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SPECIAL ISSUE: CONCEPTS AND CONTROVERSIES IN TIDAL MARSH ECOLOGY REVISITED



Human Actions Alter Tidal Marsh Seascapes and the Provision of Ecosystem Services

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Abstract

Tidal marshes are a key component of coastal seascape mosaics that support a suite of socially and economically valuable ecosystem services, including recreational opportunities (e.g., fishing, birdwatching), habitat for fisheries species, improved water quality, and shoreline protection. The capacity for tidal marshes to support these services is, however, threatened by increasingly widespread human impacts that reduce the extent and condition of tidal marshes across multiple spatial scales and that vary substantially through time. Climate change causes species redistribution at continental scales, changes in weather patterns (e.g., rainfall), and a worsening of the effect of coastal squeeze through sea level rise. Simultaneously, the effects of urbanization such as habitat loss, eutrophication, fishing, and the spread of invasive species interact with each other, and with climate change, to fundamentally change the structure and functioning of tidal marshes and their food webs. These changes affect tidal marshes at local scales through changes in plant community composition, complexity, and condition and at regional scales through changes in habitat extent, configuration, and connectivity. However, research into the full effects of these multi-scaled, interactive stressors on ecosystem service provision in tidal marshes is in its infancy and is somewhat geographically restricted. This hinders our capacity to quickly and effectively curb loss and degradation of both tidal marshes and the services they deliver with targeted management actions. We highlight ten priority research questions seeking to quantify the consequences and scales of human impacts on tidal marshes that should be answered to improve management and restoration plans.

Keywords Climate change · Ecological functions · Fisheries · Nutrients · Shoreline protection · Urbanization

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Introduction

Tidal marshes (salt marshes) are intertidal vegetated habitats dominated by grasses along coastal and estuarine shorelines that provide a suite of important benefits for people and coastal seascapes. For example, tidal marshes provide habitat for juvenile and adult life stages of a variety of fish and invertebrate species (Whitfield 2017), sequester carbon and nutrients (Huxham et al. 2018), protect coastal infrastructure from storms and tides (Costanza et al. 2008), and provide recreation opportunities for people (e.g., birdwatching, fishing) (Zedler and Leach 1998). However, anthropogenic impacts are altering the extent, composition, condition, and complexity of tidal marsh seascapes (i.e., a spatially heterogeneous area of estuarine environment dominated by the presence of extensive tidal marshes) (Bostrom et al. 2011), and this may jeopardize their capacity to provide key ecosystem services and have dire consequences for the economy and social values of coastal communities (zu Ermgassen et al. this issue).

Human impacts affect ecosystems and interact with each other at multiple spatial scales (Gedan and Silliman 2009). For example, anthropogenic impacts at small spatial scales (i.e., meters to 10s of meters) can change plant assemblage composition (e.g., Saintilan et al. 2014) and/or density (e.g., Charles and Dukes 2009), which may affect the complexity, accessibility, and habitat value of tidal marsh patches (Gedan et al. 2009). Conversely, changes at broader spatial scales (i.e., 100s of meters to kilometers) can reduce the extent and alter the shape and connectivity of tidal marsh patches (e.g., Watson et al. 2017), which may disrupt food webs and compromise beneficial life history adaptations (e.g., Meynecke et al. 2008). Changes at either scale modify coastal physical processes and landforms (e.g., geomorphology, hydrodynamics, sediment transport), thereby further degrading both the delivery of key services and the potential for marsh recovery. Identifying the drivers of change in extent, structure, and functioning of tidal marsh seascapes, the scale over which these occur and the mechanisms through which such scale-specific changes alter the ecosystem services that people desire from tidal marshes are important foci for research and natural resource management.

In this article, we summarize the key anthropogenic impacts that affect the extent, structure, and condition of tidal marshes, show how these impacts operate at different spatial scales, and address their ultimate effects on key ecological functions (i.e., processes related to the movement or storage of energy or material in ecosystems; Bellwood et al. 2018) and ecosystem services of tidal marsh seascapes (Fig. 1). While the link between seascape configuration and ecosystem condition and service provision has been long recognized, robust quantitative approaches are still needed to adequately characterize drivers of seascape change and their effects on tidal marsh functions and services (for

example, see Meyer and Posey 2013). We highlight key knowledge gaps and pose ten questions that point to critical research that can substantially improve our capacity to manage tidal marsh seascapes.

