

# *Annual Review of Environment and Resources*

## Coastal Wetlands in the Anthropocene

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## Keywords

climate change, wetland composition, wetland distribution, nitrogen, blue carbon, coastal retreat, wetland values

## Abstract

We review the functioning and sustainability of coastal marshes and mangroves. Urbanized humans have a 7,000-year-old enduring relationship to coastal wetlands. Wetlands include marshes, salt flats, and saline and freshwater forests. Coastal wetlands occur in all climate zones but are most abundant in deltas. Mangroves are tropical, whereas marshes occur from tropical to boreal areas. Quantification of coastal wetland areas has advanced in recent years but is still insufficiently accurate. Climate change and sea-level rise are predicted to lead to significant wetland losses and other impacts on coastal wetlands and the humans associated with them. Landward migration and coastal retreat are not expected to significantly reduce coastal wetland losses. Nitrogen watershed inputs are unlikely to alter coastal marsh stability because watershed loadings are mostly significantly lower than those in fertilization studies that show decreased belowground biomass and increased decomposition of soil organic matter. Blue carbon is not expected to significantly reduce climate impacts. The high values of ecosystem goods and services of wetlands are expected to be reduced by area losses. Humans have had strong impacts on coastal wetlands in the Holocene, and these impacts are expected to increase in the Anthropocene.

## Contents

INTRODUCTION .....	107
HUMANS AND COASTS .....	107
COMPOSITION OF COASTAL WETLANDS .....	109
GLOBAL DISTRIBUTION AND AREA OF DELTAS, SALT MARSHES, AND MANGROVES .....	110
COASTAL RETREAT AND TRANSFORMATION DUE TO RISING SEAS .....	113
CLIMATE CHANGE .....	114
THE UNIQUE BIOGEOCHEMISTRY OF COASTAL WETLANDS .....	115
THE PHYSIOLOGICAL BASIS FOR NITROGEN REGULATION OF PRIMARY PRODUCTION AND THE CONSEQUENCES OF EXCESSIVE NITROGEN LOADING IN SALT MARSHES .....	116
Regulation of Nitrogen Uptake on a Physiological Level ( $O_2$ , $S^{-2}$ , $Na^{+1}$ ) .....	116
Consequences of Nitrogen Source (e.g., $NH_4$ and $NO_3$ ) .....	118
The Functional Equilibrium Model .....	118
Nutrient Toxicity .....	119
Significance .....	120
COASTAL BLUE CARBON .....	120
Problems with Current Blue Carbon Budgets .....	121
Coastal Blue Carbon Systems' Potential for Carbon Dioxide Removal .....	122
THE VALUE OF COASTAL WETLANDS .....	122

## INTRODUCTION

Coastal emergent marsh and mangrove wetlands occupy large areas of the upper intertidal zone in many parts of the world (1–4). Marshes occur mainly along temperate and boreal coasts but also in tropical intertidal zones. Grasses generally dominate marshes, but shrubby vegetation sometimes replaces grasses, and succulent plants and unvegetated salt flats can dominate coastal wetlands along arid hypersaline coasts. Freshwater wetland species, both marsh and tree species, occur in many coastal intertidal communities, especially in broad wetland areas with high freshwater input, such as deltas. Mangrove forests occur in the tropics and are generally composed of trees but with many other vegetation types drawn from a diverse group of tropical plant families (4). Marsh and mangrove communities are ecologically analogous because of physical location, ecological processes, and trophic dynamics.

Many studies of coastal wetlands show they are among the most productive plant communities globally and are often a large proportion of the total area of coastal systems. Coastal wetlands have high values of ecosystem goods and services that continue to benefit humans after millennia of human use. This is not a comprehensive review, as there are a number of broad reviews covering coastal wetlands (1, 2, 5–7). The goal of those reviews was to present a synthesis of existing information on coastal wetlands, generally focusing on saline wetlands.

In this review, we address topical issues related to coastal wetlands, focusing on issues for which there is a range of opinion. We discuss coastal wetlands and human culture as well as their structure, composition, latitudinal and longitudinal distribution, productivity, functions, assessment, and human impacts on coastal wetlands. Throughout the Holocene, human culture has interacted strongly with coastal regions. Culture includes the origins of agriculture and urban civilization, the great concentration in the twentieth century of human population (50% of humans live within 200 km of an oceanic coast), and major human impacts in the coastal zone. Coastal wetlands are often thought of as synonymous with saline wetlands. Here, we also discuss the importance of coastal freshwater wetlands and their importance for coastal areas. We present an up-to-date review of the distribution of coastal wetlands both longitudinally and latitudinally and show that most coastal wetlands are found in the tropics and to a lesser extent in the Arctic. It has been postulated that migration of saline marshes onto uplands can offset marsh loss. We show that most landward migration of salt marshes comes at the expense of tidal freshwater wetlands and to a lesser extent valuable terrestrial habitats. Both natural systems and human settlements in coastal areas are at the forefront of both direct and indirect climate change impacts. We discuss the nature of these impacts and potential ways to mitigate them. With its range of saline to fresh habitats, coastal wetlands have a unique biogeochemistry. We address the role of nitrogen in the functioning of coastal wetland ecosystems and show that nitrogen loading to coastal marshes will not have a significant impact. Blue carbon, the storage of organic carbon in coastal wetland plants, has been cited as an important mechanism for mitigating climate change. We show that this is likely not the case. Through the provisioning of ecosystem goods and services, coastal wetlands provide humans with a range of benefits worth trillions of dollars annually. We document and quantify many of these services. Quantification in this area is rapidly improving. For example, the value of wetlands for storm protection has been estimated at US\$500 billion year<sup>-1</sup> globally. Human activity is threatening the sustainability of these services.

## HUMANS AND COASTS

Throughout the Holocene, humans lived in and had a strong interaction with coastal areas, especially wetlands, where they exploited wetland and estuarine resources. Gunn et al. (8) concluded that interactions between the Holocene earth system history and humans were characterized by

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**Mangrove wetlands:** coastal wetlands that are dominated by cold-sensitive trees that occur in tropical, subtropical, and warm temperate areas, mostly between 30°N and 40°S latitudes

**Landward migration:** process in which coastal wetlands migrate onto uplands or freshwater wetlands as sea level rises

**Tidal freshwater wetlands:** occur in areas that are dominated by freshwater (most common in deltas)

**Climate change:** refers to long-term shifts in temperatures and weather patterns

**Coastal marshes:** beds of intertidal rooted vegetation that are flooded and drained by tides, often facilitated by a bifurcating network of tidal channels

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important transitions or “bottlenecks” due to interaction among factors such as sea-level variation and climate change with major social and technological innovations. The stabilization of sea level approximately 5,000 years BP allowed for a great expansion of the area and productivity of coastal margin ecosystems that drove the development of initial state-level organization characterized by the first large urban areas (8–10).

Small human settlements occurred in coastal areas, especially deltas, early in the Holocene (11–13). These studies focused on early human occupation in the Danube, Rhine, Rhone, Nile, Tigris–Euphrates, and Yangtze Deltas. Human settlements in New World deltas began around the same time (8, 10). Similar patterns have been described in China in the Yangtze and Yellow River Deltas (14). In the Mississippi Delta, humans followed delta lobes as they advanced and retreated (15). Within a few centuries after sea-level stabilization, population increase in coastal margin settlements was supported by high-quality protein from aquatic animals that also provided sources of polyunsaturated omega-3 fatty acids and other nutrients essential to human nutrition (10).

Throughout the Holocene, humans altered coastal systems. Initially, impacts on coastal systems were small, such as the terpins (small, elevated mounds built by the Dutch more than 1,000 years ago). Shell middens are found in many deltas, where shells from consumed mollusks were piled up and lived on. Thousands were built in the Mississippi Delta. Settlements on natural levees occurred in several areas (16) where agriculture was practiced. Beginning in antiquity and continuing into the early twentieth century, tracts of coastal wetlands were leveed and drained on low tides for agriculture. Such agriculture on “reclaimed” lands is still common in many coastal areas, especially in deltas including the Nile, Rhone, Po, Ebro, and others. Such reclamation commonly led to subsidence as organic soils were oxidized. In some cases, as in the Mississippi Delta, these mostly failed due to high rates of subsidence and storms such as hurricanes (17). In many coastal areas, including parts of the Mississippi, Ebro, Po, Vistula, Yangtze, and many other deltas, drained areas are maintained by pumps. The Rhine is the most characteristic case, with around a quarter of its area impounded and below sea level. Many urban areas built on coastal wetlands, including parts of Amsterdam and other Dutch cities, New Orleans, Bangkok, and Shanghai, are below sea level. Large areas of some deltas, such as the Mekong and Ganges–Brahmaputra, have been converted to fish and rice farms.

During the twentieth century, the number of large, 15-m dams globally increased from 1,600 in 1900 to approximately 50,000 in 2015 (18), dramatically altering water and sediment discharge to coasts. Deltas in arid watersheds have been strongly impacted, including the Colorado (Mexico), Nile, and Tigris–Euphrates, where freshwater and sediment discharge have been reduced in some cases by more than 90% (19). Sediment input to the Mississippi Delta has been reduced by around half (17). Within many coastal areas, especially deltas, flood control levees have largely eliminated river water flowing into coastal basins, leading to wetland loss. These impacts have been extensively studied in the Mississippi Delta (9, 17).

From the middle of the twentieth century, the Earth system has been in the informally named Anthropocene (18, 20) owing to exponential growth in consumption, energy use, and population. Coastal regions, especially wetlands, are among the most impacted by Anthropocene forcings including climate change, detrimental impacts on ecosystems, and growth of the human population. Approximately 50% of the world population lives within 200 km from an oceanic coast, and most global megacities (>10 million people) are in tropical coastal zones (21). As discussed above, climate change is especially impacting coastal systems. Higher temperatures are impacting the tropical belt, affecting both natural systems and human populations. Anthropocene forcings, including both human impacts and global change forcings, are predicted to have strong negative impacts on coastal wetlands, reducing their extent globally with concomitant loss of ecosystem goods and services (1, 21).

