883–898. doi:10.1007/s12237-020-00834-w

Canepuccia, A. D., J. L. Farina, E. Fanjul, F. Botto, J. Pascual, and O. Iribarne. 2018. Driving forces behind latitudinal

variations in plant-herbivore interactions in SW Atlantic salt marshes. Mar. Ecol. Prog. Ser. **603**: 93–103. doi:10.3354/meps12705

Chapman, V. J. 1938. Studies in salt-marsh ecology sections I to III. J. Ecol. **26**: 144–179. doi:10.2307/2256416

Chapman, V. J. 1940. Studies in salt-marsh ecology: Sections VI and VII. Comparison with marshes on the East Coast of North America. J. Ecol. **28**: 118–152. doi:10.2307/2256166

Chapman, V. J. 1974. Salt marshes and salt deserts of the world, p. 3–19. *In* R. J. Reimold and W. H. Queen [eds.], *Ecology of halophytes*, v. **79**. Academic Press.

Clark, R., and K. O'Connor. 2019. A systematic survey of bar-built estuaries along the California coast. Estuar. Coast. Shelf Sci. **226**: 106285. doi:10.1016/j.ecss.2019.106285

Clarke, L. D., and N. J. Hannon. 1967. The mangrove swamp and salt marsh communities of the Sydney district: I. Vegetation, soils and climate. J. Ecol. **55**: 753–771. doi:10.2307/2258423

Clarke, L. D., and N. J. Hannon. 1969. The mangrove swamp and salt marsh communities of the Sydney district: II. The Holocoenotic complex with particular reference to physiography. J. Ecol. **57**: 213–234. doi:10.2307/2258216

Colombano, D. D., and others. 2021. Climate change implications for tidal marshes and food web linkages to estuarine and coastal nekton. Estuaries Coasts **44**: 1637–1648. doi:10.1007/s12237-020-00891-1

Cooper, J. A. G. 1993. Sedimentation in a river dominated estuary. Sedimentology **40**: 979–1017. doi:10.1111/j.1365-3091.1993.tb01372.x

Cooper, J. A. G. 2001. Geomorphological variability among microtidal estuaries from the wave-dominated south African coast. Geomorphology **40**: 99–122. doi:10.1016/S0169-555X(01)00039-3

Couvillion, B. R., M. R. Fischer, H. J. Beck, and W. J. Sleavin. 2016. Spatial configuration trends in coastal Louisiana from 1985 to 2010. Wetlands **36**: 347–359. doi:10.1007/s13157-016-0744-9

Coverdale, T. C., C. P. Brisson, E. W. Young, S. F. Yin, J. P. Donnelly, and M. D. Bertness. 2014. Indirect human impacts reverse centuries of carbon sequestration and salt marsh accretion. PloS One **9**: e93296. doi:10.1371/journal.pone.0093296

Crotty, S. M., and others. 2020. Sea-level rise and the emergence of a keystone grazer alter the geomorphic evolution and ecology of southeast US salt marshes. Proc. Natl. Acad. Sci. USA **117**: 17891–17902. doi:10.1073/pnas.1917869117

D'Alpaos, A., S. Lanzoni, M. Marani, and A. Rinaldo. 2007. Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. J. Geophys. Res.: Earth Surf. **112**: F01008. doi:10.1029/2006JF000537

Dalrymple, R. W., B. A. Zaitlin, and R. Boyd. 1992. Estuarine facies models: Conceptual basis and stratigraphic implications. J. Sediment. Res. **62**: 1130–1146. doi:10.1306/D4267A69-2B26-11D7-8648000102C1865D

Davidson, N. C., and C. M. Finlayson. 2018. Extent, regional distribution and changes in area of different classes of wetland. Mar. Freshw. Res. **69**: 1525–1533. doi:10.1071/mf17377

Davidson, N. C., and C. M. Finlayson. 2019. Updating global coastal wetland areas presented in Davidson and Finlayson (2018). Mar. Freshw. Res. **70**: 1195–1200. doi:10.1071/MF19010

Davidson, N. C., and others. 1991. *Nature conservation and estuaries in Great Britain*. Nature Conservancy Council.

Davies, J. L. 1964. A morphogenic approach to world shorelines. Z. Geomorphol. **8**: 127–142. doi:10.1127/zfg/mortensen/8/1964/127

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. *In* B. C. Parker [ed.], *Proceedings of the colloquium on conservation problems in Antarctica*. Allen Press.