Drivers of Structural Change in Tidal Marsh Seascapes

Climate Change

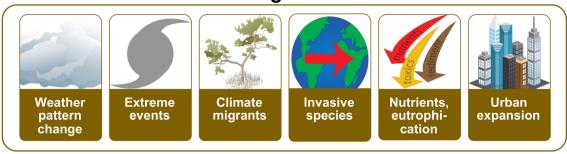
Climate change represents an existential threat to the extent and condition of tidal marshes globally (Colombano et al. this issue). For example, increased sea levels lead to changes in animal assemblages and their functional interactions, changes in tidal inundation, changes in zonation patterns of tidal marsh plants on seashores, coastal squeeze (i.e., intertidal habitat loss due to high water being fixed by coastal defenses), and increased risk of coastal erosion (Crosby et al. 2016; Leo et al. 2019) (Fig. 2). Climate change can modify evapotranspiration rates in coastal ecosystems, resulting in increased salinity levels and intrusion into estuaries, with implications for connected habitats in coastal seascapes (like seagrasses, reefs, and rivers). Weather patterns can shift on both local and continental scales causing changes in freshwater runoff regimes, coastal water chemistry (e.g., salinity, dissolved oxygen, and pH), plant and animal dominance patterns, and key ecological functions and cycles (Gabler et al. 2017). Despite the growing awareness of cumulative effects of multiple interacting stressors, studies of regional and continental climate variability (e.g., shifts in the timing, magnitude and duration of weather patterns at regional or continental scales) on tidal marshes are scant and have typically focused solely on sea level rise (Osland et al. 2016) (Table 1, question 1).

Many species are beginning to shift in both abundance and distribution in tidal marshes due to the effects of climate change. Species ranges shift as environmental conditions (principally temperature) change in order to remain within preferred environmental conditions. One of the best-known examples of temperature-induced geographical migration is the encroachment of mangrove trees into tidal marshes, which is occurring across multiple continents (Saintilan et al. 2014). As mangroves expand into tidal marshes, and in many cases fully replace marsh plants, changes in the functions and services of the ecosystem ensue (Kelleway et al. 2017). However, our understanding of the novel species interactions and ecosystem services that occur as mangroves replace tidal marshes is limited (Hobbs et al. 2009), meaning that our capacity to manage novel ecosystems is also likely limited (Table 1, question 2).

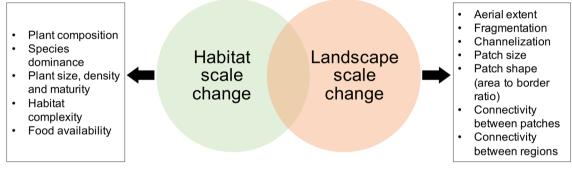
Climate change—driven modifications to tidal marshes will affect the condition of tidal marsh seascapes at both local and regional scales through habitat loss and other changes, but a



a Drivers of structural change



b Structural change at multiple spatial scales



c Changes to ecological functions and ecosystem services

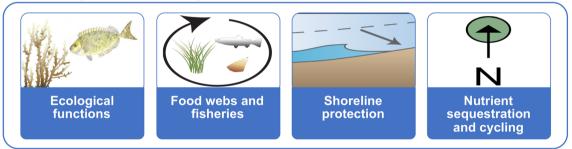


Fig. 1 Anthropogenic impacts that affect the coastal zone (a) drive significant change in the composition of tidal marshes at multiple spatial scales across seascapes (b). This can change the rate and

distribution of key ecological functions and result in subsequent reductions in the supply of a suite of socially and economically valuable ecosystem services (c)

better understanding of such effects is needed to optimize the management of these ecosystems in a changing world (Brown et al. 2013). For example, ecosystem-level effects of climate change and weather extremes can vary in periodicity (e.g., daily, seasonal, annual, or decadal). Accounting for both spatial and temporal variation in climate change effects and their complex interactions is a challenging but fundamental and often overlooked aspect of forecasting the future of tidal marsh condition and the delivery of ecosystem services (Colombano et al. this issue).

Invasive Species

Many tidal marshes have been invaded by exotic species due to their proximity to hubs of anthropogenic activities (Gedan et al. 2009). Invasive species, particularly those that act as ecosystem engineers, can substantially alter tidal marshes.

