Eco-DAS VIII
Symposium Proceedings

Eco-DAS VIII Chapter 5, 2010, 67-92

A complex-systems approach to predicting effects of sea level rise and nitrogen loading on nitrogen cycling in coastal wetland ecosystems

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Abstract

To effectively manage coastal ecosystems, we need an improved understanding of how tidal marsh ecosystem services will respond to sea-level rise and increased nitrogen (N) loading to coastal areas. Here we review existing literature to better understand how these interacting perturbations will likely impact N removal by tidal marshes. We propose that the key factors controlling long-term changes in N removal are plant-community changes, soil accretion rates, surface-subsurface flow paths, marsh geomorphology, microbial communities, and substrates for microbial reactions. Feedbacks affecting relative elevations and sediment accretion rates will serve as dominant controls on future N removal throughout the marsh. Given marsh persistence, we hypothesize that the processes dominating N removal will vary laterally across the marsh and longitudinally along the estuarine gradient. In salt marsh interiors, where nitrate reduction rates are often limited by delivery of nitrate to bacterial communities, reductions in groundwater discharge due to sea level rise may trigger a net reduction in N removal. In freshwater marshes, we expect a decrease in N removal efficiency due to increased sulfide concentrations. Sulfide encroachment will increase the relative importance of dissimilatory nitrate reduction to ammonium and lead to greater bacterial nitrogen immobilization, ultimately resulting in an ecosystem that retains more N and is less effective at permanent N removal from the watershed. In contrast, we predict that sea-level–driven expansion of the tidal creek network and the degree of surface-subsurface exchange flux through tidal creek banks will result in greater N-removal efficiency from these locations.

1. Introduction

1A. Coastal wetlands in a changing world—Coastal wetlands reside at a critical interface between land and sea, where they retain and transform nutrients, perform water purification functions, and support productivity that sustains fisheries. These ecosystem services, and several others, are important for growing human populations that are concentrated along coastlines (Craft et al. 2009). Given the small amount of land they cover, these wetlands are disproportionately valuable in terms of services they perform (Costanza et al. 1997), as well as disproportionately vulnerable to anthropogenic alterations, including the effects of sea level rise (SLR) and increased nitrogen (N) loading.

Human-induced SLR resulting from global warming threatens the long-term persistence of coastal wetlands. Urban development and hydrological alterations of coastlines worldwide have limited the ability of wetland ecosystems to retreat from

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ACKNOWLEDGMENTS

This synthesis would not have been possible without the Ecological Dissertations in the Aquatic Sciences (Eco-DAS) program under the leadership of Paul Kemp. Eco-DAS funding is provided by the National Science Foundation with contributions from the Office of Naval Research (ONR), National Oceanic and Atmospheric Administration (NOAA), and National Aeronautics and Space Administration (NASA). Eco-DAS is sponsored by the Center for Microbial Oceanography: Research and Education (C-MORE), the University of Hawaii School of Ocean and Earth Science and Technology (SOEST) and the Department of Oceanography, and the American Society of Limnology and Oceanography (ASLO). The authors additionally thank the US Geological Survey (USGS) National Research Program, the USGS Mendenhall Fellowship Program (SM), and a Woods Hole Oceanographic Institution Postdoctoral Scholar Fellowship (AES) for funding support. Three anonymous referees and Tamara Harms provided helpful suggestions that have greatly improved this paper.

Publication was supported by NSF award OCE0812838 to P.F. Kemp
ISBN: 978-0-9845591-1-4, DOI: 10.4319/ecodas.2010.978-0-9845591-1-4.67

the advancing sea (Fitzgerald et al. 2008). Furthermore, these ecosystems are currently subjected to more immediate alterations, such as increased N loading due to agriculture or urbanization. Water quality issues due to N loading affect both the structural and functional value to humans of coastal wetland ecosystems. Thus, our objective is to lay a foundation for better understanding of the interactions of multiple anthropogenic drivers (SLR and N loading) on wetland ecosystem functions (e.g., N cycling). We argue that to understand the complex, nonlinear effects of global changes such as SLR and N loading, scientists need to take a multifaceted approach that considers hydrologic, microbial, and plant community interactions.

Climate change most directly impacts tidal marshes through SLR. Human activities have accelerated SLR through an increase in the thermal expansion of the oceans from higher global air temperatures (Wigley 2005). Although thermal expansion is the leading cause of SLR, increased melting of continental ice sheets has also contributed (Shepherd and Wingham 2007). Based on International Panel on Climate Change (IPCC) temperature projections (IPCC 2007), current models project a 75- to 190-cm range in SLR for the period from 1990 to 2100 (Vermeer and Rahmstorf 2009). One of the most publicly visible implications is the predicted submergence of coastal areas, e.g., the Mississippi Delta (Blum and Roberts 2009). Although the degree of coastal inundation due to SLR will depend on many factors, it is clear that SLR has many potential negative effects including: (1) increasing erosion, (2) enhancing storm surges, (3) changing surface and groundwater quality, and (4) losing ecosystem services associated with these vulnerable wetlands.

N loading is changing along with sea level. Human activities have substantially and directly altered the N cycle by effectively doubling the amount of reactive N in the environment (Vitousek et al. 1997; Galloway et al. 2008). The impacts of N loading are particularly problematic in coastal zones, where nitrate (NO_3^-) has been found to stimulate harmful algal blooms, formation of anoxic zones, and a loss of biotic life. Increasing N availability stimulates biomass production; subsequent decomposition by oxygen-consuming microbes in turn creates low O_2 zones called "dead zones." More than 400 dead zones have recently been documented along coasts worldwide, particularly in areas of high human population density (Diaz and Rosenberg 2008). Wetland microbial and plant communities actively use and transform NO_3^-, potentially mitigating the effects of N loading to downstream ecosystems. Despite increased loading via anthropogenic sources, N remains the limiting nutrient in many coastal wetlands, and thus, N loading impacts the productivity and composition of wetland plant communities as they face SLRs.

Given the importance of tidal marshes for coastal water quality and coastal ecology, it is imperative that the dual threat of SLR and N loading on marsh ecosystem services be rigorously evaluated so that management strategies can be adjusted to minimize adverse impacts. We argue that these potential impacts can be fully understood only through a holistic, complex-systems approach that accounts for the feedbacks and interactions that occur across multiple levels of organization in tidal marshes (e.g., microbes, plants, hydrology). As we will show, these feedbacks will either exacerbate (e.g., positive feedbacks) or ameliorate (e.g., negative feedbacks) the ultimate impact of SLR on N cycling. A complex-systems approach equips us to address several challenging realities: (1) that these perturbations operate on different temporal and spatial scales, with SLR occurring more slowly and over longer time scales in many cases than N loading, and (2) that N cycling is mediated across multiple levels of organization by combinations of microbial, plant, and landscape processes. Although we focus on SLR and N loading, our complex-systems approach is relevant to numerous simultaneous changes facing wetlands, including altered hydrology (Portnoy 1999) and sedimentation, increased CO_2, and shifts in species composition due to invasive species (Levin et al. 2006).

In this synthesis we first review the literature on biotic and abiotic controls on N cycling in tidal marshes and discuss the proximal effects of SLR and N loading on each of these controls. Then, we present a new conceptual model of how SLR is likely to affect interactions and feedbacks between drivers of N cycling and the marsh's overall capacity to remove reactive N from efflux to coastal systems. Finally, in summarizing how interactions across ecosystem components are important for predicting responses of fresh and marine wetlands to SLR and N loading, we will offer future directions for research that can better embrace the complexity and multiple-scale dynamics of these valuable but vulnerable ecosystems.

1B. Overview of coastal marsh landscapes: Hydrology, geomorphology, and biology—Tidal marshes are found in coastal locations throughout the world, where different combinations of temperature, underlying geology, geomorphology of the coastline, and large-scale distribution of particular plant species present challenges for generalization. However, it is widely recognized that these diverse marshes each feature discrete functional units that are dominated by a distinct set of processes that are globally consistent (Fig. 1). We do not attempt to generalize to the species level in this article, but instead focus on N cycling processes occurring within these functional units, further described below.