Del Grosso, S., W. Parton, T. Stohlgren, D. Zheng, D. Bachelet, S. Prince, K. Hibbard, and R. Olson. 2008. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology **89**: 2117–2126. doi:10.1890/07-0850.1

Dyer, K. R. 1998. The typology of intertidal mudflats. Geol. Soc. Lond. Spec. Publ. **139**: 11–24. doi:10.1144/GSL.SP.1998.139.01.02

Elliott, M., and D. S. McLusky. 2002. The need for definitions in understanding estuaries. Estuar. Coast. Shelf Sci. **55**: 815–827. doi:10.1006/ecss.2002.1031

Eslami-Andargoli, L., P. Dale, N. Sipe, and J. Chaseling. 2009. Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. Estuar. Coast. Shelf Sci. **85**: 292–298. doi:10.1016/j.ecss.2009.08.011

Fagherazzi, S., and others. 2012. Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. Rev. Geophys. **50**: RG1002. doi:10.1029/2011RG000359

Fagherazzi, S. 2013. The ephemeral life of a salt marsh. Geology **41**: 943–944. doi:10.1130/focus082013.1

Fagherazzi, S., and others. 2013. Ecogeomorphology of salt marshes, p. 182–200. *In* J. F. Shroder [ed.], *Ecogeomorphology*. Elsevier. doi:10.1016/B978-0-12-374739-6.00329-8

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. **34**: 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419

Fanjul, E., M. Escapa, D. Montemayor, M. Addino, M. F. Alvarez, M. A. Grela, and O. Iribarne. 2015. Effect of crab bioturbation on organic matter processing in south West Atlantic intertidal sediments. J. Sea Res. **95**: 206–216. doi:10.1016/j.seares.2014.05.005

Fariña, J. M., Q. He, B. R. Silliman, and M. D. Bertness. 2018. Biogeography of salt marsh plant zonation on the Pacific coast of South America. J. Biogeogr. **45**: 238–247. doi:10.1111/jbi.13109

Feagin, R. A., and others. 2020. Tidal wetland gross primary production across the continental United States, 2000–2019. Glob. Biogeochem. Cycles **34**: e2019GB006349. doi:10.1029/2019GB006349

Feher, L. C., and others. 2017. Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands. Ecosphere **8**: e01956. doi:10.1002/ecs2.1956

Findlay, S. 2009. Tidal freshwater wetlands, p. 558–562. *In* G. E. Likens [ed.], *Encyclopedia of inland waters*. Academic Press.

Friess, D. A., E. S. Yando, J. B. Alemu, L. W. Wong, S. D. Soto, and N. Bhatia. 2020. Ecosystem services and disservices of mangrove forests and salt marshes, p. 107–141. *In* S. J. Hawkins and others [eds.], *Oceanography and marine biology*, v. **58**. Taylor & Francis.

Gabler, C. A., and others. 2017. Macroclimatic change expected to transform coastal wetland ecosystems this century. Nat. Clim. Change **7**: 142–147. doi:10.1038/nclimate3203

Gittman, R. K., and others. 2018. Living on the edge: Increasing patch size enhances the resilience and community development of a restored salt marsh. Estuaries Coasts **41**: 884–895. doi:10.1007/s12237-017-0302-6

Glooschenko, W. A., and N. S. Harper. 1982. Net aerial primary production of a James Bay, Ontario, salt marsh. Can. J. Bot. **60**: 1060–1067. doi:10.1139/b82-136

Gorham, C., P. Lavery, J. J. Kelleway, C. Salinas, and O. Serrano. 2021. Soil carbon stocks vary across geomorphic settings in Australian temperate tidal marsh ecosystems. Ecosystems **24**: 319–334. doi:10.1007/s10021-020-00520-9

Green, B., D. Smith, and G. Underwood. 2012. Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. Mar. Ecol. Prog. Ser. **466**: 177–192. doi:10.3354/meps09791

Grosholz, E., L. A. Levin, A. Tyler, and C. Neira. 2009. Changes in community structure and ecosystem funciton following *Spartina alterniflora* invasion of Pacific estuaries. *In* B. R. Silliman, E. D. Grosholz, and M. D. Bertness [eds.], *Human impacts on salt marshes: A global perspective*. Univ. of California Press.