Examples of invasive ecosystem engineers in tidal marshes include both competitors (e.g., the common reed *Phragmites* australis) and consumers (e.g., the European green crab Carcinus maenas) of marsh grasses. Competitor plant invasions such as common reed in eastern US coastal systems have led to changes in marsh elevation and the physical structure of inundated marsh surface and resulting effects on the dominant fish (Hagan et al. 2007; Weinstein et al. 2010), reduced nutrient and carbon cycling and sequestration, and modifications to the food web (Findlay et al. 2003). Similarly, faunal invasions by both grazers (e.g., nutria *Myocastor covpus* in the SE USA) and predators (e.g., European green crab across North American coastal systems) have had both direct and indirect top-down effects and competitive impacts on tidal marsh biota, including fisheries species (Jamieson et al. 1998), and have led to marsh sediment erosion (Aman and Grimes 2016). These local impacts on tidal marshes can ultimately result in



Table 1 Priority research questions to better link human impacts and their management to the capacity of tidal marshes to support ecosystem services

Field of research	Priority research question
Anthropogenic impacts	
Climate change impacts on sea levels, temperature and precipitation	To what degree will regional and continental scale climate change and variability (e.g., temperature and precipitation change) affect runoff, coastal water quality, ecological dominance, and the distribution of key ecological functions in tidal marshes?
Climate change impacts on species distribution	At what speed will climate migrants invade and then impinge upon the capacity for tidal marshes to support key ecosystem services, and should we manage to maintain what we have now or adapt to manage novel ecosystems?
3. Invasive species	How do the local-scale changes caused by invasive species com- pound to seascape-scale changes in the connectivity and com- plexity of tidal marshes?
4. Nutrients and eutrophication	What controls the nature and extent of nutrient loading impacts on the structure and function of tidal marshes, and what are the conditions at which such effects become overwhelmingly negative and lead to marsh collapse?
5. Urbanization	To what degree, and in which direction, are different ecosystem components and functions changed by urbanization and associated impacts (like trampling, fishing, boat wash) around tidal marshes?
Ecological functions and ecosystem services	3
6. Ecological functions	How do changes in tidal marsh seascape composition (at both local and regional scales) affect key ecological functions, and how do these changes link to ecosystem service provision?
7. Blue carbon storage	How will expected changes to tidal marshes and adjacent habitats affect blue carbon storage across tidal marsh seascapes as a whole?
8. Food webs and fisheries	How do the effects of climate change interact with local stressors to modify food web structure and affect the fisheries value of tidal marsh seascapes?
9. Shoreline protection	What design for restoration, living shoreline, and/or wetland re- construction methods (e.g., thin layer sedimentation) optimize shoreline protection, habitat value, and ecosystem functions and services in unison?
10. Nutrient sequestration and cycling	How do interacting anthropogenic impacts ultimately affect the capacity for nutrient sequestration in tidal marshes?

seascape-scale effects on habitat structure, nutrient cycling, trophic dynamics, and coastal geomorphology, but the characterization and understanding of such effects need further study (Table 1, question 3).

Nutrients and Eutrophication

As coastal watersheds are developed by humans, the amount of nutrients entering tidal marshes increases. Increased nutrient loading in tidal marshes may lead to increased productivity, shifts in plant community composition, and changes in plant biomass allocation between the above- and belowground compartments. Additionally, higher nutrient content in plant tissues can lead to enhanced palatability for consumers, changes in producer-consumer relationships and food web structure, and altered carbon sequestration and standing stocks (Gedan et al. 2009; Sparks and Cebrian 2015). These may

eventually result in profound changes to ecosystem service provisioning (Valiela 2006). Impacts of low to moderate nutrient loading range from positive to negative (i.e., increases or decreases in condition or functions). However, intense nutrient loading prolonged over several years can lead to tidal marsh collapse (Deegan et al. 2012) as a result of reduced below-ground biomass of tidal marsh plants and increased allocation into stems and leaves as nutrient supply increases. Higher nutrient supply can increase the decomposition of dead plant tissues and organic matter in the marsh soil. Deegan et al. (2012) showed in a major experiment in Massachusetts that, together, these processes can reduce structural integrity of the marsh soil, with consequent erosion and habitat fragmentation (Fig. 2; also see Deegan et al. 2012). The critical research question is to more thoroughly understand what controls the trajectories and thresholds of tidal marsh degradation under eutrophication (Table 1, question 4).