Tidal marshes occupy a gradient of elevations along the estuarine wedge, which is also characterized by a gradient in local water depth, salinity, and other seawater constituents such as sulfate (SO_4^{2-}). Tidal salt marshes occupy lowest elevations along that gradient and are colonized by a low-diversity but highly productive assemblage of salt-tolerant macrophytes such as *Spartina alterniflora*. Higher-elevation salt marshes are less productive and are often more diverse but may be dominated by *Spartina patens* or *Distichlis spicata*. In general, as elevations increase landward and salinities decrease, macrophyte diversity tends to increase, while productivity declines (Tiner and Burke 1995; Donnelly and Bertness 2001; Fitzgerald et al. 2006; Fitzger-

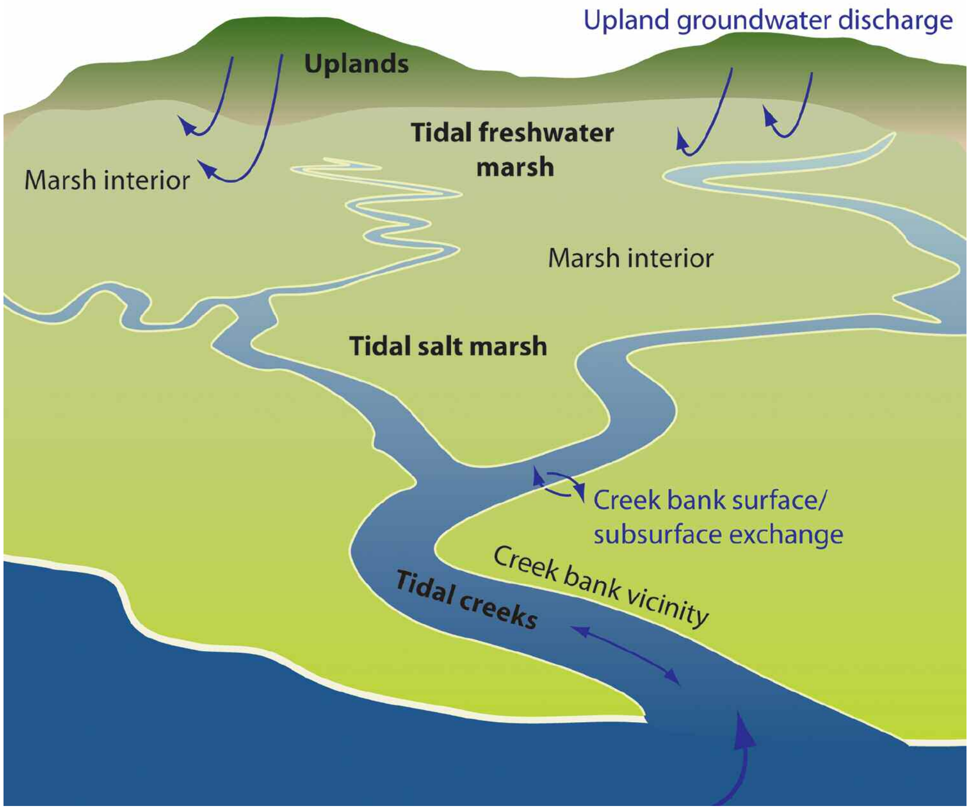

Fig. 1. Schematic diagram of portions of a tidal marsh that are likely to respond differently to SLR and N loading due to the different feedback processes that are dominant in these locations. Blue arrows show major hydrologic pathways associated with fluxes and transformations of N.

ald et al. 2008). Local water depths are typically regarded as a primary control on the zonation and succession of tidal marsh plants (Odum 1988; Silvestri et al. 2004; D'Alpaos et al. 2006), although salinity plays a dominant role in limiting the colonization and growth of freshwater species (Pennings et al. 2005). Microbial community compositions also vary systematically along the salinity gradient, as described in section 2B. Increased salinities generally result in an overall reduction in the diversity of N-cycling communities (Santoro 2010), although the mechanisms behind this pattern are poorly understood.

Seaward-to-landward declines in the amplitude of tidal fluctuations in surface-water depths constitute the dominant hydrologic change for tidal marshes along the estuarine gradient. Many marshes experience asymmetry in tidally induced hydrologic fluctuations, but these features tend to be site specific (French 2006). The sloping of water tables from uplands to the coastal zone causes many marshes to be regions of groundwater discharge (Harvey and Odum 1990; Tobias et al. 2001a; Tobias et al. 2001c). This groundwater discharge occurs along the estuarine gradient and also tends to be site specific, governed by the regional distribution of hydraulic head.

Processes governing N cycling in tidal marshes also vary in the direction parallel to the coast. A network of tidal creeks subdivides the marsh along this direction, and processes dominating N cycling in tidal creeks differ from those along the creek bank and vicinity of creek banks, which differ from those in the marsh interior. Although creek channels are unvegetated, some of the most productive vegetation in tidal marshes colonizes the creek banks, which may sometimes develop small levees. Less productive vegetation colonizes the marsh interior. The higher productivity of vegetation along creek banks is linked to the hydrology specific to this region (Wiegert et al. 1983). The interface between tidal marshes and tidal channels is a zone of strong gradients in hydraulic head, where bi-directional exchange between groundwater and surface water occurs (Harvey et al. 1987; Wilson and Gardner 2006). During the flooding portion of the tidal cycle, water from the tidal creeks moves over the banks toward the marsh interior. This water infiltrates the marsh surface, and then during ebb tide drains from the creek banks into the creek as seepage from porewater (Gardner and Wilson 2006; Wilson and Gardner 2006). Consequently, tidal creek banks are among the most aerated, best flushed portions of the marsh. Bidirectional exchange of surface water, porewater, and associated solutes also occurs to some extent in the marsh interior, where transpiration by macrophytes removes water from the subsurface, inducing infiltration of surface water (Moore et al. 1997).

1C. Overview of N cycling in tidal marshes—N cycling in coastal wetlands reflects collective activities of diverse microbial communities and the vascular plants with which they interact. N sources to wetlands include inputs from the atmosphere, surface water runoff, groundwater, and tides. In both marine and fresh tidal wetlands, bacteria convert N_2 gas to biologically available N (NH_3) through N fixation in plant rhizospheres (roots and surrounding sediments), plant shoots, and sediment surfaces. Plant rhizospheres are also hotspots for microbial activities involved in nitrification, the oxidation of ammonia to nitrite (NO_2^-) and nitrate (NO_3^-) (Bodelier et al. 1996, reviewed in Herbert 1999), as this process requires oxygen that is introduced by plant roots in otherwise mostly anaerobic sediments. The microniches formed by such oxygen gradients around plant roots (Duarte et al. 2005; Lovell 2005) or macrofaunal burrows (Kristensen and Kostka 2005) enhance microbial activities and N cycling rates. This is due to intimate coupling that often occurs in coastal ecosystems between aerobic nitrification and anaerobic denitrification (Jenkins and Kemp 1984; Herbert 1999), the latter of which converts biologically available forms of N (NO_3^-) to the biologically unavailable gaseous N_2 or N_2O. In respiratory denitrification, NO_3^- is used by microbes in the terminal oxidation of organic matter under anaerobic conditions; most of the NO_3^- is transformed to N_2, although incomplete reduction can result in the accumulation of intermediates including NO_2^- and N_2O (a potent greenhouse gas). Denitrification is not always coupled to nitrification, particularly in environments with high nitrate availability (Smith et al. 2009). Favorable conditions for respiratory denitrification include anoxia and high NO_3^- and labile organic carbon concentrations (Robertson and Groffman 2007). Alternatively, NO_3^- can be transformed to ammonium (NH_4^+) via microbes in a process called dissimilatory nitrate reduction to ammonium (DNRA).

Although denitrification has been intensively examined, relatively few studies have investigated the ecological controls on other processes that may be important for overall NO_3^- removal in wetlands (Megonigal et al. 2004; Burgin and Hamilton 2007). In contrast to denitrification, DNRA is a relatively understudied. Two forms of DNRA are known to occur: fermentative DNRA, thought to occur under conditions of high labile organic carbon (OC) availability (Tiedje 1988), and sulfur-driven DNRA (Brunet and Garcia-Gil 1996; Otte et al. 1999), thought to occur where sulfur oxidizing bacteria have access to NO_3^-. Fermentative DNRA couples electron flow from organic matter via fermentation reactions to the reduction of NO_3^- (Tiedje 1988; Megonigal et al. 2004). Sulfur-driven DNRA couples the oxidation of elemental S and H_2S to the reduction of NO_3^- to NH_4^+. While there are a number of studies documenting DNRA in wetlands (Tobias et al. 2001b; Matheson et al. 2002; Revsbech et al. 2005, Scott et al. 2008), very few investigators have discerned which form of DNRA occurs, and thus we know little about the controls on the process at the ecosystem scale.

Anaerobic ammonium oxidation (anammox) is another understudied N-removal pathway carried out by autotrophic microorganisms, which oxidize NH_4^+ using NO_2^- as an electron acceptor. Anammox organisms grow very slowly (Jetten 2001) and are thought to be out-competed by denitrifying microorganisms when there is ample organic carbon (Dalsgaard et al. 2005). Anammox is often reported as a percentage of the N_2 production, with the balance often assumed to be due to denitrification. An alternative is to report each N cycling process as a fraction of the overall NO_3^-/NO_2^- reduction; when reported in this mass-balance way, N_2 production frequently does not account for all of the NO_3^- removal (Seitzinger et al. 2006; Mulholland et al. 2008). Thus, given that the fraction of N_2 production attributable to anammox is often 1% to 20%, anammox is not currently thought to represent a significant N-removal pathway in coastal wetlands (Risgaard-Petersen et al. 2004, Trimmer et al. 2006; Rich et al. 2008; Dong et al. 2009; Koop-Jakobsen and Giblin 2009). However, it should be noted that anammox is not an extensively measured process, making it difficult to speculate on its importance or integrate it into any synthetic overview, as is our goal here. When denitrification, DNRA, and anammox are measured simultaneously (rare), anammox is consistently the least significant flux (Dong et al. 2009; Gardner and McCarthy 2009; Koop-Jakobsen and Giblin 2009).