Harris, J. M., W. R. James, J. S. Lesser, J. C. Doerr, and J. A. Nelson. 2021. Foundation species shift alters the energetic landscape of marsh nekton. Estuaries Coasts **44**: 1671–1680. doi:10.1007/s12237-020-00852-8

He, H. S., B. E. DeZonia, and D. J. Mladenoff. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. Landsc. Ecol. **15**: 591–601. doi:10.1023/A:1008102521322

He, Q., B. R. Silliman, and B. Cui. 2017. Incorporating thresholds into understanding salinity tolerance: A study using

salt-tolerant plants in salt marshes. Ecol. Evol. **7**: 6326–6333. doi:10.1002/ece3.3209

Heady, W. N., and others. 2014. *An inventory and classification of U.S. West Coast Estuaries*. The Nature Conservancy.

Heap, A. D., S. Bryce, D. A. Ryan, L. Radke, C. Smith, and R. Smith. 2001. *Australian estuaries & coastal waterways: A geoscience perspective for improved and integrated resource management*. Australian Geological Survey Organisation.

Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. Landscapemetrics: An open-source R tool to calculate landscape metrics. Ecography **42**: 1648–1657. doi:10.1111/ecog.04617

Holmquist, J. R., and others. 2018. Accuracy and precision of tidal wetland soil carbon mapping in the conterminous United States. Sci. Rep. **8**: 9478. doi:10.1038/s41598-018-26948-7

Hu, Y., B. Tian, L. Yuan, X. Li, Y. Huang, R. Shi, X. Jiang, and C. Sun. 2021. Mapping coastal salt marshes in China using time series of Sentinel-1 SAR. ISPRS J. Photogramm. Remote Sens. **173**: 122–134. doi:10.1016/j.isprsjprs.2021.01.003

Hughes, M. G., K. Rogers, and L. Wen. 2019. Saline wetland extents and tidal inundation regimes on a micro-tidal coast, New South Wales, Australia. Estuar. Coast. Shelf Sci. **227**: 106297. doi:10.1016/j.ecss.2019.106297

Human, L. R., J. Els, J. Wasserman, and J. B. Adams. 2022. Blue carbon and nutrient stocks in salt marsh and seagrass from an urban African estuary. Sci. Total Environ. **842**: 156955. doi:10.1016/j.scitotenv.2022.156955

Idaszkin, Y. L., and A. Bortolus. 2010. Does low temperature prevent *Spartina alterniflora* from expanding toward the austral-most salt marshes? Plant Ecol. **212**: 553–561. doi:10.1007/s11258-010-9844-4

Isacch, J. P., C. S. B. Costa, L. Rodríguez-Gallego, D. Conde, M. Escapa, D. A. Gagliardini, and O. Iribarne. 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-West Atlantic coast. J. Biogeogr. **33**: 888–900. doi:10.1111/j.1365-2699.2006.01461.x

James, W. R., Z. M. Topor, and R. O. Santos. 2021. Seascape configuration influences the community structure of marsh nekton. Estuaries Coasts **44**: 1521–1533. doi:10.1007/s12237-020-00853-7

Jin, B., C. Fu, J. Zhong, B. Li, J. Chen, and J. Wu. 2007. Fish utilization of a salt marsh intertidal creek in the Yangtze River estuary, China. Estuar. Coast. Shelf Sci. **73**: 844–852. doi:10.1016/j.ecss.2007.03.025

Johnson, D. S., and H. H. York. 1915. *The relation of plants to tide-levels: A study of factors affecting the distribution of marine plants*. Carnegie institution of Washington.

Jones, S. F., C. L. Stagg, K. W. Krauss, and M. W. Hester. 2018. Flooding alters plant-mediated carbon cycling independently of elevated atmospheric CO_2 concentrations. J. Geophys. Res.: Biogeosciences **123**: 1976–1987. doi:10.1029/2017JG004369

Kassas, M., and M. A. Zahran. 1967. On the ecology of the Red Sea littoral salt marsh, Egypt. Ecol. Monogr. **37**: 297–315. doi:10.2307/1942326

Kauffman, J. B., and others. 2020. Total ecosystem carbon stocks at the marine-terrestrial interface: Blue carbon of the Pacific northwest coast, United States. Glob. Change Biol. **26**: 5679–5692. doi:10.1111/gcb.15248

Keller, D. A., R. K. Gittman, M. C. Brodeur, M. D. Kenworthy, J. T. Ridge, L. A. Yeager, A. B. Rodriguez, and F. J. Fodrie. 2019. Salt marsh shoreline geomorphology influences the success of restored oyster reefs and use by associated fauna. Restor. Ecol. **27**: 1429–1441. doi:10.1111/rec.12992