Fig. 2 Anthropogenic impacts modify the structure, composition, and condition of tidal marshes across coastal seascapes. Invasive tidal marsh plants like common reed *Phragmites australis* (a) can replace native species and reduce habitat value. Similarly, with climate change, species will shift their ranges towards the poles, and this will cause structural changes to tidal marsh seascapes (e.g., intrusion of mangroves in temperate tidal marshes), and unpredictable novel species assemblages. Climate change also causes sea level rise which will result in greater tidal

inundation of tidal marshes (b). Urbanization causes fragmentation of tidal marsh seascapes, and the effects of coastal squeeze (c), especially as sea levels rise, and can significantly narrow the distribution of marshes and reduce ecological functioning. Finally, high nutrient runoff from urban and agricultural land can cause eutrophication, causing plant community change, erosion, and slumping (d) (Plum Island Estuary, Massachusetts). Images by T. Sturm, P. Bloodgood (CC BY 2.0), J. Buck (CC BY-SA 2.0) and H. Sullivan

Urbanization and Expanding Human Populations

Given their position in the intertidal swath of coastal shores, tidal marshes are particularly threatened by coastal development (Gedan et al. 2009; Halpern et al. 2019; Waltham et al. this issue). Expanding human infrastructure can fragment tidal marshes and reduce their extent, resulting in poorly connected tidal marsh seascapes, altered plant community composition, and worsened ecological condition (Bishop et al. 2017). Hardening of coastal shores can compound the effects of coastal squeeze by hindering tidal marsh expansion to higher elevations under sea level rise (Crosby et al. 2016; Leo et al. 2019). Tidal marshes near urban centers are also more likely to be exposed to heightened fishing and/or trampling, erosion from boat wakes, and sediment and pollutant runoff (Gedan et al. 2009). Urban centers also require extensive agricultural development to ensure food supply, often resulting in channelization of tidal marsh habitat (Martinez-Lopez et al. 2019) or direct replacement by other land used like grazing or cropping lands. However, the impacts of shoreline hardening are not entirely negative, as some subtidal urban structures can supplement ecological functions (e.g., Olds et al. 2018) (Table 1, question 5). Urbanization represents a conspicuous and immediate threat to tidal marshes globally, and a more thorough understanding of how urbanization interacts with other stressors is required for more effective management (Gedan et al. 2009).

Resulting Structural Change at Multiple Spatial Scales

Habitat Scale (Meters to 10s of Meters; Habitat Condition, Composition, and Complexity)

The interactive effects of anthropogenic impacts drive large and complex changes in individual patches of tidal marsh within the broader seascape. For example, rising seas alter the flooding dynamics of individual patches, which can cause loss and change the distribution and density of habitat forming marsh plants (Ziegler et al. 2019). In addition, nutrient enrichment changes above- and belowground biomass and marsh soil structural strength can interact with flooding-driven processes to further alter the condition and health of tidal marsh patches (Krause et al. 2019) and can compound the effects of climate change (Dangremond et al. 2019). Urbanization truncates the landward marsh profile, causes the loss of high elevation marsh and, importantly, precludes upland marsh migration (i.e., coastal squeeze). The result will be progressive conversion of high to low elevation marsh habitat with sea level rise and complete marsh loss if sediment supply is not adequate (Colombano et al. this issue). In turn, the structure, density, and condition of vegetation is a key driver of habitat selection for many species (Kneib 1997), so changes in these vegetation features may have substantial impacts on the habitat quality of individual marsh patches within the seascape (Smee et al. 2017). Although the regularly flooded low marsh



edge appears to be particularly important habitat for many fishery species (Minello et al. 2008), the implications of high elevation marsh loss for the dynamics and function of the rest of the marsh are unclear. Crucially, changes in structure, composition, density, and condition at the patch scale (meters to tens of meters) can propagate up to the seascape scale through cascading impacts on extent, fragmentation, and connectivity. These changes at smaller spatial scales can, in turn, alter the ecosystem services provided by tidal marsh seascapes and degrade broader-scale processes that support ongoing marsh presence and condition (like sediment transport, hydrology, and other coastal geomorphological processes) (Ziegler et al. this issue).