As water rich in NO_3^- passes through or over wetland sediments, the NO_3^- concentration typically decreases. To date, N removal is thought to be due to either assimilation into microbial, algal, or plant biomass, or to conversion to N_2 via denitrification. However, recent research has underscored the complexity of microbially driven N biogeochemistry, especially with regard to factors that control the relative importance of these multiple pathways (Brandes et al. 2007; Burgin 2007). A suite of these controlling factors may vary with SLR, including redox potential (related to the degree of inundation), salinity, availability of free dissolved sulfide (hereafter referred to as H_2S), NO_3^-, and organic carbon (OC), which are all potential controls on many N-cycling processes (Tiedje et al. 1982; Tiedje 1988; Joye and Hollibaugh 1995; Brunet and Garcia-Gil 1996). In section 2B we discuss several processes in the N cycle likely to be affected by these changes, as well as how the associated microbial communities are likely to change.

2. SLR and nitrogen loading on wetlands: Direct impacts

Effects of SLR can be parsed into effects resulting from higher water levels (i.e., increased inundation, decreased oxygen transfer to sediments) and those resulting from exposure of marsh ecosystems to higher salinities and higher concentrations of solutes in seawater, such as SO_4^{2-}. In this section we examine the direct impacts of N loading and each of these stressors on the physical environment, plant communities, and microbial ecology.

2A. Effects on the physical environment—Effects on water level/inundation frequency: SLR impacts both groundwater and surface-water hydrology by changing the distribution of water levels and hydraulic head. In surface water, the immediate effect of SLR is an increase in water level over tidal marshes. To first order, the overall aerial extent of tidal marshes is expected to decline from this increased inundation, with many salt marshes converting to open water areas (Craft 2007) and brackish marshes replacing many tidal freshwater marshes (Craft et al. 2009). However, because of feedback between water level and sediment accretion (see section 3A), it is inappropriate to estimate the extent of SLR-driven marsh loss simply by comparing current topography and SLR predictions (Kirwan and Guntenspergen 2009). As a result of this feedback, some marshes may not experience long-term changes in water depth (French 2006). Still, although many marshes exhibit vertical accretion rates that equal SLR rates, they remain prone to loss of coverage through lateral expansion of the tidal channel network (Williams and Hamilton 1995; Hartig et al. 2002; Van der Wal and Pye 2004). Modeling results (Kirwan et al. 2008) suggest that this expansion can be in part due to localized and temporary disturbance of vegetation, e.g., by crab burrowing (Hughes et al. 2009), at the creek heads. Exposed, unvegetated sediment may be submersed below the threshold for vegetation colonization under accelerated SLR, converting these disturbed patches permanently to open water.

Effects on surface water/groundwater exchange: In groundwater, the increase in sea level will often result in a decrease in coastal hydraulic head gradients, which can cause a reduction in the volume of groundwater discharge to tidal marshes (Tobias et al. 2001a). This effect can be exacerbated by an increased fraction of upland runoff at the expense of infiltration, due to higher water tables in the near-coastal zone that also result from SLR (Nuttle and Portnoy 1992). Upland groundwater is typically high in NO_3^- from anthropogenic sources. Under climate-change scenarios, the N load that would be delivered to tidal marshes as groundwater discharge may instead be delivered to the subtidal zone (Tobias et al. 2001a). As a result of diminished freshwater flushing by groundwater discharge, marsh interiors could experience a salinity buildup (Tobias et al. 2001a). Enhanced evapotranspiration resulting from the higher temperatures expected to accompany global change may partially counteract this effect by enhancing bidirectional exchange between tidal surface water and marsh porewater (see Moore et al. 1997).

The level and duration of inundation also exerts a strong control on flow paths and groundwater residence times in the vicinity of tidal creeks. Flow paths and residence times are longer with greater inundation, and the total flushing of water through creek banks is larger (Wilson and Gardner 2006). Because the total creek/marsh interface length is expected to increase under SLR (Kirwan and Murray 2007; Kirwan et al. 2008), the magnitude of surface-subsurface exchange through creek banks will likely increase both on a per-unit-area basis and on a total basis. This enhanced tidal flushing will locally deliver additional solutes and nutrients to shallow porewater (Harvey et al. 1987; Wilson and Gardner 2006).

Effects on mean surface-water velocities and turbulence: In open-water environments, changes in water level are directly and positively correlated to changes in flow velocities, turbulence intensities, and bed shear stress (Middleton and Wilcock 1994). Sediment entrainment is positively related to the excess bed shear stress (i.e., the stress above an entrainment threshold) (Knighton 1998), so it follows that increased water levels will be associated with enhanced sediment erosion at marsh/open water interfaces (e.g., Boorman et al. 2001). In addition, the inundation of low marshes or breaching of barrier islands by SLR results in a longer fetch for waves and greater erosion further inland (Fitzgerald et al. 2008).

In the marsh interior water depth has less of an effect on mean velocities and turbulence intensity. When emergent vegetation is present, the influence of the bed on flow velocity diminishes within several centimeters of the soil-water interface (Nepf 1999), and flow is instead dominated by vegetative drag. In emergent vegetation, vegetative drag increases proportional to water levels (Harvey et al. 2009; Larsen et al. 2009b), so SLR would be expected to have minimal effect on velocity. Only very rarely are bed shear stresses in dense emergent marsh sufficient to suspend sediment (Stevenson et al. 1985; Christiansen et al. 2000; Larsen and Harvey 2010). However, in low-density vegetation, where stems do not limit eddy development, turbulent wakes form in the lee of stems (Nepf 1999). Thus, in sparsely vegetated marsh environments (e.g., hypersaline *Sarcocornia/Suaeda* marsh), found in the lowest, fluvially dominated portions of the estuarine gradient (Snedaker 1995; Bertness and Ewanchuk 2002), SLR may enhance turbulence and erosion.

In tidal channels enhanced erosion will cause a similar enhancement in sediment deposition at the vicinity of the channel/marsh interface. Higher turbulence and higher bed shear stresses will also result in greater entrainment of relatively coarse, dense inorganic sediment that will settle rapidly relative to fine-grained and organic particles (Larsen et al. 2009a) and deposit over a wider area around tidal channels and the marsh front (Christiansen et al. 2000). This mineral sediment augments local soil elevations and provides a source of iron and manganese to marsh communities, enhancing the precipitation of sulfide metals, thereby decreasing dissolved H_2S and the resulting stress on macrophytes (King et al. 1982). In addition, nutrients sorbed to fine mineral sediment (e.g., phosphorus) may provide limiting substances to primary producers and decomposers (Slocum et al. 2005).

Effects of increased salinities: Increased salinities that result from SLR enhance flocculation of both inorganic and organic material (Winterwerp and van Kesteren 2004). Flocculated sediments have been described as "suspended biofilms" that can provide a source of labile carbon and nutrients and serve as a substrate for a variety of microbial reactions (Liss et al. 1996). Flocculation is further enhanced by intermediate levels of turbulence, which promote the collision and aggregation of particles without causing particle shearing (Winterwerp and van Kesteren 2004; Larsen et al. 2009c). Although enhanced levels of turbulence near the marsh front may induce the breakup of flocs, the net effect of SLR will likely be an enhancement of the degree of flocculation, due to the expansion of the relatively low-turbulence tidal channel network. By increasing settling velocities and particle mass, flocculation would decrease the distance within the marsh over which allocthonous fine particles and associated constituents are distributed.

2B. Effects on microbial biogeochemistry—Effects of increased SO_4^{2-}: Increases in SO_4^{2-} concentrations in coastal wetlands due to SLR may shift tidal freshwater wetlands from being net methanogenic to SO_4^{2-} reducing ecosystems. SO_4^{2-} reduction produces reduced sulfur compounds, including H_2S, which has significant effects on all processes in the N cycle. Along redox transitions in stratified water columns and sediments, nitrification and NO_2^- and NO_3^-reduction are tightly coupled in space, with nitrification supplying NO_2^- for anammox (Lam et al. 2007) or the NO_3^- needed for denitrification (Seitzinger 1988; Seitzinger et al. 2006). Nitrification is inhibited by low (60-100 µM) H_2S concentrations (Joye and Hollibaugh 1995). Thus, the presence of increasing amounts of H_2S may uncouple these processes, potentially altering the microbial consortia that perform them (Joye and Hollibaugh 1995). Although H_2S has been shown to impact nitrification, other work in coastal systems has found that nitrification rates are unrelated to H_2S concentrations, (Caffrey et al. 2003) and that the presence of Fe(III)-containing minerals such as ferrihydrite can relieve sulfide inhibition of nitrification (Dollhopf et al. 2005), suggesting a complex interplay between the N cycle and other geochemical cycles in coastal sediments.