## COMPOSITION OF COASTAL WETLANDS

Salt marshes dominate coastal marsh vegetation in temperate and boreal areas. There is an abundant literature about salt marsh wetlands (1, 3, 7). Coastal marshes are beds of intertidal rooted vegetation that are flooded and drained by tides, often facilitated by a bifurcating network of tidal channels. **Table 1** presents a general account of the taxonomic composition of coastal marshes.

Mangroves are coastal wetlands that are dominated by cold-sensitive trees that occur in tropical and subtropical areas, mostly between 30°N and 30°S latitudes. Other species that occur in mangrove swamps include shrubs, palms, ferns, and succulent plants. True mangroves occur only in the intertidal zone, are taxonomically distinct from terrestrial relatives, often form pure stands, and have special adaptations for existence in the intertidal zone (e.g., aerial roots, vivipary—seed

**Vivipary:** precocious or premature germination of offspring while still attached to the parent plant

**Table 1** Worldwide classification of salt marshes based on geographic distribution, floristic composition, and physiognomy<sup>a</sup>

Group	Geographic distribution	Dominant plants	Important controlling parameters
Arctic	Greenland, Iceland, and arctic coasts of North America, Scandinavia, and Russia	<i>Puccinellia phryganodes</i> , <i>Carex</i> spp.	Ice, extremely low temperatures
Northern Europe	Iberian Peninsula north to Norway and southwestern Sweden, west coast of Great Britain, Scandinavian coasts of Baltic Sea along English Channel, and other muddy coasts	<i>Puccinellia maritima</i> , <i>Juncus gerardii</i> , <i>Salicornia</i> spp., <i>Spartina</i> spp., <i>Festuca rubra</i> , <i>Agrostis stolonifera</i> , <i>Carex paleacea</i> , <i>Juncus bufonius</i> , <i>Scirpus</i> spp., <i>Spartina townsendii</i>	Sufficient precipitation, sandy to muddy substrate, moderate climate, coasts with a high proportion of sand, low to moderate salinity, muddy coasts
Mediterranean	Along Mediterranean coasts	Much low shrubby vegetation, <i>Arthrocnemum</i> , <i>Limonium</i> , <i>Juncus</i> , <i>Salicornia</i> spp.	Arid to semiarid, rocky to sandy coasts, generally high salinity, moderate precipitation
Eastern North America	Temperate Atlantic and Gulf of Mexico coasts of North America	<i>Spartina alterniflora</i> , <i>Spartina patens</i> , <i>Juncus roemerianus</i> , <i>Distichlis spicata</i> , <i>Salicornia</i> spp., <i>Puccinellia maritima</i> at higher latitudes	Generally muddy coasts and moderate climate, broad development of marshes
Western North America	Temperate Pacific coasts of North America	<i>Spartina gracilis</i> , <i>Spartina foliosa</i> , <i>Frankenia</i> spp., <i>Salicornia</i> spp.	Arid in south to high precipitation in north, rugged high-relief coasts, limited marsh development
Sino-Japanese region	Temperate Pacific coasts of China, Japan, Russia, and Korea	<i>Triglochin maritima</i> , <i>Limonium japonicum</i> , <i>Zoysia macrostachya</i> , and <i>Salicornia</i> spp.	Rugged, uplifting coasts, limited marsh development, moderate precipitation
South America	Principally along South American coasts too cold for mangroves, but also limited extent along mangrove coasts	Unique species of <i>Spartina</i> , <i>Limonium</i> , <i>Distichlis</i> , <i>Juncus</i> , <i>Heterostachys</i> , <i>Allenrolfea</i> , <i>Salicornia</i>	Rugged coasts, geographic isolation
Australia	South Australia, New Zealand, and Tasmania	<i>Hemibroa</i> spp., <i>Arthrocnemum</i> spp., <i>Salicornia</i> spp.	Tropical, temperate to arid for Australia, temperate elsewhere; soft substrates in estuaries, in coastal lagoons, and on low-relief continental shelves
Tropical	Saline flats not occupied by mangroves	<i>Salicornia</i> spp., <i>Limonium</i> spp., <i>Spartina brasiliensis</i>	Rainfall, geographic isolation, high salinity

<sup>a</sup>Data are from Reference 7 (with additions), using classifications from Reference 25.

**Table 2 Area of tidal freshwater ecosystems in the conterminous United States<sup>a</sup>**

Coastal region	Fresh tidal marsh (ha) <sup>b</sup>		Fresh tidal forest and scrub (ha) <sup>b</sup>	
Atlantic	39,983	(73,896)	91,055	(683,031)
Gulf of Mexico	36,220	(183,040)	10,805	(172,640)
Pacific	5,706	(6,637)	9,065	(164,101)

<sup>a</sup>Data calculated from appendix D of Reference 29.

<sup>b</sup>Numbers in parentheses add the unspecified to the tidal area. Most wetland inventories lump the tidal systems with the freshwater systems.

sprouts on trees—and special physiological adaptations including salt exclusion, salt excretion, and salt accumulation). The term mangrove generally refers to a specific type of tree, whereas mangrove wetland or mangrove forest refers to the whole community assemblage in intertidal zones. Many tropical estuaries are dominated by mangroves (4, 22–24).

Along arid tropical and temperate coastlines, the proportion of unvegetated tidal flats (i.e., salt flats, salt pans, salt barrens, sabkhas, and salinas) increases with hypersaline conditions that are physiologically stressful to vascular plants. Due to the higher salinities along arid and semiarid coasts, salt-tolerant succulent plants are also more abundant and dominant in tidal wetlands.

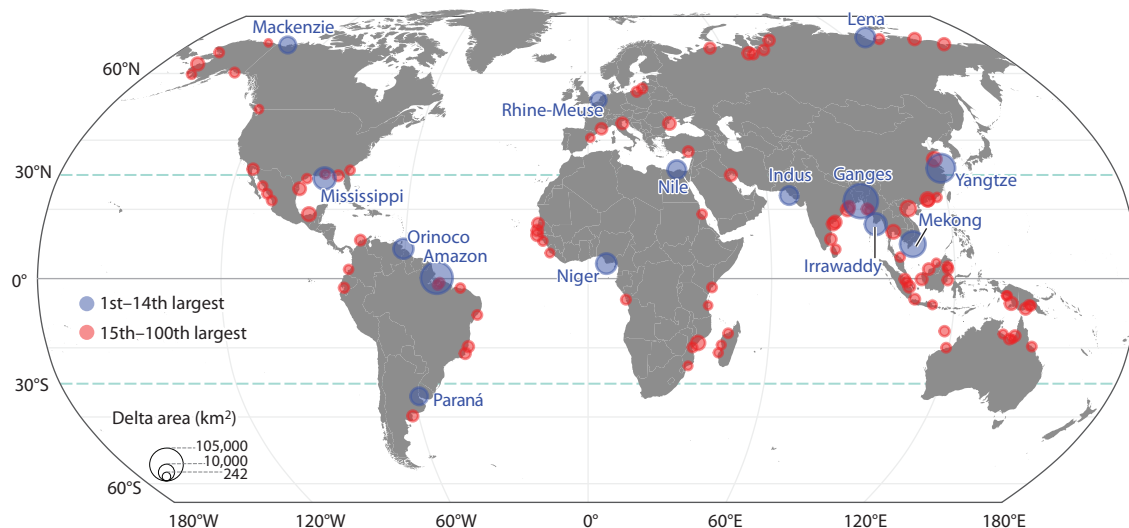
Although coastal marshes are often considered synonymous with salt marshes, along some coasts there are large areas of coastal freshwater wetlands (**Table 2**). Tidal freshwater marshes can be found throughout the world, but no comprehensive inventory of these systems exists (26). Freshwater tidal wetlands are found in at least three different coastal geomorphic settings. The first is the upper parts of estuaries, where riverine input keeps the environment fresh (26). The second is in river deltas, where freshwater can dominate almost to the land–sea interface (26). The third occurs in areas with low tidal range with significant freshwater input where uplands slope gently to the sea, such as the Everglades in Florida and parts of the Yucatan Peninsula. Tidal amplitude depends on the geomorphology of the estuary and can reach more than 10 m in some estuaries, such as the Bay of Fundy. However, eventually the tide decreases gradually in amplitude and velocity against the gradient of the river, and the system becomes nontidal. Like their saline and brackish counterparts, freshwater wetlands can be dominated by trees, shrubs, and herbaceous plants.

Many freshwater tidal wetlands have been converted to urban or agricultural land (26). Conversion to rice fields is widespread in southern Europe, southeastern North America, and Asia. For example, in coastal Texas (United States), there is very little freshwater wetland left, because large areas have been converted to rice fields (27). Because the tidal signal decreases gradually and species composition is often similar between tidal and nontidal freshwater wetlands, most wetland inventories lump the tidal systems with the freshwater systems (28). Field et al. (29) used the estuarine drainage areas identified by the United States to estimate the extent of coastal wetlands in the United States (**Table 2**). Hartley et al. (30) reported 657,433 ha of coastal freshwater wetlands, and Sasser et al. (31) reported 188,100 ha of swamp forest in the Mississippi Delta. The discrepancy with the Field et al. (29) data is probably because there are areas that were not specified as either tidal or not tidal. Adding the unspecified area to the tidal area (**Table 2**) makes these estimates closer.

## GLOBAL DISTRIBUTION AND AREA OF DELTAS, SALT MARSHES, AND MANGROVES

From a global perspective, the distribution and areal coverage of deltas, coastal marshes, and mangroves follow similar patterns (**Figures 1 and 2**). These data have been captured with increasing





**Figure 1**

Location of the largest 105 deltas by area globally based on analysis using recent satellite imagery in Reference 32. Most are between 30°N and 30°S. The 100 largest deltas are shown as colored bubbles, and the bubble sizes are equivalent to the delta areas. The 14 largest deltas are labeled (*blue bubbles*); 11 are in the tropical zone. Except for the Mississippi, which is fed by snowmelt and precipitation in the temperate zone, these deltas are fed by rains from tropical weather systems. The second most important area for deltas is in the Arctic (e.g., Mackenzie, Lena).