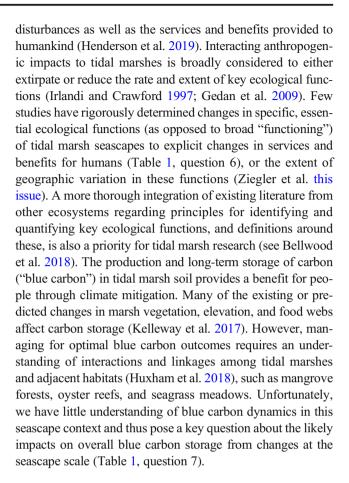
Seascape Scale (100s of Meters to Kilometers; Extent, Fragmentation, Connectivity)

Human impacts modify the condition of tidal marsh seascapes at scales of 100s of meters to kilometers in diverse ways. Perhaps most importantly, human impacts reduce the aerial extent of tidal marshes within coastal seascapes through replacement with unvegetated flats or hardened shorelines of lower habitat value (Bishop et al. 2017). The fragmentation of tidal marshes causes reductions in patch sizes, increasing prevalence of edge effects, including higher exposure to coastal erosion from wind, waves and boat wakes, and poorer connectivity among tidal marsh patches. Poorer connectivity reduces biodiversity by reducing gene flow, fragments and changes the demographics of animal populations that perform key ecological functions across seascapes, and reduces the delivery of nutrient or energy from tidal marshes to surrounding ecosystems which rely upon these subsidies (Irlandi and Crawford 1997; Kneib 1997; Jinks et al. 2020). Seascape scale processes that underpin the resilience and persistence of tidal marshes, like sediment supply and hydrodynamics, are substantially modified by climate change, urbanization, and channelization at scales of 10s to 100s of kilometers (Vincent et al. 2013; Osland et al. 2016). More thoroughly understanding the spatial scale of influence of human impacts and the consequences of tidal marshes becoming increasingly fragmented and poorly connected is an important need to enhance our capacity to manage and restore marsh seascapes (Table 1, question 5) (Gilby et al. 2018).

Changes to Ecological Functions and Ecosystem Services

Rates and Distributions of Key Ecological Functions

The rates and distribution of key ecological functions like predation, herbivory, and detritivory are pivotal in determining the resilience of ecosystems to natural and anthropogenic



Food webs and Fisheries

Maintaining well-connected, complex food webs with a diversity of ecological niches linked by key ecological functions performed by multiple species (i.e., functional redundancy) is crucial for the generation of ecosystem services (Henderson et al. 2019). For example, well-connected, complex food webs in tidal marshes provide refuge and food for coastal fisheries across seascapes (Sheaves et al. 2015; Whitfield 2017) and support threatened species (Gilby et al. 2017). Autochthonous tidal marsh production (localized production like organic matter or larvae) is an important subsidy for many ecosystems across coastal seascapes (Kneib 1997; Jinks et al. 2020). In addition, food webs of other coastal habitats are linked to tidal marshes by the movement of animals among patches of diverse systems within broader seascapes (Nagelkerken et al. 2015). More diverse and abundant coastal animal communities supported by healthy and expansive marshes also have greater capacity to resist, and recover from, disturbances due to higher redundancy in key ecological functions (Henderson et al. 2019). The degradation of tidal marshes reduces the trophic roles of tidal marsh seascapes (Whitfield 2017; Gilby et al. 2018), including support of fisheries, adjacent systems, and autochthonous and allochthonous food webs. The extent and mechanisms through which such



reduction propagates from patch to seascape scales, including interactions between local and global factors, remain unclear (Table 1, question 8).

Shoreline Protection

The shoreline protection provided by tidal marshes has significant economic value (Barbier et al. 2011), particularly in areas at risk severe storms (Rao et al. 2015). This key ecosystem service will become even more valuable as the frequency and intensity of severe storms increases (Barbier 2015). The likelihood of tidal marshes continuing to provide this service is compromised by losses at the patch level due to climate change (Arkema et al. 2013), eutrophication (Deegan et al. 2012), urbanization (Waltham and Sheaves 2015), and replacement by other species such as mangroves (Kelleway et al. 2017). While hardened shorelines provide similar benefits to tidal marshes in terms of wave and erosion protection, they do not provide the same habitat and fishery benefits. Seeking effective designs for shoreline protection that embrace environmentally friendly practices and enhance habitat creation (Dafforn et al. 2015), including living shorelines (Bilkovic et al. 2016), under current and future conditions is a growing and important area of research (Table 1, question 9).