Just as H_2S can have significant effects on nitrification, sulfur availability influences NO_3^- reduction processes as well. H_2S is toxic to many sensitive biomolecules (e.g., enzymes); high ambient H_2S can inhibit the final two reductases (Sorensen 1978) of the denitrification sequence, thereby shunting the denitrification sequence over to an alternative process, such as DNRA (Brunet and Garcia-Gil 1996; Senga et al. 2006). In addition to the microcosm and lab culture evidence for H_2S affecting a shift to DNRA, ecosystem-level measurements also suggest increased DNRA under higher sulfide conditions (Gardner et al. 2006). However, H_2S may also serve as an electron donor in a chemolithoautotrophic form of denitrification, in which case the H_2S can be oxidized to elemental S or SO_4^{2-} with a simultaneous reduction of NO_3^- to N_2 (and possibly NH_4^+). Increasing H_2S enhances denitrification in environments with high chemolithoautotrophic S-driven denitrification (Burgin et al., unpubl. data). Thus, the effects of H_2S on denitrification are nonlinear and may vary considerably between environments. It is likely that at sufficiently low concentrations, H_2S may enhance denitrification; however, once it reaches toxic levels, it may inhibit key enzymes, allowing alternative processes to be favored (Senga et al. 2006). On the other hand, metal-bound sulfides such as FeS also can be oxidized by these bacteria but do not show the enzymatic inhibition of denitrification (Brunet and Garcia-Gil 1996), and these often are abundant in sediments (Holmer and Storkholm 2001). Anammox, too, is sensitive to high sulfide concentrations, as has been documented in hypolimnetic Baltic Sea waters (Jensen et al. 2008). However, there is little information about how sediment anammox responds to increased H_2S concentrations. In the Thames estuary, anammox rates decreased along the length of the estuary, which the authors attributed to an increase in sulfide concentrations (Trimmer et al. 2003). However, many parameters covary along the gradient, making it difficult to separate the effects of H_2S from changes in organic matter and salinity.

Effects of increased salinity: Of the different N-cycling microbial communities, we know the most about how nitrifiers change along salinity gradients. Nitrifiers have shown distinct community composition along salinity gradients in diverse estuarine environments including large estuaries such as San Francisco Bay, USA, (Mosier and Francis 2008) and Chesapeake Bay, USA, (Francis et al. 2003), smaller estuaries such as Plum Island Sound, Massachusetts, USA, (Bernhard et al. 2005), New England, USA, salt marshes (Moin et al. 2009), and the coastal subsurface (Santoro et al. 2008). In all the aforementioned cases, overall genetic richness of the nitrifer community was lowest at the highest salinity sites, suggesting that increased sea level will result in reduced nitrifier diversity where marshes cannot trangress landward. When observed as a function of salinity, nitrification rates have shown a variety of responses. In sediments of the Scheldt estuary, Netherlands, (Andersson et al. 2006) as well as in a survey of nine North American estuaries (Caffrey et al. 2007), increased salinity decreased nitrification rates. Other estuarine studies have found the highest nitrification rates at intermediate salinities including Plum Island Sound (Bernhard et al. 2007) and the Douro River estuary in Portugal (Magalhaes et al. 2005). Increased salinity results in a greater efflux of NH_4^+ from sedimentary environments (Rysgaard et al. 1999), further suggesting a potential decrease in nitrification rates.

The impact of salinity on N fixation, denitrifying, and anammox microbial communities is even less clear (reviewed in Santoro 2010). Few studies have examined relationships of salinity to N fixation, but mesocosm manipulations of salinity within the range of 0.2 to 4 ppt found no effect on N fixation rates of cyanobacterial mats from oligotrophic Carribean marshes (Rejmankova and Komarkova 2005). A laboratory experiment testing sediments of the Pawcatuck River estuary in Rhode Island, USA, found no effect of salinity on denitrification rates (Nowicki 1994). In sediments from the Randers Fjord estuary, Denmark, denitrification decreased as salinity was experimentally increased from 0 to 10 psu, but further increases showed no impact (Rysgaard et al. 1999). In terms of the microbial community, diversity of denitrifiers has been shown to be highest at intermediate salinities (Santoro et al. 2006) in the coastal subsurface, but greatest at low salinities in the Chesapeake Bay (Bulow et al. 2008). Alhough studies of the response of anammox and DNRA organisms to increased salinity are few, two studies have shown decreased rates of anammox along increasing salinity gradients (Trimmer et al. 2003; Rich et al. 2008). A recent study in the Cape Fear River estuary (North Carolina, USA), however, found an increased richness of anammox organisms along an increasing salinity gradient (Dale et al. 2009). A lower abundance of *nrfA* genes, a marker for DNRA organisms, was found at higher salinities in the Colne River estuary, UK (Smith et al. 2007).

Because so many environmental factors covary in estuarine systems, several laboratory experiments have attempted to directly test the effect of increased salinity on multiple N-cycling processes. Laboratory experiments offer the advantage of controlling for the effects of other variables to isolate the effects of salinity on microbial communities and geochemical rates. For example, Weston et al. (2006) incubated freshwater river sediments from the Altahama River (Georgia, USA) for 1 month with artificial saline media. The saline treated cores had decreased methanogenesis, increased sulfate reduction, and decreased denitrification activity compared to controls. Overall carbon mineralization rates were also higher in the salinity treatment, suggesting that as freshwater marshes become more saline, N-removal capacity may be reduced and become a net source of NH_4^+. Similar predictions arise from the results of an experimental manipulation carried out with lake sediments from the Netherlands (Laverman et al. 2007). In these experiments using flow-through reactions and a salinity increase to 10 psu, the investigators observed an increase in DNRA of 35 nmol cm^{-3} h^{-1} relative to freshwater controls. Denitrification was not significantly affected by salinity and accounted for approximately 50% of the NO_3^- removal in both the salinity amended cores and the freshwater cores.

Effects of increased inundation: An important effect of increased tidal marsh inundation will be decreased porewater oxygen concentrations. As estuaries transition to anoxia, a respiratory succession occurs in the microbial community as electron acceptors are used up in the order of their thermodynamic favorability: magnesium (Mn) (IV), iron (Fe) (III), NO_3^-, and finally SO_4^-. However, a study in the Chesapeake Bay found that the microbial community did not shift until SO_4^- metabolisms began to dominate (Crump et al. 2007).

Because all processes in the N cycle are redox dependent, the transition to increasing anoxia associated with SLR is likely to shift both the rates and microbial communities associated with all aspects of the N cycle. Nitrification, by definition an aerobic process, is likely to be affected the most. However, nitrification at relatively low oxygen concentrations has been documented in wastewater treatment plants (Park and Noguera 2004). It has been suggested that the ammonia-oxidizing archaea, a group only recently discovered to carry out nitrification (Koenneke et al. 2005), might be low-oxygen specialists carrying out ammonia oxidation in environments where oxygen is too low for nitrifying bacteria (Lam et al. 2007; Santoro et al. 2008). New discoveries about dynamics of the N cycle in low oxygen conditions are still occurring (Lam et al. 2009); thus, the precise dynamics of how the N cycling community will change in response to reduced oxygen conditions is difficult to predict. Responses of microbes to SLR are mediated by landscape dynamics (section 2A) and plant communities (section 2C), the interactions of which are considered in further detail below (section 3).

Effects of N loading: When limited by N, microbial communities will respond to an increase in N concentrations with shifts in species composition and an increase in productivity under N-loading conditions (Howarth and Hobbie 1982; Morris and Bradley 1999). However, tidal marsh microbial communities are often limited by the supply of labile OC. Although refractory detrital OC is readily available in marshes, labile OC from benthic microalgae is often the primary source of carbon for denitrifying bacteria (Boschker et al. 1999; Tobias et al. 2003). Primary production by benthic microalgae is stimulated by N loading, but only when light is not a limiting factor. Thus, in marshes in which bacteria involved in N cycling are limited by carbon, microbial responses to N enrichment may be spatially variable, with the largest increases in bacterial productivity in tidal creek bottoms and sparsely shaded creek banks and little increase in bacterial productivity in the more shaded marsh interior (Deegan et al. 2007). Meanwhile, N enrichment can cause algal species shifts (e.g., more diatoms, less cyanobacteria) that, while increasing the lability of algal carbon, also result in a decrease in the abundance of N-fixing bacteria (Deegan et al. 2007).

2C. Effects on plant communities—A combination of stressors can have a greater impact on tidal marsh plant communities than exposure to a single stress (McKee and Mendelssohn 1989). In tidal marshes, seawater inundation often acts in combination with increased salinity (Flynn et al. 1995) and H_2S (Gribsholt and Kristensen 2003) concentrations. Therefore, the following paragraphs review not only the effect of SLR inundation on plant communities, but also the added impacts of increased H_2S, salinity, and evapotranspiration (ET), along with the interacting stressor of N loading.