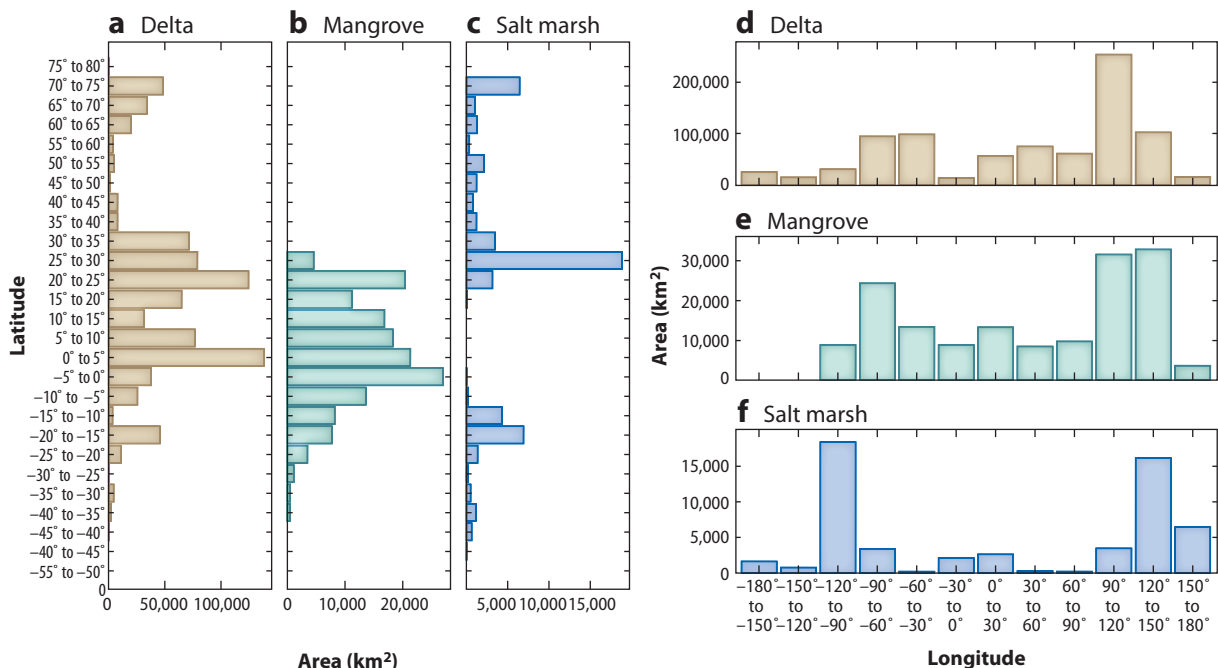
accuracy and resolution due to advances in remote-sensing technologies (sensors and algorithms) and an increased abundance of ground referencing. There are still limitations to the accuracy of these projections, but the general patterns provide an excellent perspective (for a discussion of these issues, see the **Supplemental Material**).

Most of the 105 largest deltas are located in the broader tropical zone between 30°N and 30°S (**Figure 1**). These deltas are fed by tropical weather systems associated with the Intertropical Convergence Zone. The largest area of nontropical deltas occurs in the Arctic, where they are generally fed by rivers draining the north temperate zone.

Of the 14 largest deltas, the Mississippi, Orinoco, Amazon, Niger, Nile, Indus, Ganges–Brahmaputra, Irrawaddy, Mekong, and Yangtze are in the broader tropical belt (**Figures 1 and 2a,d**). Total delta area per 5° latitude interval ranges from approximately 30,000 to nearly 140,000 km<sup>2</sup>. Delta area is around 100,000 km<sup>2</sup> per 30° interval between 30°W and 90°W and includes the Mississippi, Orinoco, and Amazon. In the Eastern Hemisphere, delta area is around 50,000 km<sup>2</sup> from 0°E to 150°E, with a large peak of around 250,000 km<sup>2</sup> between 90°E and 120°E. This area includes the Niger, Nile, Indus, Ganges–Brahmaputra, Irrawaddy, Mekong, and Yangtze deltas, with the latter four from 90°E to 120°E.

The abundance of mangroves and salt marshes mimics that of deltas (**Figure 2b–d,f**). More than 75% (or 640,188 km<sup>2</sup>) of the total global delta geomorphic area (e.g., 35) is in the tropics (32), where nearly all global mangroves exist (33). Indeed, more than 40% (or 54,972 km<sup>2</sup>) of the world's mangroves grow on deltas (36). Although these aerial estimates differ both conceptually and methodologically, their conjunction suggests that mangroves occupy at least 9% of global tropical deltaic geomorphic area and likely much more if relative only to coastal deltaic intertidal floodplains. Mangrove area is generally highest near the equator and declines to very low levels at 30°N and 30°S (**Figure 2b,e**).

**Supplemental Material** >



**Figure 2**

(a,d) Delta area across latitude (5° intervals) and longitude (30° intervals). Data from Reference 32 (for a discussion of the limitations of these data, see the **Supplemental Material**). (b,e) Variation of mangrove areal distribution by latitude and longitude. Data from References 33 and 35. (c,f) Variation of salt marsh areal distribution data by latitude and longitude. Data from Reference 34.

Within latitudinal range limits, mangroves and salt marshes occupy distinct coastal environmental settings (or typologies), deltas, estuaries, lagoons, open coasts, and carbonate (or karstic) soils, characterized by varying relative contributions of riverine to tidal to wave energies in addition to regional climate and salinity regimes (37, 38). For salt marshes, ranking aerial estimates by coastal typologies is not yet feasible owing to the lack of high-resolution maps such as those available for mangroves (e.g., 36).

In the tropics and subtropics, inactive coastal deltaic floodplains are generally covered by mangrove vegetation. By contrast, fresh and low-salinity or reduced-salinity freshwater and brackish marshes and swamps occur in active coastal deltaic floodplains. But even where tropical mangroves dominate the landscape, salt marshes still co-occur, usually bordering the transitional zones between mangroves and mudflats (so-called low marshes) or as more interior patches amid mangrove forests (so-called high marshes). Unvegetated tidal flats can develop upslope of mangrove forests due to hypersaline conditions, and the proportional areal coverage of tidal flat to mangrove forest increases where hypersaline conditions are more common in arid and semiarid coastlines. In temperate and boreal deltas, freeze-tolerant freshwater marshes and forested swamps occur upstream and by brackish and salt marsh communities toward the sea.

Global tidal marsh extent in 2020 ranged from 90,800 km<sup>2</sup> of saline and brackish but generally not freshwater marshes (39) to 52,880 km<sup>2</sup> of salt marshes (36). Large areas of tidal freshwater vegetation are likely not included in these estimates. Global mangrove extent in 2020 was estimated as 147,359 km<sup>2</sup> (35). Because of variability in the different estimates of coastal wetlands, there is a need for more detailed inventories of coastal wetland area (see the **Supplemental Material**).



## COASTAL RETREAT AND TRANSFORMATION DUE TO RISING SEAS

Land-use change in the twentieth century and earlier was the primary driver of coastal wetland loss due to reclamation for urban, agricultural, and industrial land uses (5, 40). In recent decades, land-use regulations have slowed the rate of coastal wetland loss, but these ecosystems are now threatened by accelerated sea-level rise (41, 42), which is expected to become the primary driver of coastal wetland loss across the globe.

Coastal wetlands are resilient ecosystems that have the potential to adapt to small changes in sea level through upward and landward movement across the landscape. The geological concept of accommodation is valuable for considering the effects of sea-level rise on coastal wetlands (43, 44). Within the context of sea-level rise, accommodation space refers to the vertical and horizontal (e.g., volumetric) space that becomes available for coastal wetland adaptation with rising seas (44). With gradual changes in sea level, coastal wetlands can move vertically or horizontally to occupy newly available accommodation space. However, sediment supply, biogenic accretion, and the rate of increase in accommodation space govern whether coastal wetlands are lost or gained in response to sea-level rise. Geological records show that the seaward loss of coastal wetlands due to retreat occurs when sea levels rise rapidly without concomitant increases in sediment supply (44, 45) or biogenic accretion. These records show that the full colonization of new accommodation space under rapidly rising seas is unlikely. Thus, coastal wetland retreat is likely in response to accelerated sea-level rise where an adequate sediment supply is not assured.

Are there sea-level rise thresholds for wetland loss? Under moderate rates of sea-level rise, coastal wetlands have the potential to adapt vertically by accumulating sediments and organic matter to build wetland soil elevations at rates that enable plants to adjust to increasing water levels (46, 47). Dynamic feedbacks among inundation, plant root growth, and sedimentation can enable some coastal wetlands to move upward to adjust to gradual sea-level increases (38, 48, 49). However, coastal wetland loss and transformation are likely when sustained sea-level rise rates exceed upper thresholds for vertical adjustment. Recent publications indicate that upper thresholds for coastal wetland loss are 6–9 mm year<sup>-1</sup> for marshes in Louisiana (United States) (50), 4.6–7.1 mm year<sup>-1</sup> for UK marshes (51, 52), 5 mm year<sup>-1</sup> for marshes along the eastern US coast (53), 6 mm year<sup>-1</sup> for mangroves in various parts of the world (54), and 3.6–7.6 mm year<sup>-1</sup> for marshes in various parts of the world (52). In some regions (e.g., the north-central Gulf of Mexico), widespread wetland loss (55) is already occurring owing to rates of relative sea-level rise that exceed vertical adjustment thresholds (50). In the coming decades, rates of sea-level rise in many areas (41, 42) are expected to cross thresholds for wetland drowning and loss.