Kim, D., D. M. Cairns, J. Bartholdy, and C. L. S. Morgan. 2012. Scale-dependent correspondence of floristic and edaphic gradients across salt marsh creeks. Ann. Am. Assoc. Geogr. **102**: 276–294. doi:10.1080/00045608.2011.620520

Kimball, M. E., and others. 2021. Novel applications of technology for advancing tidal marsh ecology. Estuaries Coasts **44**: 1568–1578. doi:10.1007/s12237-021-00939-w

Kirwan, M. L., G. R. Guntenspergen, and J. A. Langley. 2014. Temperature sensitivity of organic-matter decay in tidal marshes. Biogeosciences **11**: 4801–4808. doi:10.5194/bg-11-4801-2014

Kirwan, M. L., D. C. Walters, W. G. Reay, and J. A. Carr. 2016. Sea level driven marsh expansion in a coupled model of marsh erosion and migration. Geophys. Res. Lett. **43**: 4366–4373. doi:10.1002/2016GL068507

Kneib, R. T. 1997. Early life stages of resident nekton in intertidal marshes. Estuaries **20**: 214–230. doi:10.2307/1352732

Lacy, J. R., M. R. Foster-Martinez, R. M. Allen, M. C. Ferner, and J. C. Callaway. 2020. Seasonal variation in sediment delivery across the bay-marsh interface of an estuarine salt marsh. J. Geophys. Res.: Oceans **125**: e2019JC015268. doi:10.1029/2019JC015268

Lesser, J. S., O. Floyd, K. Fedors, L. A. Deegan, D. S. Johnson, and J. A. Nelson. 2021. Cross-habitat access modifies the 'trophic relay' in New England saltmarsh ecosystems. Food Webs **29**: e00206. doi:10.1016/j.fooweb.2021.e00206

Levin, L. A., and others. 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems **4**: 430–451. doi:10.1007/s10021-001-0021-4

Li, B., and others. 2009. *Spartina alterniflora* invasions in the Yangtze River estuary, China: An overview of current status and ecosystem effects. Ecol. Eng. **35**: 511–520. doi:10.1016/j.ecoleng.2008.05.013

Liu, W., X. Chen, D. R. Strong, S. C. Pennings, M. L. Kirwan, X. Chen, and Y. Zhang. 2020. Climate and geographic adaptation drive latitudinal clines in biomass of a widespread saltmarsh plant in its native and introduced ranges. Limnol. Oceanogr. **65**: 1399–1409. doi:10.1002/lno.11395

Lugo, A. E., and S. C. Snedaker. 1974. The ecology of mangroves. Annu. Rev. Ecol. Syst. **5**: 39–64. doi:10.1146/annurev.es.05.110174.000351

Mahmoud, A., A. M. El-Sheikh, and F. Isawi. 1982. Ecology of the littoral salt marsh vegetation at Rabigh on the Red Sea coast of Saudi Arabia. J. Arid Environ. **5**: 35–42. doi:10.1016/S0140-1963(18)31461-7

Martinson, H. M., W. F. Fagan, and R. F. Denno. 2012. Critical patch sizes for food-web modules. Ecology **93**: 1779–1786. doi:10.1890/11-1497.1

Mazarrasa, I., and others. 2021. Factors determining seagrass blue carbon across bioregions and geomorphologies. Glob. Biogeochem. Cycles **35**: e2021GB006935. doi:10.1029/2021GB006935

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the Univ. of Massachusetts, Amherst.

McLaren, J. R., and R. L. Jefferies. 2004. Initiation and maintenance of vegetation mosaics in an Arctic salt marsh. J. Ecol. **92**: 648–660. doi:10.1111/j.0022-0477.2004.00897.x

Mcowen, C. J., and others. 2017. A global map of saltmarshes. Biodivers. Data J. **5**: e11764. doi:10.3897/BDJ.5.e11764

McSweeney, S. L., D. M. Kennedy, I. D. Rutherfurd, and J. C. Stout. 2017. Intermittently closed/open lakes and lagoons: Their global distribution and boundary conditions. Geomorphology **292**: 142–152. doi:10.1016/j.geomorph.2017.04.022