Effects of increased inundation: The amplitude of tidal inundation is an important predictor for plant species occurrence in both fresh and marine tidal marshes (Bockelmann et al. 2002). McKee and Patrick (1988) found that the elevation growth range of *Spartina alterniflora* directly increased with an increase in tidal amplitude. Common North American tidal marsh species (e.g., *Juncus gerardi* and *Spartina maritima*) are adapted to the unique hydrologic conditions of aquatic ecosystems. One specific adaptation to increased inundation is the amount of aerenchymous tissue, which facilitates delivery of oxygen to the sediment (Castellanos et al. 1994; Hacker and Bertness 1995). Not all plant species are equally adapted to tolerate flooding; thus, increasing inundation substantially decreases species richness, stem length, and seedling emergence and growth in species such as *Impatiens capensis* and *Pilea pumila* (Baldwin and Mendelssohn 1998; Middleton

1999; Hopfensperger and Engelhardt 2008). Baldwin et al. (2001) found flooding to affect annual species more dramatically than perennials. Increased inundation can also cause a shift in energy allocation by increasing root:shoot ratios in plants (Gribsholt and Kristensen 2003). However, even though plants may produce more roots, there have been conflicting results on whether or not the amount of aerenchymous tissue increases with inundation (Burdick and Mendelssohn 1987; Pearson and Havill 1988).

Water-storage changes in areas with low plant cover are driven by the process of evaporation, while storage in areas with high plant cover is driven by plant transpiration (Gribsholt and Kristensen 2003; Paquette et al. 2004). A positive-feedback relationship exists by which high transpiration rates enhance soil oxidation and enlarge the aerated layer (Hemond and Fifield 1982; Dacey and Howes 1984; Howes et al. 1986), thus creating conditions for plant community development that further loosen the soil and increase ET rates (Ursino et al. 2004; Li et al. 2005). Plant canopy structure can also influence ET rates, whereas transpiration rates are highly correlated with leaf-area index (Hussey and Odum 1992). In tidal freshwater marshes where leaf density is high, transpiration dominates over evaporation; however, in salt marshes where there is lower leaf density, evaporation and transpiration rates are approximately equal (Hussey and Odum 1992). Not only do ET rates influence soil aeration, but ET can indirectly influence soil surface elevation through biomass production and soil compressibility (Paquette et al. 2004). Therefore, a rise in sea level could shift the system to a salt marsh, resulting in decreased transpiration rates and soil aeration. However, the effect of SLR on marsh ET could be countered if the marsh received high N loads at the same time; then biomass, transpiration rates, and soil aeration could all increase.

Effects of increased SO_4^{2-}: An increase in SO_4^{2-} reduction to H_2S, due to increased seawater inundation, has multiple effects on tidal marsh plants. H_2S directly suppresses the activity of enzymes responsible for anaerobic respiration in the roots of wetland plants (Allam and Hollis 1972; Pearson and Havill 1988; Koch et al. 1990). The dramatic decrease in plant respiration causes a direct decrease in growth of roots, shoots, and leaves (Pezeshki et al. 1988; Koch et al. 1990; Armstrong et al. 1996). Growth reduction due to H_2S can limit rhizosphere aeration (Armstrong et al. 1996) and lead to plant death (Wiessner et al. 2007). Increased concentrations of H_2S have also been found to inhibit N uptake and assimilation in a variety of tidal marsh plant species (DeLaune et al. 1984; McKee and Mendelssohn 1989; Koch et al. 1990; Chambers et al. 1998; Wiessner et al. 2008). The synergistic interaction between the effects of increased inundation and H_2S on N uptake and energy production in plants results in a greater response in the plant community compared to when the stressors are isolated (Koch et al. 1990; Webb and Mendelssohn 1996). The inhibition of N uptake due to high H_2S results in higher C/N ratios in plant tissues (Chambers et al. 2002). In addition, decreased plant uptake of N can result in higher porewater NH_4^+ concentrations (Flynn et al. 1995). However, in marshes significantly enriched in N, H_2S inhibition of plant N uptake can be overcome (Portnoy and Giblin 1997). Last, sulfide can also harm plants in aerobic conditions by reducing root respiratory capacity and lowering root energy production (Allam and Hollis 1972; Havill et al. 1985; Pearson and Havill 1988). Thus, once a pulse of salt water brings sulfide into the system, damage to plants will occur whether the system is aerobic or anaerobic.

Although marsh plants are negatively affected by H_2S in many ways, they have several positive- and negative-feedback effects on H_2S concentrations in the sediment. Plant roots release oxygen, creating aerobic microhabitats (Howes et al. 1986; Gribsholt and Kristensen 2003; Choi et al. 2006), which substantially decrease SO_4^{2-} reduction rates (Stribling and Cornwell 2001; Wiessner et al. 2007). Stribling and Cornwell (2001) found a decrease in root oxygen production during plant senescence. However, while plants inhibit SO_4^{2-} reduction through sediment oxidation, they may also facilitate SO_4^{2-} reduction by providing a high carbon load, which fuels the microbial reduction process (Gribsholt and Kristensen 2003; Miley and Kiene 2004; Wiessner et al. 2007). The relative influence of plants on these opposite processes may vary between species and over time. In a *Spartina alterniflora*–dominated salt marsh, Hines et al. (1989) found SO_4^{2-} reduction rates increased in the spring with plant growth and high dissolved organic carbon (DOC) root delivery and then decreased in the fall with a decrease in DOC delivery, whereas reduction generates toxic H_2S. Many of the SO_4^{2-}–reducing bacteria associated with plant roots in salt marshes and seagrass beds also fix N, which is rapidly transferred to plants and is particularly high during seasons of plant growth (Lovell 2002). However, these types of plant-microbe associations can be quite specific (Bagwell et al. 2001), and the general effects of increased H_2S concentrations on these interactions are not well known.

Effects of increased salinity: Increased salinity can have devastating effects on freshwater plants through two direct mechanisms: (1) increased salt concentrations that change the water potential gradient, creating a water deficit in plant tissues, and (2) direct plant uptake of toxic concentrations of sodium and chloride ions (Greenway and Munns 1980; Flynn et al. 1995). Pezeshki et al. (1987) found decreased stomatal conductance and photosynthesis as a consequence of increased salinity. In addition, saline waters can decrease above and belowground plant growth (Portnoy and Valiela 1997; Van Zandt et al. 2003) and species richness (Howard and Mendelssohn 2000) and lead to death (Grace and Ford 1996). A larger scale implication of saltwater intrusion is an increase in abundance of invasive species, particularly those adapted to brackish conditions, such as nonnative *Phragmites australis* in North America (Baldwin and Mendelssohn 1998; Chambers et al. 2003; Packett and Chambers 2006). In marine tidal marshes, from which some of the invasive plants may originate, plant tolerance of saline conditions is linked to N demand, as N-rich compounds such as proline and glycine betaine are thought to be used in osmotic regulation by halophytes (Stewart and Lee 1974; Cavalieri and Huang 1979).

Importantly, both local water depths and salinity are expected to change with SLR. Although many studies have examined the independent effects of local salinity and local water depths on tidal marsh zonation and succession (e.g., Odum 1988; Silvestri et al. 2004; Pennings et al. 2005; D'Alpaos et al. 2006), few studies have examined their joint effect, highlighting a research need.

Effects of N on plant response to SLR: N loading may constrain the responses of plant communities to SLR by favoring above-ground rather than below-ground biomass production (Tyler et al. 2007; Langley et al. 2009). Increases in productivity that occur as a consequence of N loading to an N-limited system (e.g., salt marshes) may not translate into increased organic matter accretion that is required for these wetland ecosystems to maintain elevation, particularly when productivity is altered by shifts in community structures of primary producers as in cases of algal blooms and hypoxia (Havens et al. 2001). In fact, the loss of below-ground biomass accumulation that resulted from a 36-year nutrient experiment in salt marsh plots in Massachusetts, USA caused a negative elevation change in the marsh surface of 1.5 mm yr^{-1} (Turner et al. 2009). N loading may also shift competitive interactions between macrophytes in a way that favors the rapid spread of invasive species (Tyler et al. 2007).

3. Effects of SLR and N loading on wetlands: hypotheses from a complex-systems approach

Predicting the manner in which SLR will affect the transformations, residence times, and ultimate fate of N in tidal marshes is complex due to the involvement of several driving variables (e.g., water depth, dissolved oxygen, microbial activities, macrophyte abundance and root density, hydrologic retention times, DOC and N supply) and multiple feedback loops in tidal marsh N cycling (Figs. 2-5). Even the effects of SLR on marsh ecosystem structure—the first-order control on marsh ecosystem function—are complex. We begin this section by examining the feedbacks governing tidal marsh elevation relative to sea level and hence ecosystem structure. Second, we examine the feedbacks that control the efficiency of that marsh structure in transforming N. This "efficiency" will differ between marsh locations along and across the estuarine gradient (Fig. 1). We predict responses that key regions are likely to exhibit from the interacting perturbations of SLR and N loading: interior of salt or brackish marshes (section 3B), tidal creeks (section 3C), and tidal freshwater marshes (section 3D). We also examine in detail the hypothesized feedbacks that likely influence N cycling efficiency in those regions.