In the face of seaward wetland losses, the landward migration of wetlands is viewed as a potential option for facilitating wetland adaptation to rising sea levels (56, 57). There has been much debate regarding the extent to which landward migration could offset seaward losses. Although some studies indicate that wetland migration could offset losses (58), others conclude that wetland migration cannot compensate for seaward losses (59). In many estuaries, coastal wetland migration is typically constrained by flood barriers (57, 60, 61). A recent analysis of 166 estuarine drainage areas across the conterminous United States shows that two-thirds of the potential area available for tidal saline wetland migration (i.e., salt marsh or mangrove forest landward migration) are expected to occur at the expense of valuable freshwater tidal coastal or near-coastal wetlands (i.e., freshwater marshes and forested wetlands) (59). The remaining one-third of potential wetland migration is expected to occur at the expense of valuable uplands (i.e., croplands, forests, pastures, and grasslands). The landward migration of salt marshes and mangrove forests occurs at the expense of valuable freshwater wetlands and is a wetland transformation rather than a net coastal wetland gain. Thus, landward migration of wetlands is not expected to compensate for

seaward wetland losses. Collectively, these analyses highlight the importance of (a) considering both tidal saline and tidal freshwater wetlands when evaluating the potential for wetland migration and (b) considering the societal and ecological benefits of the adjacent terrestrial and wetland ecosystems affected by wetland migration. Studies that focus only on the migration of tidal saline wetlands likely overestimate the potential for wetland migration to offset seaward losses by not considering the loss of freshwater wetlands.

Rising sea levels interact with other aspects of climate change to transform coastal wetlands and adjacent coastal ecosystems (62, 63). At the global scale, macroclimatic drivers, extreme events, and geomorphology greatly influence ecosystem structure and function in coastal wetlands. For example, extreme drought can lead to mangrove and salt marsh dieback (64, 65). Warming winters can facilitate the poleward range expansion of mangroves at the expense of salt marsh (66, 67). Stronger hurricanes can trigger mangrove (68, 69) and marsh (70) dieback. Saltwater intrusion can kill upland and freshwater forests, leading to landscapes covered by ghost forests (71). Along arid coastlines, changes in precipitation, freshwater inflow (a major driver of change), and salinity can lead to changes in the areal coverage of vegetated wetlands (72). In the coming century, climate change, sea-level rise, and coastal land-use change will interact to transform our coastal wetlands. There is a need to better anticipate and prepare for these changes.

## CLIMATE CHANGE

Both natural systems and human settlements in coastal areas are at the forefront of both direct and indirect climate change impacts of increasing temperature, sea-level rise, tropical cyclones, drought and water stress, wildfires, and extreme precipitation events (73–81).

Extreme heat is affecting increasingly larger areas of the globe. Global temperatures have increased by slightly more than 1°C since 1880 and are projected to increase by an additional 1.5–2.0°C or more by midcentury, coinciding with a disproportionate increase in the frequency, duration, and geographic extent of heat wave events (82). Xu et al. (83) reported that for the past six millennia, humans, crops, and livestock occupied a relatively narrow part of the global climate envelope. The position of this climate envelope is projected to shift more in the next half century than it did in the past 6,000 years. A third of the human population will experience a mean annual temperature greater than 29°C by 2070, compared to 11–15°C for the past six millennia. The most dramatic reduction of temperature suitability is projected to occur in the tropics, subtropics, and subtemperate zone, especially along tropical coasts, which will facilitate the replacement of coastal marshes by mangroves. Projected climate change will lead to temperatures that often exceed human thermoregulatory capacity and 30% of the world's population is already currently exposed to lethal temperature–humidity conditions (84). By 2100, this percentage is likely to increase by 48–74% depending on future emissions. Increased mortality from high heat is likely and may be further exacerbated by greenhouse gas emissions. Loeb et al. (85) reported that the amount of heat stored by the earth system doubled from 2005 to 2021. The use of nonmetabolic energy to mitigate high temperatures through air conditioning is less accessible in the lower-income tropics than in high-income countries (e.g., 86).

Increasing heat waves also pose challenges for food security, especially in low-income countries in the tropical belt. Extreme heat can affect wild and domestic food production and storage (87), especially in coastal zones where livelihoods are often dependent on local and regional harvest and trade. The oceans are warming, and there has been an increase in the frequency and duration of marine heat waves (88).

Eustatic sea-level rise (due to an increase in the volume of the ocean) is projected to increase by up to 1 m or more by 2100 and increasingly impact coastal wetlands in large areas of near-sea-level land such as deltas (21, 89, 90). Oppenheimer et al. (91) reported mean eustatic sea-level rise

estimates and projections from 1986–2005 to 2081–2100 (ranges in brackets): 0.43 m [0.29–0.59]-RPC2.6, 0.55 m [0.39–0.72]-RPC4.5, and 0.84 m [0.61–1.10]-RCP8.5. Especially vulnerable are low-lying coastal regions in the wider tropics (see **Figure 1**) with large deltas and high populations (17, 19, 21, 89, 90). Coastal flooding is projected to increase due to climate-induced tidal and storm events (92). Changes in drainage basins of large deltas (freshwater withdrawal, sediment retention behind dams) and local changes (reclamation, hydrologic alteration) are decreasing the resilience of coastal wetlands (17, 21, 90, 93). High subsidence rates in deltas lead to high rates of relative sea-level rise, which are exacerbated by subsurface fluid withdrawal (17, 21, 94). Sea-level rise can interact with ocean circulation to exacerbate coastal flooding and saltwater intrusion (95–97).

Increasing warming of ocean surface waters has amplified the intensity of tropical cyclones (73, 75, 98, 99). Mei et al. (80) predict that climate change will increase already-high average typhoon intensity in the Pacific area by 14% by 2100. Tropical cyclones are also intensifying more rapidly (100), as are large surge events (101), and losing strength more slowly over land (102). Countries bordering the western Pacific and Indian oceans are among the most populous in the world, with many coastal megacities (19, 21). Thus, the frequency of the strongest tropical cyclones is projected to increase, and these storms will be larger, intensify faster, have more precipitation, move slower, decay more slowly over land, and, as noted above, negatively impact coastal wetlands. Extreme precipitation events are becoming more common worldwide (3, 78, 103). For example, Hurricane Harvey in 2017 had peak rainfall of approximately 1.5 m in 3 days along the Texas coast.

In summary, the implications of climate change are enormous and existential for the human species: Future climate forcings are predicted to affect almost all of Earth's coasts from the tropics to high-latitude coastal areas. A broad zone that includes tropical to subtemperate regions is expected to be affected by most of the forcings discussed above (**Figure 1**). It includes a large proportion of the world's population, almost all of the world's major deltas, most coastal megacities, and large areas of coastal wetlands. It should be noted that climate change forcings that are not normally considered "coastal" forcings, such as drought, can impact coastal areas both directly and indirectly. For example, wildfires are becoming more intense, and the length of the wildfire season in many areas is increasing. Direct effects include the burning of coastal carbon stores in soils and peat bogs and the destruction of root zone reproductive potential (21). Indirect effects are also significant. Coastal areas, including coastal wetlands, that are affected by both direct and indirect impacts of wildfires can become less resilient and sustainable because of global change-fueled forcings such as intensification of wildfires and drought, especially when combined with other global change drivers. These areas include southern California and northwestern Mexico, the Mediterranean and Middle East, central Chile, and the southeastern coast of Australia.

## THE UNIQUE BIOGEOCHEMISTRY OF COASTAL WETLANDS

Soil biogeochemistry, or nutrient transformations, is fundamentally different in flooded wetland soils compared with terrestrial or upland systems (104). The diffusion of oxygen is 10,000 times slower in water than in air; therefore, flooded/wet soils experience anaerobic conditions because of slow  $O_2$  diffusion and high  $O_2$  consumption from reduced chemicals and soil microbial metabolism. Once under anaerobic conditions, there is a predictable stepwise reduction of alternate electron acceptors from  $NO_3^-$ ,  $Mn^{++}$ ,  $Fe^{+3}$ ,  $SO_4^{2-}$ , and  $CO_2$  (104). If one of these is supplied in excess, then the soil reduction level, or Eh, does not drop below that. The Eh spans from +300 at the aerobic/anaerobic threshold down to -300, though the theoretical range is larger and is influenced by pH. Tidally influenced coastal wetland soils typically have a large proportion of the soil microbial metabolism under sulfate-reducing redox conditions, as tides provide regular input of sulfate associated with salinity in sea water. This supply of  $SO_4^{2-}$  maintains the soil redox level

above methanogenesis, significantly reducing the formation and release of  $\text{CH}_4$  to the atmosphere in these coastal systems (104). Freshwater systems in the coastal zone can constitute a significant proportion of total wetland area (17). In these systems, continuous freshwater flow from rivers prevents salt from entering wetland soils, so that river deltas provide a freshwater system within the otherwise saline coastal zone (105). Consequently, the surface deltaic wetland soils tend to be maintained at higher redox potential because most rivers globally contain elevated  $\text{NO}_3^-$  concentrations (106). Upon contacting the deltaic wetland soils, nitrate becomes reduced to  $\text{N}_2$  gas by the microbial metabolism of denitrification (107). The consequence of this denitrification activity is improved water quality reaching the coastal waters, as these freshwater coastal wetlands can reduce the bioavailable nitrogen load and maintain the redox potential of the surface soils above methanogenesis. However,  $\text{NO}_3^-$  is consumed at the surface and does not penetrate deeply into the organic soil (108). Therefore, the deeper soils can become reduced to an Eh supporting methanogenic activity (105). As a result of this situation, river deltas are important systems in the coastal zone not only for improving water quality but also as hot spots of methane production and release, adding a potent greenhouse gas to the atmosphere (104).