Meyer, D. L., and M. H. Posey. 2019. Salt marsh habitat size and location do matter: The influence of salt marsh size and landscape setting on nekton and estuarine finfish community structure. Estuaries Coasts **42**: 1353–1373. doi:10.1007/s12237-019-00555-9

Moles, A. T., and others. 2014. Which is a better predictor of plant traits: Temperature or precipitation? J. Veg. Sci. **25**: 1167–1180. doi:10.1111/jvs.12190

Möller, I., and T. Spencer. 2002. Wave dissipation over macrotidal saltmarshes: Effects of marsh edge typology and vegetation change. J. Coast. Res. **36**: 506–521. doi:10.2112/1551-5036-36.sp1.506

Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. Ecology **83**: 2869–2877. doi:10.1890/0012-9658(2002)083[2869:ROCWTR]2.0.CO;2

Morzaria-Luna, L., J. C. Callaway, G. Sullivan, and J. B. Zedler. 2004. Relationship between topographic heterogeneity and vegetation patterns in a Californian salt marsh. J. Veg. Sci. **15**: 523–530. doi:10.1111/j.1654-1103.2004.tb02291.x

Mozdzer, T. J., K. J. McGlathery, A. L. Mills, and J. C. Zieman. 2014. Latitudinal variation in the availability and use of dissolved organic nitrogen in Atlantic coast salt marshes. Ecology **95**: 3293–3303. doi:10.1890/13-1823.1

Mueller, P., and others. 2018. Global-change effects on early-stage decomposition processes in tidal wetlands–implications from a

global survey using standardized litter. Biogeosciences **15**: 3189–3202. doi:10.5194/bg-15-3189-2018

Nixon, S. W. 1980. Between coastal marshes and coastal waters—A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, p. 437–525. *In* P. Hamilton and K. B. Macdonald [eds.], *Estuarine and wetland processes*. Springer. doi:10.1007/978-1-4757-5177-2_20

Nolte, S., E. C. Koppenaal, P. Esselink, K. S. Dijkema, M. Schuerch, A. V. De Groot, J. P. Bakker, and S. Temmerman. 2013. Measuring sedimentation in tidal marshes: A review on methods and their applicability in biogeomorphological studies. J. Coast. Conserv. **17**: 301–325. doi:10.1007/s11852-013-0238-3

Noto, A. E., and J. B. Shurin. 2017. Mean conditions predict salt marsh plant community diversity and stability better than environmental variability. Oikos **126**: 1308–1318. doi:10.1111/oik.04056

Osland, M. J., N. Enwright, and C. L. Stagg. 2014. Freshwater availability and coastal wetland foundation species: Ecological transitions along a rainfall gradient. Ecology **95**: 2789–2802. doi:10.1890/13-1269.1

Ouyang, X., and S. Y. Lee. 2014. Carbon accumulation rates in salt marsh sediments suggest high carbon storage capacity. Biogeosci. Discuss. **10**: 19155–19188. doi:10.5194/bgd-10-19155-2013

Owers, C. J., C. D. Woodroffe, D. Mazumder, and K. Rogers. 2022. Carbon storage in coastal wetlands is related to elevation and how it changes over time. Estuar. Coast. Shelf Sci. **267**: 107775. doi:10.1016/j.ecss.2022.107775

Pedersen, J. B., and J. Bartholdy. 2007. Exposed salt marsh morphodynamics: An example from the Danish Wadden Sea. Geomorphology **90**: 115–125. doi:10.1016/j.geomorph.2007.01.012

Peer, N., G. M. Rishworth, N. A. Miranda, and R. Perissinotto. 2018. Biophysical drivers of fiddler crab species distribution at a latitudinal limit. Estuar. Coast. Shelf Sci. **208**: 131–139. doi:10.1016/j.ecss.2018.05.001

Pennings, S. C., and R. M. Callaway. 1992. Salt marsh plant zonation: The relative importance of competition and physical factors. Ecology **73**: 681–690. doi:10.2307/1940774

Pennings, S. C., and M. D. Bertness. 1999. Using latitudinal variation to examine effects of climate on coastal salt marsh pattern and process. Curr. Top. Wetland Biogeochem. **3**: 100–111.

Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: Latitudinal variation in plant–herbivore interaction strength. Ecology **86**: 2310–2319. doi:10.1890/04-1022

Peterson, G. W., and R. E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries **17**: 235–262. doi:10.2307/1352573

Poffenbarger, H. J., B. A. Needelman, and J. P. Megonigal. 2011. Salinity influence on methane emissions from tidal marshes. Wetlands **31**: 831–842. doi:10.1007/s13157-011-0197-0

Pritchard, D. W. 1952. Estuarine hydrography, p. 243–280. *In* H. E. Landsberg [ed.], *Advances in geophysics*, v. **1**. Elsevier. doi:10.1016/S0065-2687(08)60208-3

Purer, E. A. 1942. Plant ecology of the coastal salt marshlands of San Diego County, California. Ecol. Monogr. **12**: 81–111. doi:10.2307/1948423

Ragotzkie, R. A. 1959. Proceedings: Salt Marsh Conference held at the Marine Institute of the University of Georgia, Sapelo Island, Georgia.

Raupp, M. J., and R. F. Denno. 1979. The influence of patch size on a Guild of sap-feeding Insects that inhabit the salt marsh grass *Spartina patens*. Environ. Entomol. **8**: 412–417. doi:10.1093/ee/8.3.412

Ravera, O. 2000. The Lagoon of Venice: The result of both natural factors and human influence. J. Limnol. **59**: 19–30. doi:10.4081/jlimnol.2000.19

Raw, J. L., C. L. Julie, and J. B. Adams. 2019. A comparison of soil carbon pools across a mangrove-salt marsh ecotone at the southern African warm-temperate range limit. S. Afr. J. Bot. **127**: 301–307. doi:10.1016/j.sajb.2019.11.005

Raw, J. L., T. Riddin, J. Wasserman, T. W. K. Lehman, T. G. Bornman, and J. B. Adams. 2020. Salt marsh elevation and responses to future sea-level rise in the Knysna estuary, South Africa. Afr. J. Aquat. Sci. **45**: 49–64. doi:10.2989/16085914.2019.1662763

Redfield, A. C., and M. Rubin. 1962. Age of salt marsh peat in relation to recent changes in sea level. Science **48**: 1728–1735. doi:10.1126/science.136.3513.328-c

Redfield, A. C. 1972. Development of a New England salt marsh. Ecol. Monogr. **42**: 201–237. doi:10.2307/1942263

Riddin, T., and J. B. Adams. 2012. Predicting macrophyte states in a small temporarily open/closed estuary. Mar. Freshw. Res. **63**: 616–623. doi:10.1071/MF11224

Rogers, K., P. Boon, C. E. Lovelock, and N. Saintilan. 2017. Coastal halophytic vegetation, p. 544–569. *In* D. A. Keith [ed.], *Australian vegetation*, 3rd ed. Cambridge Univ. Press.

Rogers, K., and others. 2019. Wetland carbon storage controlled by millennial-scale variation in relative sea-level rise. Nature **567**: 91–95. doi:10.1038/s41586-019-0951-7

Rountree, R. A., and K. W. Able. 2007. Spatial and temporal habitat use patterns for salt marsh nekton: Implications for ecological functions. Aquat. Ecol. **41**: 25–45. doi:10.1007/s10452-006-9052-4

Rovai, A. S., and others. 2018. Global controls on carbon storage in mangrove soils. Nat. Clim. Change **8**: 534–538. doi:10.1038/s41558-018-0162-5

Runca, E., A. Bernstein, L. Postma, and G. Di Silvio. 1996. Control of macroalgae blooms in the Lagoon of Venice. Ocean Coast. Manag. **30**: 235–257. doi:10.1016/0964-5691(95)00065-8

Saintilan, N. 2009. Biogeography of Australian saltmarsh plants. Austral Ecol. **34**: 929–937. doi:10.1111/j.1442-9993.2009.02001.x

Sánchez, J. M., D. G. SanLeon, and J. Izco. 2001. Primary colonisation of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain: Vegetation structure and sediment accretion. Aquat. Bot. **69**: 15–25. doi:10.1016/S0304-3770(00)00139-X

Schrama, M., F. van der Plas, M. P. Berg, and H. Olff. 2017. Decoupled diversity dynamics in green and brown webs during primary succession in a saltmarsh. J. Anim. Ecol. **86**: 158–169. doi:10.1111/1365-2656.12602

Schutte, C. A., W. S. Moore, A. M. Wilson, and S. B. Joye. 2020. Groundwater-driven methane export reduces salt marsh blue carbon potential. Glob. Biogeochem. Cycles **34**: e2020GB006587. doi:10.1029/2020GB006587