3A. Biophysical feedbacks on marsh elevation—Autochthonous processes (peat accretion): Organic sediments are deposited autochthonously when the rate of organic matter production exceeds that of decomposition. With other environmental factors held constant, autochthonous sediment accretion in a given vegetation community exhibits a humped response to local water depths, with an optimum water depth for accretion (Morris et al. 2002; Larsen et al. 2007). At depths that exceed the optimum, plant community productivity is limited by anaerobic stress, whereas at depths shallower than the optimum, productivity is limited by soil salinization stress (Phleger 1971; Morris et al. 2002), and/or more aerobic redox potentials make decomposition more efficient (Brinson et al. 1981; DeBusk and Reddy 1998). Because they are more productive, low marsh communities often have larger autochthonous peat accretion rates than high marsh communities (Fitzgerald et al. 2008). However, other interacting factors (e.g., soil or water chemistry, specific vegetation community composition) may also contribute to local variability in autochthonous sediment accretion rates and could overwhelm the influence of local water depth (Stribling et al. 2007; Kirwan and Murray 2008; Turner et al. 2009).

Because of organic matter production and decomposition dynamics (Fig. 6), marsh communities approach a stable equilibrium elevation with respect to constant tidal forcing within a range of hydrologic perturbation. Biophysical feedbacks maintain that equilibrium: perturbations that increase local water depth cause a decrease in organic matter decomposition and possibly an increase in plant productivity, resulting in accretion to the equilibrium; perturbations that decrease local water depth cause subsidence and a return to the equilibrium. Consequently, SLR that initially causes an increase in local water depths may promote faster autochthonous sediment accretion, so that the vegetation community asymptotically approaches a new, dynamic equilibrium with the shifting mean high water level (Hussein et al. 2004; Mudd et al. 2004; Temmerman et al. 2004; D'Alpaos et al. 2007).

In freshwater tidal marshes, the autochthonous accretion response to SLR is complicated by the effects of saltwater intrusion (Fig. 3). Field surveys (Craft 2007) and laboratory experiments (Weston et al. 2006) have demonstrated that high salinities increase decomposition and decrease soil accretion rates. Increasing salinity increases aerobic decomposition by expanding the habitat range for burrowing marine crabs (Craft 2007) and reduces plant productivity (discussed in Section 2C), resulting in a decreased equilibrium elevation for the vegetation community (Wheeler 1999; Mendelssohn and Morris 2000; Pezeshki 2001) (Fig. 6). In addition, the SO_4^{2-} introduced by seawater favors sulfate-reducing bacteria over slow-growing methanogenic bacteria that typically dominate decomposition processes in freshwater wetlands (Keller and Bridgham 2007). This shift from methanogenesis to sulfate reducing conditions may create concomitant increases in organic matter decomposition (e.g., Portnoy and Giblin 1997), which could further contribute to decreased wetland elevations. Over longer timescales, the shift in vegetation to more salt-tolerant

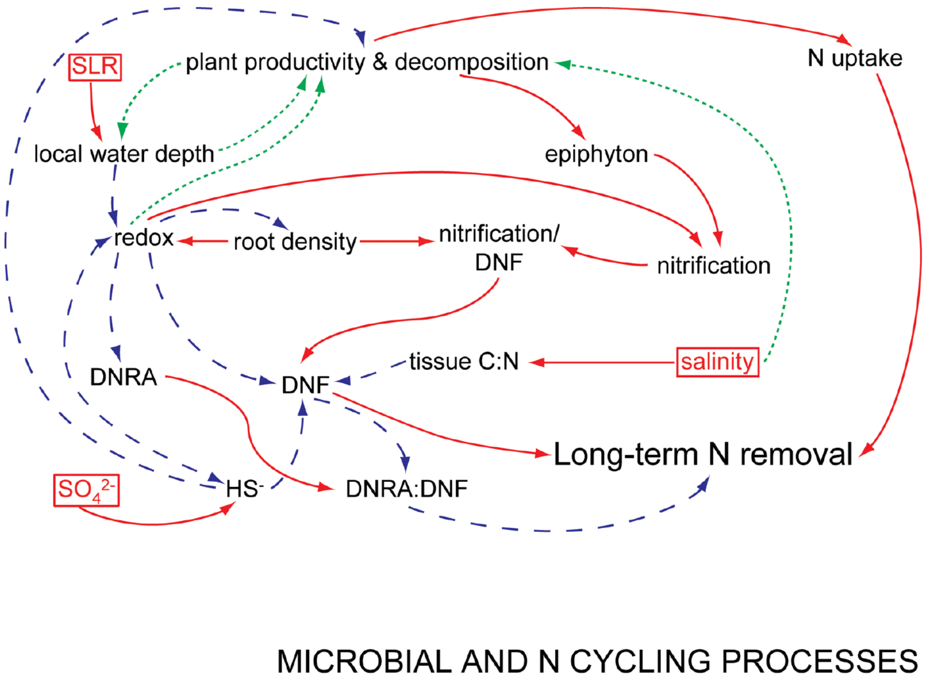

Fig. 2. Biogeochemical feedbacks and interactions affecting long-term N removal in tidal marshes. Proximal stressors expected to increase in magnitude as a result of SLR are shown in red boxes. Red solid and blue dashed arrows indicate positive and negative effects, respectively; green dotted arrows indicate effects that may be positive or negative, depending on environmental specifics. Arrows are multiplicative; determining the indirect influence of a stressor on a variable requires tracing the path of the effect, where a positive increase in a driver that has a negative impact on a proximal variable will lead to a decrease in that proximal variable. If that variable has a negative impact on a second proximal variable, that variable will increase in response to the distal driver.

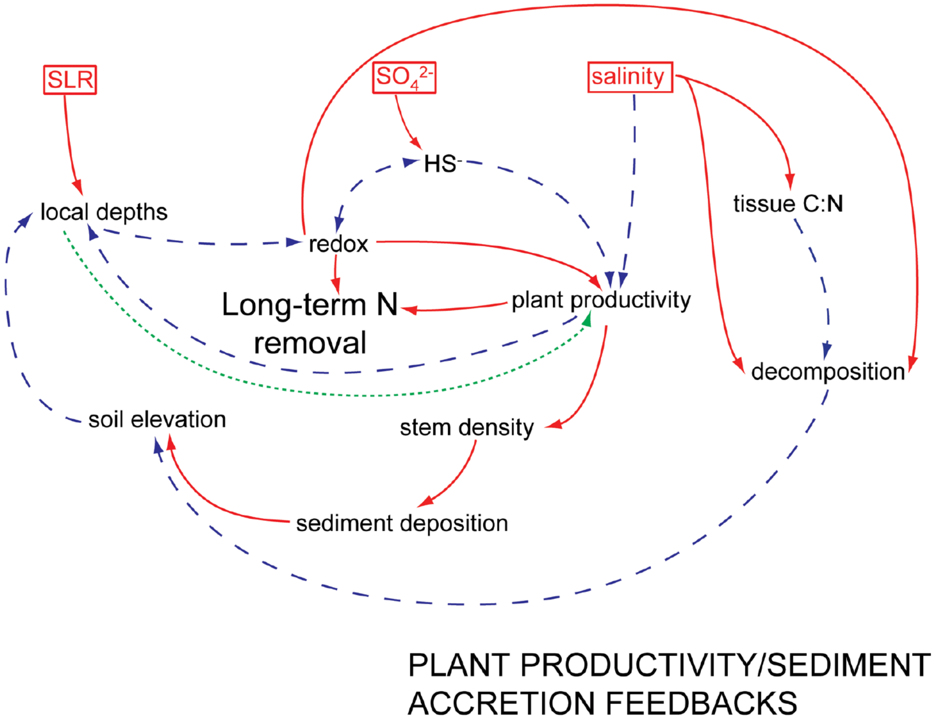

Fig. 3. Autochthonous and allochthonous sediment accretion feedbacks affecting N removal in tidal marshes. This figure shows in detail processes that are collapsed in Figs. 2, 4, and 5. See the Fig. 2 caption for a guide to interpreting the diagram.