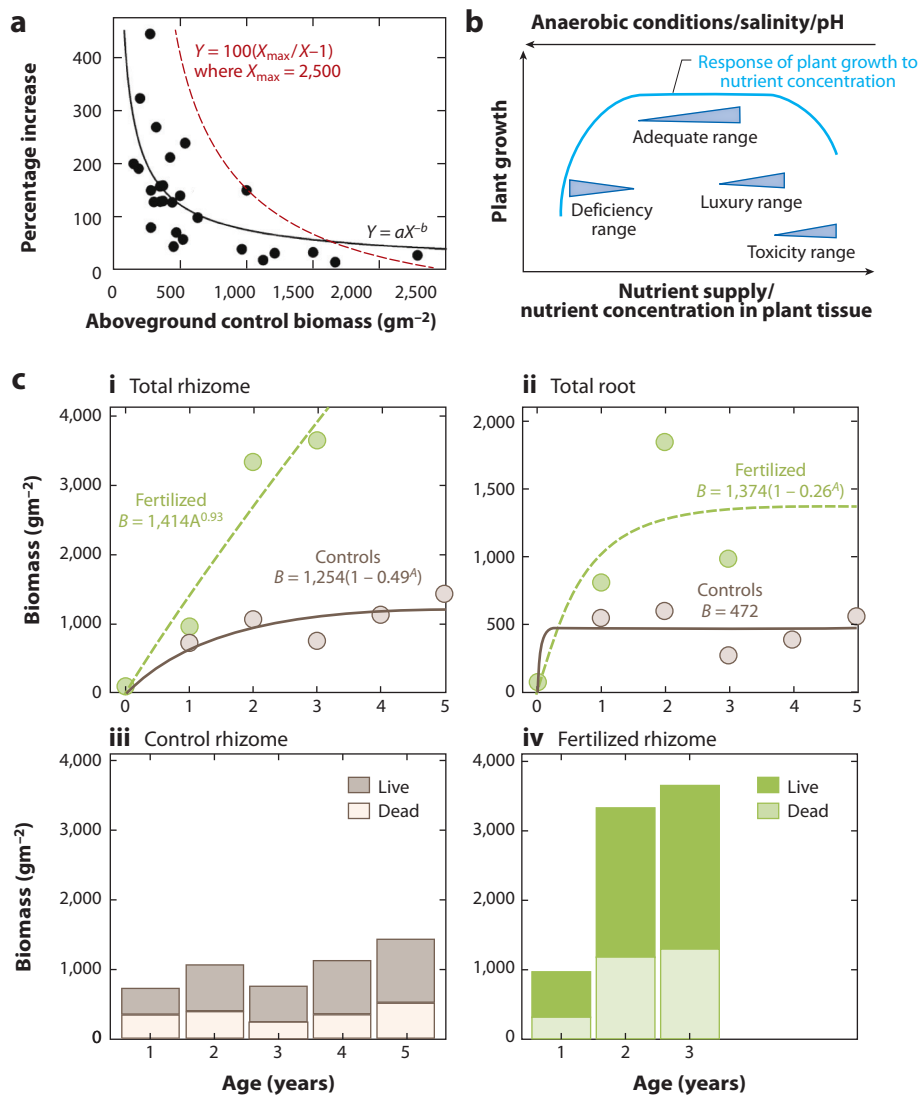
### THE PHYSIOLOGICAL BASIS FOR NITROGEN REGULATION OF PRIMARY PRODUCTION AND THE CONSEQUENCES OF EXCESSIVE NITROGEN LOADING IN SALT MARSHES

An increase in the supply of nitrogen to coastal areas has hastened the need to understand the effects of nitrogen loading on wetland productivity and soil organic matter accumulation. Here, we focus on what is known about the physiological basis for regulation of primary production and address the question of impacts of increased nitrogen loading on coastal salt marshes. Nitrogen is recognized to be universally limiting of primary production in salt marshes dominated by *Spartina alterniflora* (Figure 3a), but the response of salt marsh vegetation to nitrogen fertilization decreases as the in situ control biomass increases; in other words, primary production is limited ultimately by energy efficiency. When the control standing biomass is high,  $2,500 \text{ g m}^{-2}$ , little can be gained in the way of added production from fertilization, but when biomass is low, there is a large potential for increasing productivity (Figure 3a). If nitrogen alone were able to raise the biomass to the hypothetical maximum of  $2,500 \text{ g m}^{-2}$ , the predicted relationship would appear, as depicted in Figure 3a. The gap between a line fitted to the empirical data and a hypothetical maximum (Figure 3a) is a result of colimitation by other factors or stressors such as osmotic stress, hypoxia, herbivory, disease, soil chemistry (toxicity and/or micronutrient deficiencies), and probably others. Productivity, especially of rhizomes, can be expected to follow a similar trend.

Plant productivity and nutrient uptake in salt marshes are also strongly regulated by abiotic stress, primarily anaerobic conditions, sulfide concentrations, and salinity. Thus, the relationship between nutrient supply and utilization is not necessarily directly proportional (Figure 3b) and can have indirect effects. For example, high inputs of  $\text{NO}_3^-$  may affect plants by inhibiting iron reduction, reducing iron availability for plant uptake, and reducing the bioavailability of phosphorus due to the formation of less soluble Fe–P compounds (65).

### Regulation of Nitrogen Uptake on a Physiological Level ( $\text{O}_2$ , $\text{S}^{2-}$ , $\text{Na}^{+1}$ )

Salt marsh plant productivity can be nitrogen limited despite a large pool of available porewater nitrogen, mainly  $\text{NH}_4$  (112). Nutrient uptake by plants is best described by Michaelis–Menten kinetics (113):  $U = R C V_{\max} / (k_m + C)$ . Here,  $V_{\max}$  is the maximum specific rate of uptake, usually based on root dry weight;  $k_m$  is the half-saturation constant;  $R$  is root weight; and  $C$  is the concentration of a specific ion in the rhizosphere.



**Figure 3**

(a) Summary results of 14 studies of effects of 1 or more years of fertilization with nitrogen or a combination of nitrogen and other nutrients on the dry standing biomass of *Spartina alterniflora*. Plotted is the percent increase in aboveground biomass relative to the maximum biomass observed during a growing season on control plots. Also shown is the best fit of a power function to the empirical data and a theoretical upper limit (red dashed line). (b) Relationship between plant growth and nutrient supply showing limitations from deficiency and surplus. (c) Time series of root and rhizome biomass from marsh organs harvested sequentially for 3 to 5 years. The distributions of live and dead tissue are cumulative. Note that the fertilized treatment was discontinued after 3 years due to crowding in the marsh organ pipes. The  $A$  and  $B$  in the biomass equations denote age (years) and biomass, respectively. Panel *a* adapted from Reference 109. Panel *b* adapted with permission from Reference 110. Panel *c* adapted with permission from Reference 111.

$V_{\max}$  and  $k_m$  are not constants, which explains why salt marsh vegetation can be nitrogen limited when the concentrations of ammonium in the porewater are relatively high.  $V_{\max}$  and  $k_m$  are affected by temperature, the concentrations of competing ions, toxins, and oxygen availability (114, 115). Competing ions, such as seawater cations competing with  $\text{NH}_4$  for carriers, increase  $k_m$ , a process known as competitive inhibition. Known toxins such as sulfide lower  $V_{\max}$  and increase  $k_m$  (112).

Nutrient uptake is an active metabolic process in which ions are moved against a gradient, which generally requires oxygen. Wetland plants passively deliver oxygen to their roots through processes such as Venturi flow, Knudsen diffusion (116), or hygrometric pressurization (117), but *Spartina* is less efficient at transporting oxygen compared with other wetland plants, and its uptake of  $\text{NH}_4$  increases when the roots are supplied an external source of nitrogen (114).

### Consequences of Nitrogen Source (e.g., $\text{NH}_4$ and $\text{NO}_3$ )

Angiosperms generally assimilate nitrogen as either ammonium or nitrate, with some species showing a strong preference for one ionic form over the other (118, 119). The pathways of reduction of  $\text{NO}_3^-$  to  $\text{NH}_4^+$  require energy inputs additional to those involved when utilizing ammonium ions directly (120). Wetland soils are anoxic throughout much of the profile; hence, many wetland plants have adapted to taking up  $\text{NH}_4$  because  $\text{NO}_3$  availability is low (121). Although the majority of fertilization studies have focused on the enrichment of  $\text{NH}_4\text{-N}$  (rather than  $\text{NO}_3$ ) on plant productivity, there is mounting evidence that salt marsh plants have a greater growth response to  $\text{NH}_4$  than  $\text{NO}_3$  (122–124). This raises the possibility that excessive anthropogenic  $\text{NO}_3$  inputs could have a negative impact on marsh ecosystems, given that  $\text{NO}_3$  is a thermodynamically favorable electron acceptor during anaerobic decomposition (125) while having a limited effect on plant productivity.

*Spartina alterniflora* grown aerobically in hydroponic cultures at three levels of  $\text{NO}_3$  (0.07 to  $2 \text{ g N m}^{-2} \text{ day}^{-1}$ ) and an intermediate level of  $\text{NH}_4$ , with N-Serve to inhibit nitrification, had total production in unshaded treatments spanning 10.1 to  $41.6 \text{ dry g plant}^{-1}$  in  $\text{NO}_3$  treatments (126). Intermediate loading rates produced equivalent and intermediate growth. Plants assimilated  $\text{NO}_3$  with a lower  $V_{\max}$  than  $\text{NH}_4$ , 0.108 versus  $0.136 \text{ mg N g root}^{-1} \text{ h}^{-1}$ , and a higher  $k_m$ ,  $0.124 \text{ mg NO}_3\text{-N L}^{-1}$  versus  $0.057 \text{ mg NH}_4\text{-N L}^{-1}$  (127). The results of field experiments in which  $\text{NO}_3$  is added to anaerobic soil will differ, as discussed in Reference 128.