Nutrient Sequestration and Cycling

Tidal marshes are hotspots of nutrient sequestration and removal and so can buffer anthropogenic nutrient inputs to coastal systems (Gedan et al. 2009; Piehler and Smyth 2011). However, anthropogenic impacts like invasive species introductions, urbanization, shoreline erosion, climate change, and eutrophication have cascading effects on the ability of tidal marshes to sequester nutrients (Gedan et al. 2009). Principally, these impacts cause the conversion of vegetated to unvegetated habitat and consequent reduction in the capacity for nutrient processing (Piehler and Smyth 2011; Deegan et al. 2012). In addition to loss of tidal marsh habitat, changes such as saltwater intrusion, warmer temperatures, invasive species, and eutrophication can alter vegetation assemblages with implications for rates of nutrient cycling (Yang et al. 2015). Mangrove encroachment and invasion of the common reed in tidal marshes, for example, may lead to higher rates of nutrient uptake and larger long-term sinks of nutrients (Findlay et al. 2003; Kelleway et al. 2017). Conversely, the replacement of diverse plant communities by monocultures can decrease nitrogen retention, although the scale of this response is often species-specific (Yang et al. 2015). Loss of habitat and shifts in vegetation can have counteracting effects on nutrient cycling; therefore, future research should elucidate how interacting drivers of change will ultimately affect nutrient sequestration in tidal marshes (Table 1, question 10).

Discussion

Anthropogenic impacts are diversifying and expanding in geographic scope globally as the human population increases and expands, and these impacts are often focused in the coastal zone (Halpern et al. 2019). This results in the breakdown of key ecological functions and the loss of valuable ecosystem services (Barbier et al. 2011). We show that there are clear links between key anthropogenic impacts, the condition and extent of tidal marsh seascapes at multiple spatial scales (from local to regional scales), and their capacity to deliver key ecosystem services. Having a capacity to accurately predict how combinations of impacts will affect future ecosystem service delivery is therefore paramount in optimizing management interventions (Brown et al. 2013).

While many of the impacts covered in this article are well understood in isolation, overcoming the dearth of information about their interacting effects is a priority for management and restoration plans (Brown et al. 2013; Gilby et al. 2018). We identified ten priority research questions that should be addressed to more thoroughly disentangle these complex effects (Table 1). Each question addresses a research gap regarding the trajectory or interacting nature of human impacts and their consequences for tidal marsh seascapes, the spatial scales over which these impacts modify tidal marshes and their ecosystem services and/or the optimal design of conservation, restoration, or broader management actions to overcome them. There are, to the best of our knowledge, no major obstructions to answering these priority questions; the need is for more investigative focus on them. Perhaps most importantly, however, the authors noted that the majority of studies conducted in this space have occurred in North America, so expanding research to marshes outside of this region that may have different pressures, environmental conditions (e.g., tidal extent), and species composition (especially of habitat forming marsh plants) is a priority (Ziegler et al. this issue). Due to the diversity of tidal marsh composition and positions on shorelines globally, there are challenges in generalizing results for particular impacts across different continents (Ziegler et al. this issue). The intensity of human impacts to ecosystems can often vary substantially over temporal scales. For example, anthropogenic climate change interacts with natural variability in weather and climate resulting in weather and climate extremes changing over decadal scales (e.g., El Nino Southern Oscillation), and the effects of runoff from modified watersheds may fluctuate depending on rainfall. Expanding the geographic and temporal scope of studies into the consequences of human impacts on tidal marsh ecosystem services and the scales over which these occur is a global priority for tidal marsh ecologists.

More thoroughly understanding the intricacies of human impacts on tidal marshes and their consequence for ecosystem services will maximize our capacity to optimize management



plans and enable us to more thoroughly anticipate the outcomes of different management interventions. For example, we can use the results of such quantitative studies to optimize ecological restoration plans to reduce fragmentation at regional scales (Waltham et al. this issue), to maximize the effectiveness of marine reserves in coastal seascapes (Olds et al. 2016), to design environmentally friendly structures for coastal ecosystems (Bilkovic et al. 2016), and to predict the results of management interventions, thereby increasing our capacity to more thoroughly incentivize coastal management and restoration actions (Borgström et al. 2016). Such seascape-wide management plans can help reduce and mitigate the consequences of coastal development and other exogenous threats (Zedler and Leach 1998). Examples of successful application exist, but there is a pressing need to upscale efforts to scales of kilometers to 10s of kilometers to provide more meaningful habitat enhancements and conservation actions across estuarine seascapes to support ecosystem services (Gilby et al. 2018). The time is now for tidal marsh ecologists to fill these crucial knowledge gaps relating to humans impacts and the scale of their consequences for ecosystems services to maximize our capacity to salvage and enhance these valuable coastal ecosystems.

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