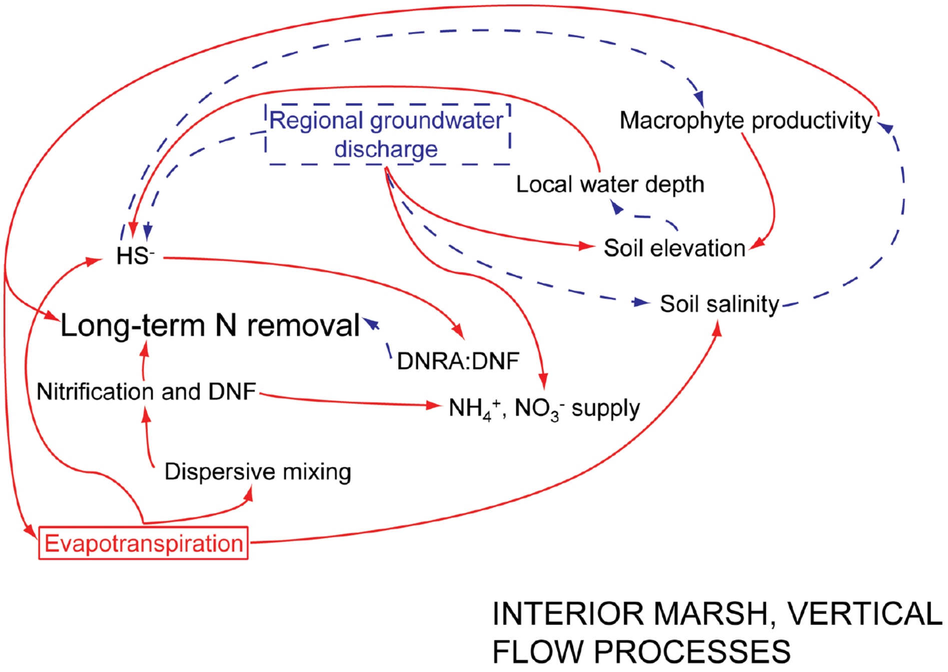

Fig. 4. Effects of global change on vertical flow processes affecting N removal in interior tidal marshes. Away from creek banks, horizontal flow is minimal, and most N removal is driven by vertical flow paths that bring nutrients in contact with organic carbon and microbial communities. As described in part 2, SLR is expected to decrease groundwater discharge to tidal marsh interiors, and warmer temperatures associated with climate change are expected to increase rates of evapotranspiration. See the Fig. 2 caption for a guide to interpreting the diagram. Blue boxes represent proximal stressors expected to decrease in magnitude with SLR.

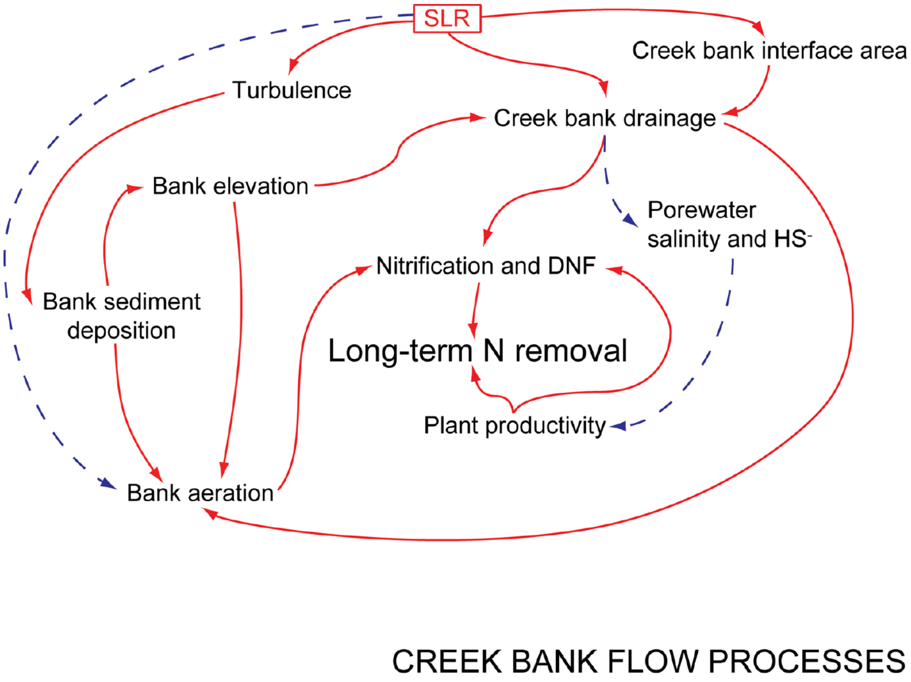

Fig. 5. Nitrogen removal driven by horizontal and vertical flow through creek banks associated with tidal forcing. This process is hypothesized to be a prime mechanism for removal of N originating in surface-water. See the Fig. 2 caption for a guide to interpreting the diagram.

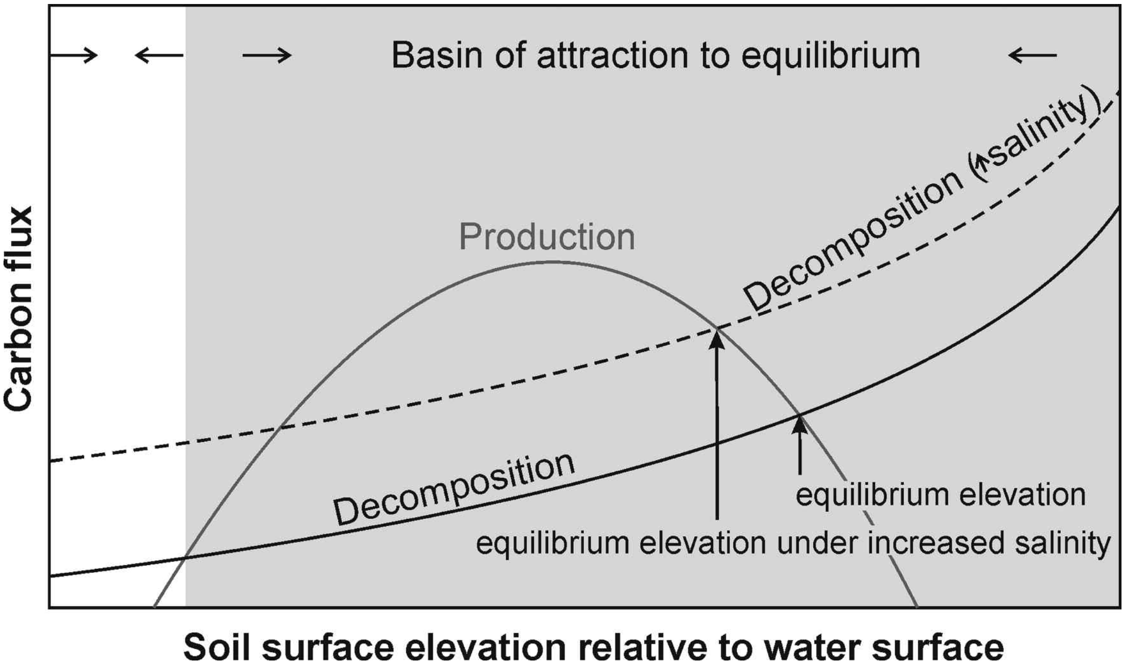

Fig. 6. Carbon fluxes contributing to net autochthonous soil accretion in tidal marshes. Autochthonous soil accretion occurs when rates of organic matter production exceed rates of organic matter decomposition; the soil surface elevation is in equilibrium with respect to water level when production and decomposition rates are equivalent. Production and decomposition of organic matter are both highly sensitive to local water depths, or the difference between the water surface elevation and soil surface elevation. Both of these processes are also sensitive to salinity. This diagram depicts only the response of decomposition to salinity, because the response of primary production is community specific. The dynamics of production and decomposition result in a basin of attraction—a range of soil surface elevations that eventually aggrade or degrade over time (shown by thin arrows) to the equilibrium elevation.

communities that accompanies salinity changes would decrease the lability of the organic matter produced (Odum 1988; Craft et al. 2009), which could counteract the effect of increased decomposition rates.

For tidal salt marsh vegetation communities to sustain a dynamic equilibrium with SLR, perturbations to local water depth must be within the basin of attraction (Fig. 6) for the equilibrium point. Large perturbations may increase local depths to a point where the community succumbs to anoxic stress, is outcompeted by a lower-elevation marsh community, or produces organic matter at a rate that no longer exceeds decomposition. These perturbations, which occur when SLR is rapid relative to maximum rates of soil accretion, result in replacement of high marsh communities with low marsh communities, or of high or low marsh communities by open water. In many locations worldwide, current rates of SLR are exceeded by maximum rates of low marsh soil accretion but approximately match maximum rates of high marsh soil accretion (Fitzgerald et al. 2008). Thus, if SLR accelerates in a manner consistent with predictions (IPCC 2007), many high marsh communities may be replaced by less diverse but more productive low marsh communities (Boorman et al. 2001); in several locations, this replacement is already occurring (Donnelly and Bertness 2001). Where diverse high marsh communities persist, soil elevations tend to exhibit greater variance than marshes with a dominant species (D'Alpaos et al. 2007).

Allochthonous processes (sedimentation): Allochthonous delivery of sediment to tidal marshes can significantly impact overall marsh accretion rates. Marshes with high incoming suspended sediment concentrations are considered best equipped to persist under conditions of rapid SLR (Temmerman et al. 2004), but suspended sediment loads of many of the world's rivers have decreased during the Holocene (Day et al. 2008). Storm events, which are expected to increase in frequency as a result of SLR (IPCC 2007), are commonly associated with substantial sedimentation (Slocum et al. 2005; Cahoon 2006; Day et al. 2008). Suspended sediment concentrations tend to increase roughly linearly with maximum inundation height (Temmerman et al. 2003), and several researchers have suggested that enhanced flooding of tidal marshes would lead to greater allocthonous sedimentation (Baumann et al. 1984; Reed 1995; Anthony 2004). However, changes in suspended sediment delivery to coastal systems that result from urbanization or altered water management practices may overwhelm the response of tidal marshes to SLR (Watson 2008). Furthermore, the extent and location of sediment deposition tends to be site specific (Reed 1995; French 2006), and is a function of sediment characteristics, the existence of conditions that promote flocculation, and vegetation characteristics (Pasternack and Brush 2002).