An increasing supply of nitrogen, primarily  $\text{NO}_3\text{-N}$  to coastal waters, has the potential to increase decomposition through denitrification and lead to loss in soil carbon. In addition to lowering the carbon sink function, the consequences of greater soil organic matter decomposition may be a lower net accretion and overall ability to keep pace to relative nitrogen-limited sea-level rise. Experimental  $\text{NO}_3\text{-N}$  addition studies have illustrated that microbial respiration rates are stimulated with added nitrate (125, 129), but field studies showing the impact on soil carbon are needed. Day et al. (130) showed that at loading rates less than about  $30 \text{ g N m}^{-2} \text{ year}^{-1}$ , denitrification could support oxidation of no more than a few percent of soil organic matter. Furthermore, though salt marsh plants are primarily nitrogen limited, soil bacteria can respond more readily to phosphorus enrichment (131).

### The Functional Equilibrium Model

Plant root-to-shoot ratios decline as nutrient loading increases (132–134), and it has been argued that higher nutrients lead to lower root biomass because fewer roots are necessary to supply nutrients to plants (135). The observation that root-to-shoot ratios are variable and subject to control by nutrient availability has inspired a well-known theory in the plant literature, known



as the balanced root and shoot activity theory. These models are discussed in an excellent review by Wilson (136). The model predicts that the root weight increases less than leaf weight as the root-weight-specific uptake rate increases. Consequently, the root-to-shoot ratio will decrease. The uptake kinetics also must be considered. The root-weight-specific uptake rate is limited by physiology ( $V_{\max}$ ), not by loading rate. An increase in nitrogen concentration in the range of  $V_{\max}$  is inconsequential. It does not increase uptake. Thus, the root-to-shoot ratio has a lower limit set by the physiological upper limit of uptake. These generalities are supported by experimental results involving more than 20 plant species showing that, as increasing nutrient supply increased total plant weight, the mean ratio of root-to-shoot total plant weight decreased, but root weight increased 70% (137).

The effect of nutrients on belowground production has been a controversial topic, with evidence that nitrogen either decreases (135, 138, 139) or increases (109, 140, 141) belowground production (**Figure 3c**). To be clear, the term roots is used loosely in much of the ecological literature to mean roots plus rhizomes. Rhizome biomass must be considered a different organ with different responses to nutrients (**Figure 3c**). Rhizomes are functionally like the branches in a forest canopy. They are perennial organs with meristems that grow roots, and the evidence from a well-controlled bioassay experiment shows that belowground biomass is dominated by rhizomes (**Figure 3c**) and that their biomass increases when leaf weight increases (111).

North Inlet Estuary, South Carolina (United States), has been the site of a fertilization study since 1984, with applications of 30 mol N and 15 mol P m<sup>-2</sup> year<sup>-1</sup>. The elevations of these fertilized marsh plots have increased at a rate four times that of controls, and the evidence, including bioassay data (111) and computed tomography scans of sediment cores (142), points to an expansion of belowground biomass as the primary mechanism. In a bioassay (marsh organ) with the same dosage as used in the field, the growth of belowground biomass was dominated by rhizomes, which grew to 3,648 g m<sup>-2</sup> in the fertilized treatments after 3 years and 1,439 g m<sup>-2</sup> in the control treatments after 5 years (111).

## Nutrient Toxicity

An important mechanism of ammonium toxicity in plants is a reduction in soil pH (143). During ammonium uptake, cations are taken up more readily than anions, producing a compensatory proton efflux that causes rhizosphere acidification (143). Internal mechanisms of ammonium toxicity are not fully understood but are thought to be due to (a) uncoupling of ATP production during electron transport of photosynthesis (144), (b) intracellular depletion of cations (e.g., K<sup>+</sup>, Mg<sup>+</sup>) and increase of anions (phosphate) (145), (c) an increase in respiratory and structural carbon demand, and (d) the high energetic cost of pumping out ammonium (146). Thus, a high availability of nonstructural carbohydrate reserves has been shown to reduce the relative toxicity of ammonium (147).

Overall, nitrogen toxicity in salt marsh plants has not been well documented. Part of the reason may be due to abiotic stress limitations on uptake as well as the slightly acidic to circumneutral pH in salt marshes. NH<sub>4</sub> toxicity occurs when a significant portion of ammonium is present as its conjugate base (ammonia; NH<sub>3</sub>) at a high soil pH (>8.5) (145), not typically found in salt marsh soils (pH 6–7.5) (148) but prevalent in other marine environments. For example, ammonium concentrations of 125 μM under alkaline conditions were toxic to *Zostera marina* (145). Ammonium concentration in salt marsh soils typically increases with depth and distance from a tidal creek. In the Great Sippewissett salt marsh in Massachusetts (United States), NH<sub>4</sub> concentrations were less than 20 μM 5 to 10 cm below the surface and greatest (averaging 90 to 175 μM) at a depth of 40 cm (149). Freshwater marsh species exposed to ammonia (NH<sub>3</sub> + NH<sub>4</sub>OH + NH<sub>4</sub><sup>+</sup>)



**NEP:** net ecosystem production

**CDR:** carbon dioxide removal

concentrations in excess of 11.7 mM at a pH of 6 to 7 experienced a reduction in relative growth rate, including *Juncus effusus*, *Sagittaria latifolia*, *Schoenoplectus tabernaemontani*, and *Typha latifolia* (150). The relationship between nutrient supply and productivity also depends on nutrient utilization efficiency. C4 grasses, such as *Spartina alterniflora*, have higher nitrogen use efficiency, producing more biomass per unit tissue nitrogen than C3 species due to the lower investment of nitrogen in photosynthesis (110). As discussed above, the main effect of experimental nutrient enrichment on marsh grasses has been an increase in biomass and a change in biomass allocation from root-to-shoot production.

## Significance

An important issue over the past several decades has been the extent to which nutrient input to coastal wetlands can result in reduced belowground biomass and the increased decomposition of soil organic matter resulting from high  $\text{NO}_3$  inputs and increased denitrification in the anaerobic root zone (122, 130). Increased nitrogen loading was negatively correlated with dead belowground biomass (151). There is a labile pool of soil necromass that probably decomposes faster when enriched with nitrogen, which would be seen as a step decline in soil organic matter, but the labile pool does not add new volume to the soil. It decays, and its speed of decay is irrelevant. What matters are the production and preservation of refractory organic matter.  $\text{NO}_3$  can serve as an oxidant, but then there is a question of mass balance.

To address these questions, many fertilization experiments have been conducted in which nutrients were added to marshes either in situ or to cores. Many nutrient additions were very high, in some cases in excess of  $600 \text{ g N m}^{-2} \text{ year}^{-1}$ , which is far in excess of ambient loading rates. There are several examples from the Mississippi Delta, where river water enters coastal basins with large areas of coastal wetlands. In the Atchafalaya coastal basin that receives around one-third of total Mississippi River discharge, loading rates to mixed inshore waters and stratified near-shore waters were  $66\text{--}136 \text{ g NO}_3\text{--N m}^{-2} \text{ year}^{-1}$ , and 40–47% of  $\text{NO}_3$  was removed from the water column (152) with little discernable loss of wetlands (153). In the Breton Sound basin, loading rates onto the upper basin containing around  $1,000 \text{ km}^2$  of water bodies and wetlands were 4.1 to  $12.2 \text{ g N m}^{-2} \text{ year}^{-1}$  with no demonstrable impacts on biomass or soil organic matter decomposition (130, 154). These results show that very high nitrogen-loading rates in fertilization experiments are much higher than ambient loading rates and nitrogen loading from coastal watersheds that generally do not have negative impacts, but in a positive direction, as shown in a well-controlled bioassay experiment (**Figure 3c**). The increase in biomass is attributed largely to rhizome growth.

## COASTAL BLUE CARBON

The concentration of atmospheric  $\text{CO}_2$  was controlled for the past several hundred million years by a combination of natural weathering processes balanced with plate tectonics and volcanism and a very slight positive rate of global net ecosystem production (NEP).  $\text{CO}_2$  varied between approximately 180 and 300 ppm over the past 800,000 years as the balance between global ecosystem primary production and respiration increased or decreased with cyclical variations in global temperature controlled by Milankovitch orbital variations. The positive NEP has led to vast global stores of organic carbon in the form of coal, oil, methane, and peat. However, since the industrial revolution, atmospheric  $\text{CO}_2$  levels have been increasing due to combustion of fossil fuels and forest clearing, which has led to rapid global warming.

Currently, much research is focused on identifying natural and artificial processes to limit and possibly reduce  $\text{CO}_2$  levels—carbon dioxide removal (CDR) research—to mitigate impacts of climate change. Two reports by the US National Academies of Science, Engineering, and Medicine

**Table 3** Blue carbon sequestration by tidal wetlands and seagrass meadows of the world<sup>a</sup>

	Area (km <sup>2</sup> )	Stock (Pg CO <sub>2</sub> )	Sequestration rate (g C m <sup>-2</sup> year <sup>-1</sup> )	Annual burial (Pg C year <sup>-1</sup> )	Annual burial (Pg CO <sub>2</sub> year <sup>-1</sup> )
Mangrove	137,600	14.8–42.9	226	0.03	0.11
Salt marsh	54,950	5.7	242	0.01	0.05
Seagrass meadow	344,958	15.4–30.8	138	0.05	0.17
Total	NA	NA	NA	0.09	0.34

<sup>a</sup>Data from References 22, 43, 165, 167, and 186–188.

Abbreviation: NA, not applicable.

(NASEM) summarize CDR research and the potential for terrestrial and coastal regions (155) and open ocean regions (156) to lower CO<sub>2</sub> levels.

Coastal blue carbon sequestration is one form of CDR that has been studied over the past two decades (157–159). Coastal blue carbon refers to the stocks of undecomposed plant-derived organic carbon in soils of tidal wetlands and seagrass meadows that have accumulated over the past 4,000–6,000 years, when rates of sea-level rise slowed to below approximately 4 mm year<sup>-1</sup>. The slowdown allowed sediment infilling of shallow coastal areas, the formation of deltas, and the development of tidal wetlands and seagrass meadows. The areal expanse of these systems increased as they advanced into open water estuarine areas with sediment infilling and transgressed uplands that were flooded by rising seas.