Shakeri, L. M., K. M. Darnell, T. J. B. Carruthers, and M. Z. Darnell. 2020. Blue crab abundance and survival in a fragmenting coastal marsh system. Estuaries Coasts **43**: 1545–1555. doi:10.1007/s12237-020-00738-9

Sievers, M., and others. 2021. Global typologies of coastal wetland status to inform conservation and management. Ecol. Indic. **131**: 108141. doi:10.1016/j.ecolind.2021.108141

Silvestri, S., A. Defina, and M. Marani. 2005. Tidal regime, salinity and salt marsh plant zonation. Estuar. Coast. Shelf Sci. **62**: 119–130. doi:10.1016/j.ecss.2004.08.010

Simpson, L. T., T. Z. Osborne, L. J. Duckett, and I. C. Feller. 2017. Carbon storages along a climate induced coastal wetland gradient. Wetlands **37**: 1023–1035. doi:10.1007/s13157-017-0937-x

Smee, D. L., J. A. Sanchez, M. Diskin, and C. Trettin. 2017. Mangrove expansion into salt marshes alters associated faunal communities. Estuar. Coast. Shelf Sci. **187**: 306–313. doi:10.1016/j.ecss.2017.02.005

Smith, D. L., C. J. Bird, K. D. Lynch, and J. McLachlan. 1980. Angiosperm productivity in two saltmarshes of Minas Basin. Proc. Nova Scotian Inst. Sci. **30**: 109–118.

Stagg, C. L., D. R. Schoolmaster, S. C. Piazza, G. Snedden, G. D. Steyer, C. J. Fischenich, and R. W. McComas. 2017. A landscape-scale assessment of above-and belowground primary production in coastal wetlands: Implications for climate change-induced community shifts. Estuaries Coasts **40**: 856–879. doi:10.1007/s12237-016-0177-y

Taillardat, P., B. S. Thompson, M. Garneau, K. Trottier, and D. A. Friess. 2020. Climate change mitigation potential of wetlands and the cost-effectiveness of their restoration. Interface Focus **10**: 20190129. doi:10.1098/rsfs.2019.0129

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology **43**: 614–624. doi:10.2307/1933451

Temmerman, S., T. J. Bouma, G. Govers, Z. B. Wang, M. B. D. Vries, and P. M. J. Herman. 2005. Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh. J. Geophys. Res.: Earth Surface **110**: F04019. doi:10.1029/2005JF000301

Temmerman, S., P. Meire, T. J. Bouma, P. M. Herman, T. Ysebaert, and H. J. De Vriend. 2013. Ecosystem-based coastal defence in the face of global change. Nature **504**: 79–83. doi:10.1038/nature12859

Thom, B. G. 1984. Transgressive and regressive stratigraphies of coastal sand barriers in Southeast Australia. Mar. Geol. **56**: 137–158. doi:10.1016/0025-3227(84)90010-0

Thorne, K. M., K. J. Buffington, S. F. Jones, and J. L. Largier. 2021. Wetlands in intermittently closed estuaries can build elevations to keep pace with sea-level rise. Estuar. Coast. Shelf Sci. **257**: 107386. doi:10.1016/j.ecss.2021.107386

Turner, R. E., E. M. Swenson, and C. S. Milan. 2002. Organic and inorganic contributions to vertical accretion in salt marsh sediments, p. 583–595. *In* M. P. Weinstein and D. A. Kreeger [eds.], *Concepts and controversies in tidal marsh ecology*. Springer. doi:10.1007/0-306-47534-0_27

Twilley, R. R., V. H. Rivera-Monroy, R. Chen, and L. Botero. 1999. Adapting an ecological mangrove model to simulate trajectories in restoration ecology. Mar. Pollut. Bull. **37**: 404–419. doi:10.1016/S0025-326X(99)00137-X

Uhran, B., L. Windham-Myers, N. Bliss, A. M. Nahlik, E. T. Sundquist, and C. L. Stagg. 2021. Improved wetland soil organic carbon stocks of the conterminous US through data harmonization. Front. Soil Sci. **1**: 706701. doi:10.3389/fsoil.2021.706701

Van de Koppel, J., T. J. Bouma, and P. M. J. Herman. 2012. The influence of local- and landscape-scale processes on spatial self-organization in estuarine ecosystems. J. Exp. Biol. **215**: 962–967. doi:10.1242/jeb.060467

van Niekerk, L., and others. 2020. An estuary ecosystem classification that encompasses biogeography and a high diversity of types in support of protection and management. Afr. J. Aquat. Sci. **45**: 2199–2216. doi:10.2989/16085914.2019.1685934

Vasey, M. C., V. T. Parker, J. C. Callaway, E. R. Herbert, and L. M. Schile. 2012. Tidal wetland vegetation in the San Francisco Bay-Delta estuary. San Franc. Estuary Watershed Sci. **10**: 1–16. doi:10.15447/sfews.2012v10iss2art2

Veldkornet, D. A., J. B. Adams, and A. J. Potts. 2015. Where do you draw the line? Determining the transition thresholds between estuarine salt marshes and terrestrial vegetation. S. Afr. J. Bot. **101**: 153–159. doi:10.1016/j.sajb.2015.05.003

Veldkornet, D. A., A. J. Potts, and J. B. Adams. 2016. The distribution of salt marsh macrophyte species in relation to physicochemical variables. S. Afr. J. Bot. **107**: 84–90. doi:10.1016/j.sajb.2016.08.008

Waltham, N. J., and others. 2021. Tidal marsh restoration optimism in a changing climate and urbanizing seascape. Estuaries Coasts **44**: 1–10. doi:10.1007/s12237-020-00875-1

Wang, X., F. G. Blanchet, and N. Koper. 2014. Measuring habitat fragmentation: An evaluation of landscape pattern

metrics. Methods Ecol. Evol. **5**: 634–646. doi:10.1111/2041-210X.12198

Ward, M. A., and others. 2021. Blue carbon stocks and exchanges along the California coast. Biogeosciences **18**: 4717–4732. doi:10.5194/bg-18-4717-2021

Wasson, K., and others. 2019. Pattern and scale: Evaluating generalities in crab distributions and marsh dynamics from small plots to a national scale. Ecology **100**: e02813. doi:10.1002/ecy.2813

Watson, E. B., and R. Byrne. 2013. Late Holocene marsh expansion in southern San Francisco Bay, California. Estuaries Coasts **36**: 643–653. doi:10.1007/s12237-013-9598-z

Wegscheidl, C., M. Sheaves, I. McLeod, and J. Fries. 2015. *Queensland's saltmarsh habitats: Values, threats and opportunities to restore ecosystem services*. Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER) publication, James Cook Univ.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Conserv. Biol. **6**: 237–256.

Woodroffe, C. 1992. Mangrove sediments and geomorphology. *In* A. I. Robertson and D. M. Alongi [eds.], *Tropical Mangrove Ecosystems*. American Geophysical Union. doi:10.1029/CE041p0007

Yan, J., Z. Zhu, J. Zhou, X. Chu, H. Sui, B. Cui, and T. van der Heide. 2021. Saltmarsh resilience controlled by patch size and plant density of habitat-forming species that trap shells. Sci. Total Environ. **778**: 146119. doi:10.1016/j.scitotenv.2021.146119

Yando, E. S., M. J. Osland, J. M. Willis, R. H. Day, K. W. Krauss, and M. W. Hester. 2016. Salt marsh-mangrove ecotones: Using structural gradients to investigate the effects of woody plant encroachment on plant–soil interactions and ecosystem carbon pools. J. Ecol. **104**: 1020–1031. doi:10.1111/1365-2745.12571

Ziegler, S. L., K. W. Able, and F. J. Fodrie. 2019. Dietary shifts across biogeographic scales alter spatial subsidy dynamics. Ecosphere **10**: e02980. doi:10.1002/ecs2.2980

Ziegler, S. L., and others. 2021a. Geographic variation in salt marsh structure and function for nekton: A guide to finding commonality across multiple scales. Estuaries Coasts **44**: 1497–1507. doi:10.1007/s12237-020-00894-y

Ziegler, S. L., L. R. Clance, A. R. McMains, M. D. Miller, and F. J. Fodrie. 2021b. Influence of marsh island size on nekton communities: Intermediate optima rather than single-large-or-several-small (SLOSS). Mar. Ecol. Prog. Ser. **672**: 45–56. doi:10.3354/meps13780

Ziegler, S. L., M. D. Miller, C. S. Smith, and F. J. Fodrie. 2021c. Abiotic cycles mediate the strength of cross-boundary consumption within coastal food webs. Estuaries Coasts **44**: 1147–1156. doi:10.1007/s12237-020-00829-7