Rates of organic carbon burial are high in tidal systems due to low decomposition rates (160) and soil accretion (161, 162), the process whereby tidal wetlands build and maintain elevation relative to the rate of sea-level rise. Integrated for all tidal wetlands and seagrass meadows of the world, it is estimated that ~0.1 Pg C are sequestered annually and that there are 36–79 Pg CO<sub>2</sub> in the surface meter of soil (**Table 3**). As blue carbon ecosystem soil profiles often reach depths greater than 1 m (e.g., 163), organic carbon content is likely considerably higher. Without blue carbon sequestration, atmospheric CO<sub>2</sub> would be higher and climate change exacerbated.

Organic carbon burial in coastal blue carbon ecosystems is the product of soil organic carbon burial rate and the area of each ecosystem (157). The area of tidal wetland vegetation is typically quantified from a combination of remote-sensing approaches (164, 165).

Carbon burial rates are calculated as soil organic carbon density times sedimentation rate (157). There are challenges in measuring and interpreting either of these terms. Carbon burial is the net result of several processes operating concomitantly. There are strong vertical gradients in carbon stocks and density that reflect the processes of in situ root and rhizome production, surface deposition, decomposition, compaction, and erosion. Factors that influence these rates include solar radiation, temperature, water level, flooding frequency, wave and current energy, and nutrient enrichment.

### Problems with Current Blue Carbon Budgets

Accurate estimates of the global areal expanse of blue carbon ecosystems remain a challenge. Over the past 20 years, areal estimates have decreased by almost 50%. Organic carbon sequestration rates used in most global blue carbon budgets have not been rigorously compared with detailed ecosystem carbon budgets, and it is largely unknown whether the NEP of these systems is high enough to support burial rates used in global compilations. For example, seagrass budgets often use a burial rate of 138 g C m<sup>-2</sup> year<sup>-1</sup> (e.g., **Table 3**), yet measures of NEP suggest an upper limit in the range of 3–66 g C m<sup>-2</sup> year<sup>-1</sup> (166). Carbon fingerprinting techniques show that, in general, only 50% of soil organic carbon in seagrass meadows is derived from seagrass tissues

**NASEM:** National Academies of Science, Engineering, and Medicine

**Coastal blue carbon:** refers to stocks of undecomposed plant-derived organic carbon in soils of coastal wetlands and seagrasses

**Organic carbon burial:** the product of locally derived soil organic carbon burial rate and area of each ecosystem in coastal blue carbon ecosystems

and that the other 50% is derived from phytoplankton and terrestrial organic matter (167). NEP constraints have not been employed for mangrove or salt marsh blue carbon systems.

Another major problem facing the use of sequestration burial as the measure of blue carbon sequestration by coastal systems is that it ignores the continued loss of these ecosystems through both direct and indirect human actions, such as clearing and filling for land-use change, logging of mangroves, and erosion from sea-level rise (168). Blue carbon budgeting should also account for both erosion/loss and wetland gain through upland transgression (39, 169) (as described in this section). It also ignores the emission of methane from these systems (170–172), which negates blue carbon burial sequestration if large enough. With a 30:1 greenhouse gas multiplier of CH<sub>4</sub> versus CO<sub>2</sub> effect, as little as 8 g CH<sub>4</sub> negates 242 g C organic carbon burial m<sup>-2</sup> year<sup>-1</sup>. Mississippi Delta saline marshes release around 11 g CH<sub>4</sub> C m<sup>-2</sup> year<sup>-1</sup>, which is equal to 333 g C CO<sub>2</sub> (173).

### Coastal Blue Carbon Systems' Potential for Carbon Dioxide Removal

To qualify for CO<sub>2</sub> removal status, the rate of blue carbon sequestration must be greater than a baseline level of sequestration. This is termed additionality. The rates in **Table 3** could be considered baseline levels because they are based on measurements made in the past decade or so. A NASEM report (155) identified five approaches for accelerating CDR through 2060 and potentially for the rest of the century. Each varies in potential cost, technological readiness, and social barriers to implementation. They include the following:

1. Actively manage blue carbon ecosystems to increase CO<sub>2</sub> removal.
2. Restore blue carbon ecosystems where they were originally located or degraded.
3. Remove hardened shoreline barriers to allow conversion to natural shorelines in conjunction with coastal adaptation projects.
4. Manage wetland transgression into uplands.
5. Increase carbon storage capacity in wetlands by augmentation with carbon-rich materials.

Aspects of activities 1–3 are ongoing in several coastal systems of the United States. In the Mississippi Delta, freshwater diversions have been created to control salinity intrusion associated with subsidence and sea-level rise in the attempt to maintain healthy tidal wetland plant communities. Sediment diversions are also being put in place to expand wetland area and enable existing wetlands to maintain elevation relative to eustatic sea-level rise. In Massachusetts, several tidally restricted wetlands have been restored by increasing tidal saltwater flow, allowing seawater and sediment to enter (174). A major benefit of this type of restoration is salinization, which greatly reduces methanogenesis and CH<sub>4</sub> release to the atmosphere (175, 176). Moreover, all of these techniques are extremely expensive, and the ability to implement activities nationwide or globally is very unlikely.

### THE VALUE OF COASTAL WETLANDS

Coastal wetlands provide a broad range of ecosystem services (ES) that support and enhance human well-being. There has been ongoing and extensive research to understand ES and value their contributions to the well-being of humans and the rest of nature. For example, a recent Scopus search (May 5, 2023) for articles with “coastal wetlands” OR “mangroves” OR “salt marsh” AND “value” in the title, abstract, or keywords yielded 7,206 documents.

Probably the first attempt to comprehensively value coastal wetlands in monetary units was a 1974 study by Gosselink et al. (177) on “the value of the tidal marsh.” These authors provided a succinct and relevant rationale for why this kind of valuation of ES is needed:

The shortcomings of evaluating environment only in terms of direct uses or products is [*sic*] that such cost-accounting ignores the extremely valuable life-support work natural areas carry out without any development or direct use by man. It is this “free work of nature” that is grossly undervalued, simply because it has always been taken for granted, or assumed to be unlimited in capacity. (177, p. 9)

This study was criticized by some economists at the time (178) because of its attempt to go beyond the conventional market-based approach to valuation and include the multifaceted “free work of nature” and its contributions to human well-being. However, it has become increasingly clear from subsequent studies that most of the contribution of coastal ecosystems, especially wetlands (and natural ecosystems in general), to human well-being is outside the market. They are nonmarketed “public goods” and include storm protection, fisheries habitat, recreation, nutrient cycling, and carbon sequestration and storage. They therefore require diverse types of analysis and modeling to reveal that value.

The 7,206 articles mentioned above on coastal wetlands valuation are among the more than 15,000 articles on “ecosystem services” AND “value” picked up by Scopus. Clearly, coastal wetlands are among the most-studied ecosystems in terms of their ES value. They are also among the most valuable on a per hectare basis. The reasons why are detailed in other sections of this review. They relate to the position of coastal wetlands at the interface of marine and terrestrial ecosystems with high energy inputs from both sides and the history of human settlement to take advantage of these energy flows.

There have been several earlier reviews on the value of coastal ecosystems, including References 179–181. There is also a new open access database, the Ecosystem Services Valuation Database (ESVD; <https://www.esvd.net>), that contains estimates of the values for a range of ES from more than 900 studies resulting in over 6,700 value estimates. **Table 4** is a summary of the value estimates (in 2017 US\$ ha<sup>-1</sup> year<sup>-1</sup>) from the ESVD for mangroves and salt marshes for a range of ES. As of the search date (May 9, 2023), there were 672 value estimates for mangroves and 150 for salt marshes for a total of 822 estimates. **Table 4** lists the number of estimates and mean, minimum, and maximum values for each of the 20 ES listed in the table. These are compared with equivalent values from a global synthesis by de Groot et al. (182) using an earlier version of the ESVD database. One can see the consistency in the total value estimates of around \$200,000 ha<sup>-1</sup> year<sup>-1</sup> (adjusted to 2017 dollars) as well as substantial differences in some of the categories as new studies are added. Compare this value with the estimate from Costanza et al. (183) of just over \$15,000 ha<sup>-1</sup> year<sup>-1</sup> (adjusted to 2017 dollars) for mangroves and salt marshes. This increase in estimated value is consistent with Costanza and colleagues’ estimation that “as more and better information becomes available we expect the total estimated value to increase” (183, p. 258). As we learn more about the complex connections between ecosystems and human well-being, it is expected that these value estimates will continue to increase and become more nuanced.

It is also clear that more sophisticated data and modeling can be employed to understand and value ES of coastal wetlands. For example, coastal wetlands reduce the damaging effects of tropical cyclones on coastal communities by absorbing storm energy in ways that neither solid land nor open water can (184, 185). The mechanisms involved include decreasing the area of open water (fetch) for wind to form waves; increasing drag on water motion and, hence, the amplitude of a storm surge; reducing direct wind effects on the water surface; and directly absorbing wave energy. Wetland vegetation contributes by decreasing surges and waves and maintaining shallow water depths that have the same effect. Wetlands also reduce flood damages by absorbing floodwaters caused by rain and moderating their effects on built-up areas. But these effects are highly variable in space and time, depending on the interaction of wetland area, storm intensity and frequency, and coastal infrastructure to be protected. Because mangroves are trees, they are better at reducing

Table 4 Estimated values (US\$ ha<sup>-1</sup> year<sup>-1</sup>) for a range of ecosystem services from the ESVD database,<sup>a</sup> compared with estimates from Reference 182<sup>b</sup>

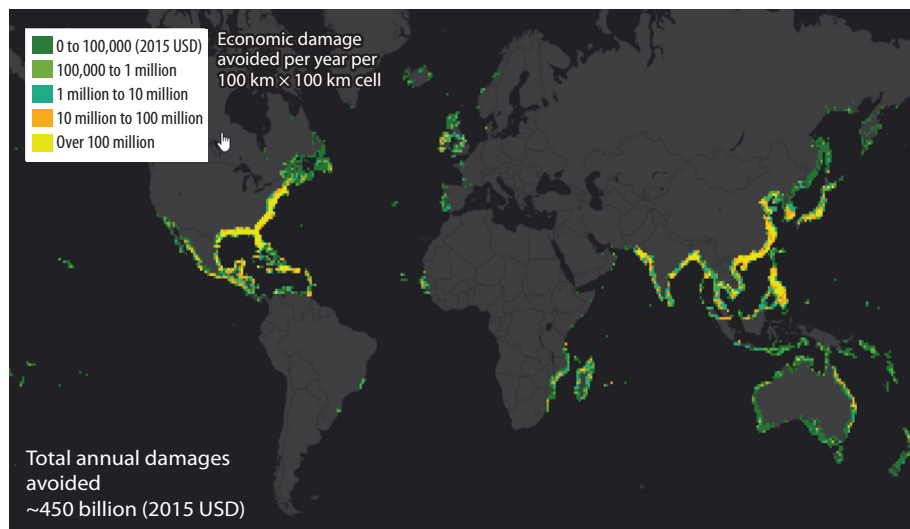
Ecosystem services	Estimates from study of coastal wetlands ES values (182)	Weighted average of mangroves and salt marshes (calculated for this article) <sup>c</sup>	Mangroves			Salt marshes				
			<i>n</i>	Mean	Min	Max	<i>n</i>	Mean	Min	Max
Provisioning services	\$2,998	\$26,132	411	\$33,537			51	\$6,112		
Food	\$1,111	\$20,762	281	\$27,271	\$1	\$4,313,157	32	\$3,165	\$4	\$48,142
Water	\$1,217	\$1,204		\$1,025	\$28	\$4,757	2	\$1,688	\$2	\$3,374
Raw materials	\$348	\$4,112	127	\$5,171	\$1	\$389,622	16	\$1,248	\$5	\$5,645
Genetic resources	\$10	\$3					1	\$11	\$11	\$11
Medicinal resources	\$301	\$51	3	\$70	\$15	\$173				
Regulating services	\$171,515	\$105,559	151	\$136,515			43	\$21,862		
Air quality regulation		\$1,026	2	\$1,323	\$552	\$2,094	7	\$223	\$2	\$1,238
Climate regulation	\$65	\$14,697	50	\$20,077	\$3	\$880,239	8	\$152	\$54	\$507
Disturbance moderation	\$5,351	\$14,642	39	\$13,372	\$13	\$263,804	7	\$18,076	\$70	\$47,686
Regulation of water flows										
Waste treatment	\$162,125	\$3,991	20	\$4,319	\$1	\$27,827	19	\$3,103	\$51	\$15,658
Erosion prevention	\$3,929	\$68,558	28	\$93,801	\$5	\$2,492,592	2	\$308	\$29	\$587
Nutrient cycling	\$45									
Biological control		\$2,645	12	\$3,623	\$10	\$24,190				
Habitat services	\$17,138	\$5,536	10	\$5,982			5	\$4,331		
Nursery service	\$10,648	\$165					3	\$612	\$19	\$1,739
Genetic diversity	\$6,490	\$5,371	10	\$5,982	\$23	\$46,613	2	\$3,719	\$2,688	\$4,749
Cultural services	\$2,193	\$70,172	100	\$94,706			51	\$3,839		
Aesthetic information		\$15,083	5	\$20,455	\$273	\$120,357	15	\$559	\$10	\$996
Recreation	\$2,193	\$15,103	68	\$19,769	\$1	\$690,831	33	\$2,488	\$2	\$15,658
Inspiration/existence		\$38,897	20	\$53,284	\$1	\$938,814				
Spiritual experience		\$1					1	\$4	\$4	\$4
Cognitive development		\$1,087	7	\$1,198	\$5	\$3,890	2	\$788	\$87	\$1,488
Total economic value	\$193,845	\$207,399	672	\$270,740			150	\$36,144		

<sup>a</sup> See <https://www.esvd.net>.

<sup>b</sup> Values from Reference 182 are in 2007 US dollars; values calculated for this article are in 2017 US dollars.

<sup>c</sup> Assuming a total of 200,250 km<sup>2</sup> of coastal wetlands, with 147,350 km<sup>2</sup> (73%) mangroves and 52,900 km<sup>2</sup> (27%) salt marsh.

<sup>d</sup> Blank cells indicate data not available.



**Figure 4**

Spatial distribution of estimated avoided damages per year by coastal wetlands from tropical cyclones. Estimates were based on the probabilities of particular locations being hit by a tropical cyclone of a given magnitude in a typical year based on historical storm frequency by storm category striking  $100 \times 100$  km pixels. We then applied the results of a statistical model of the relationship of damages to wetland area and gross domestic product (GDP) in the swath of storms, storm strength, and time to each  $100 \times 100$  km pixel globally to produce maps of the value of coastal wetlands for storm protection in terms of property damages avoided for each pixel. Figure adapted with permission from Reference 185.

storm surge than coastal marshes, but there are no simple relationships between storm intensity and the response of coastal wetlands.

In 2008, coastal wetlands in the United States were estimated to provide storm protection services worth \$23 billion year<sup>-1</sup> (184). A more recent global study estimated the global value of coastal wetlands for storm protection services at \$450 billion year<sup>-1</sup> (in 2015 dollars) with 4,600 lives saved annually (185). To make this calculation, the records of more than 1,000 tropical cyclones since 1902 that caused property damage and/or human casualties in 71 countries were mapped and overlaid with coastal wetland maps and built infrastructure maps. The study (185) took advantage of improved storm tracking and better global land-use mapping and damage-assessment databases, along with improved computational capabilities, to model the relationships between coastal wetlands and avoided damages and deaths from tropical cyclones. **Figure 4** is a map of avoided damages provided by coastal wetlands from Reference 185.

The 40 million ha of coastal wetlands in storm-prone areas provided an average of \$11,000 ha<sup>-1</sup> year<sup>-1</sup> in storm damages avoided. This value is fairly consistent with the \$14,800 ha<sup>-1</sup> year<sup>-1</sup> estimate from the ESVD database for disturbance regulation, shown in **Table 4**. Consistent with **Table 4**, the range of values is quite large, but the spatial distribution of these values is much more explicit, as shown in **Figure 4**.

This is just one example of the many studies attempting to understand, quantify, and value coastal wetland ES. There will always be uncertainty about the value of coastal wetland ES. The basic conclusions are that coastal wetlands in their natural state are extremely valuable and that their conservation and restoration significantly benefit both humans and the rest of nature.

## SUMMARY POINTS

1. Humans have benefited from and strongly impacted coastal wetlands.
2. Coastal wetlands are composed of salt marshes, mangroves, and tidal freshwater wetlands. Coastal wetlands are particularly abundant in marine deltas.
3. Coastal migration of coastal wetlands onto uplands is not expected to significantly reduce coastal wetland loss.
4. Climate change (global warming; sea-level rise; frequency of strong tropical cyclones, extreme precipitation events, droughts) can strongly and negatively impact coastal wetlands. In coming decades, sea-level rise rates in many areas are expected to cross thresholds for wetland drowning and loss.
5. Watershed nitrogen loadings are not expected to strongly impact coastal wetland stability.
6. Carbon sequestration (blue carbon) is not expected to significantly reduce climate impacts.
7. The total area of coastal wetlands and the total value of ecosystem goods and services of coastal wetlands are predicted to decline substantially in this century unless climate change is halted.
8. There will always be uncertainty about the value of coastal wetland's ecosystem services. The basic conclusions are that coastal wetlands in their natural state are extremely valuable and that their conservation and restoration significantly benefit both humans and the rest of nature.

## FUTURE ISSUES

1. The accuracy of quantification of the area of coastal wetlands, particularly for nonmangrove cover types, needs to be increased.
2. A better understanding of the trade-offs between coastal retreat and the loss of valuable coastal freshwater wetland and upland ecosystems is necessary.
3. Researchers should advance our understanding of how climate change impacts—both chronic (sea-level rise) and acute (changing storminess)—affect coastal wetlands and determine how to increase the resiliency of coastal wetlands to these changes.
4. Improvements to global land-use mapping and damage-assessment databases are needed to increase understanding of how the value of ecosystem goods and services will change as coastal wetlands adapt to climate change and human impacts.
5. Improved quantification of all positive and negative pathways of coastal blue carbon sequestration balanced against wetland net ecosystem production is needed, especially with regard to how climate change and human impacts will affect wetland land loss and the oxidation and release to the atmosphere of previous blue carbon stores.
6. Researchers should advance our understanding of how humans can coexist more sustainability with coastal wetlands.
7. Improved modeling and valuation of coastal wetlands' ecosystem services and the costs and benefits of coastal wetland conservation and restoration are important.



## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

## AUTHOR CONTRIBUTIONS

Author contributions to the efforts of this review are as follows: J.D. led the completion of the manuscript and was in charge of overall organization and conceptualization. All authors contributed to the Introduction and development of the article. The section titled Humans and Coasts was written by J.G. and J.D. Composition of Coastal Wetlands was written by J.V., T.S., and D.E. Global Distribution and Area was written by A.R., Ja.S., E.A, D.E., and R.T. Coastal Retreat and Transformation was written by M.O. Climate Change was written by J.D., M.M., and Ja.S. Physiological Basis for Nitrogen Regulation was written by J.M. and T.Q. Coastal Blue Carbon was written by C.H., J.R., and J.R.W. Value of Coastal Wetlands was written by R.C. Efforts by Je.S. included article organization, logistics, and literature review.

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