Predicting tidal marsh persistence under SLR: Predicting the persistence, transgression, or changing zonation patterns of tidal marshes in response to SLR is an active area of research (reviewed in Fitzgerald et al. 2008). Inundation of tidal marshes and shifts in species composition (e.g., salt-intolerant to salt-tolerant or annual to perennial dominance) resulting from SLR may occur at a relatively constant rate (e.g., for sloping marsh surfaces) or exhibit a threshold response (e.g., inundation of a tidal platform and/or rapid inundation following breaching of barrier islands (Fitzgerald et al. 2006; Fitzgerald et al. 2008). In general, allochthonously dominated marshes accrete more rapidly than autochthonously dominated marshes and are more likely to persist under rapid SLR, although many may still succumb to inundation (Temmerman et al. 2004; French 2006). Highly organic autochthonous marshes also have a more compressible substrate, resulting in greater subsidence when subject to SLR (Paquette et al. 2004). While the rapid accretion rates of *Spartina* monocultures will minimize the loss of tidal marsh area in some locations, in other locations, tidal marsh communities will experience inundation (Smith et al. 2000).

Although measurements suggest that many tidal marshes are accreting at a rate sufficient to keep pace with SLR (Williams and Hamilton 1995; Hartig et al. 2002; Van der Wal and Pye 2004), tidal marsh loss remains likely around the expanding tidal channel network (Kirwan and Murray 2007), in locations where subsidence is occurring, e.g., Gulf coast wetlands (Callaway et al. 1997; Turner 1997), where upland mineral inputs are curtailed (Temmerman et al. 2004; French 2006), where vegetation is stressed or eliminated due to other factors (e.g., marsh dieback phenomenon) (McKee et al. 2004; Kirwan et al. 2008), or where local rates of change in the water surface elevation are relatively rapid. In these locations, tidal marshes along the estuarine gradient may shift inland in the short term (Smith et al. 2000; Craft et al. 2009). However, unless feedback between the new vegetation community distribution and soil accretion results in net accretion rates that are greater than or equal to SLR, portions of the marsh will continue to become subtidal. Along developed coastlines net marsh loss will be accelerated, because inland shifting of tidal marshes may be blocked by development.

Due to the number of interacting factors affecting tidal marsh persistence, responses of tidal marsh structure to SLR will be highly site-specific (French 2006). A number of models have been developed to predict how different combinations of environmental conditions affect salt marsh persistence and structure through their impacts on feedback between vegetation, sedimentation, and sea-level rise (Mudd et al. 2004; D'Alpaos et al. 2007; Kirwan and Murray 2007). Other models have also incorporated sediment compaction and belowground biomass production (Mudd et al. 2009) or sediment accretion relationships specific to brackish marsh communities (Kirwan and Murray 2008). In general, however, due to the greater diversity of brackish and freshwater marsh communities and more complex, more poorly understood relationships between soil accretion and water level in those communities, the persistence and structure of these marsh zones in response to SLR is less well understood, a situation that highlights a research need.

3B. Predictions for salt or brackish marshes: Marsh interior—Hydrology and the physical environment: Regional groundwater discharge to tidal marshes will likely decrease with SLR (Nuttle and Portnoy 1992; Tobias et al. 2001a), which in turn will immediately reduce delivery of groundwater NO_3^- to tidal marshes. Decreased rates of groundwater discharge to tidal marshes could have large and adverse consequences for N budgets in several estuaries of the Atlantic US coast where groundwater is a dominant source of NO_3^- (e.g., Chesapeake Bay, embayments of Cape Cod). In these estuaries, groundwater discharge locations would likely shift to subtidal zones (Tobias et al. 2001a), increasing the estuarine NO_3^- concentrations and possibly promoting eutrophication and the development of dead zones.

Although diminished groundwater discharge to marsh interiors is expected to cause less delivery of reactive N species, the increased temperatures associated with global climate change are expected to increase global ET rates, which in tidal marshes will contribute to enhanced bidirectional dispersion of the near-surface porewater (Harvey and Nuttle 1995; Harvey et al. 1995). This enhanced hydrologic mixing will initially bring more parcels of surface water rich in NO_3^- into contact with DOC-enriched and anaerobic portions of the subsurface, resulting in greater rates of microbial NO_3^- reduction. However, the diminished delivery of freshwater to these systems via groundwater discharge, combined with enhanced ET, will also lead to salt and solute accumulation in the rhizosphere (Harvey et al. 1995; Tobias et al. 2001a). Thus, salt marshes will likely experience higher soil salinities. Furthermore, the decrease in the supply of dissolved Fe and Mn from groundwater in salt marshes will lead to less precipitation of sulfides (King et al. 1982; Slocum et al. 2005; Day et al. 2008) and more accumulation of H_2S, with subsequent increased sulfide stress in macrophytes.

Plant community dynamics: We predict that macrophyte productivity will decline in response to SLR due to increased inundation, salinity, and H_2S, particularly in the absence of N loading. As a result, interior marshes will likely deepen to a lower equilibrium elevation than expected based on surface-water elevations alone. Deepening will be more pronounced in highly organic marshes, where soil compression will occur due to loss of groundwater discharge (Paquette et al. 2004; Whelan et al. 2005; Cahoon et al. 2006), and in locations where the thinning of stems results in less deposition of suspended sediments. As plant productivity decreases, total ET rates will also decrease, diminishing dispersive mixing. Thus, initial increases in NO_3^- reduction rates that may accompany global climate change as a result of enhanced global ET are not likely to persist over the long term (Fig. 4). Increased inundation increases root:shoot ratios of vascular plants (Gribsholt and Kristensen 2003), although N loading decreases root:shoot ratios (Langley et al. 2009). Belowground biomass is critical for maintaining marsh elevation and the effectiveness of N removal; therefore, future research is needed to predict changes in root:shoot ratios in salt marshes facing an increase in both sea level and N concentrations.

N biogeochemistry: Tidal marshes can remove up to 90% of the NO_3^- in a groundwater plume (Tobias et al. 2001c). However, alterations in NO_3^- loading caused by SLR-driven hydrologic changes will have cascading effects on N cycling, potentially diminishing this removal capacity. Decreased groundwater discharge to tidal marshes will likely cause a decrease in overall NO_3^- reduction via microbial processes such as denitrification and DNRA. Additionally, an increase in H_2S may decrease the relative importance of denitrification compared to DNRA. The NH_4^+ produced from DNRA will either be immediately exported from the marsh or taken up by plants or microbes and cycled internally rather than removed as N_2 (via denitrification) to the atmosphere. Concentrations of labeled $^{15}NH_4^+$ exported from a New England, USA, marsh in an ^{15}N tracer enrichment experiment were substantially lower than predicted on the basis of measured DNRA rates, suggesting that the NH_4^+ produced by DNRA was cycled internally rather than immediately exported (Drake et al., 2009).

Marsh deepening and the reduction in plant biomass will have further cascading effects on N cycling (Fig. 4). In the marsh interior, the main effect of increased local water depths will be a decrease in dissolved oxygen in the benthos, which may limit aerobic processes like nitrification, particularly as rhizosphere oxygenation declines with plant biomass. Because benthic nitrification is five to nine times greater than water-column nitrification in tidal marshes (Gribsholt et al. 2005), this effect will significantly change N dynamics. Further, epiphyton communities, key centers for nitrification in tidal marshes (Eriksson and Weisner 1999), will likely be reduced in extent in stressed, lower-density macrophyte communities. Consequently, the portion of denitrification that is coupled to nitrification, which can be substantial in coastal sediments (Jenkins and Kemp 1984; Bodelier et al. 1996; Herbert 1999), will decline. Although denitrification could continue with nitrate from other sources, most N may be present as NH_4^+ as DNRA increases. These effects will all be exacerbated if N loading is sufficient to induce hypoxia (in which most N is present as NH_4^+ rather than NO_3^-).

Synergistic interactions: The hypothesized response of interior portions of tidal marshes underscores the tenet that the synergistic effects of multiple ecosystem stressors are substantially greater than the effects of any of these stressors acting alone (Day et al. 2008). Alone, increased inundation can decrease transpiration rates in a salt marsh, but increased inundation plus increased N loading can increase plant biomass and transpiration rates, leading to a more oxidized substrate with greater rates of NO_3^- reduction. Likewise, increased local water depths can cause a longitudinal (i.e., upriver) displacement of macrophyte zonation and functionality. When groundwater discharge also diminishes, positive feedbacks discussed above cause a rapid buildup of salts and sulfides, deepening, and loss of macrophyte productivity, leading to greatly reduced N turnover and diminished ecosystem function. Added stress on these ecosystems via N loading may further exacerbate impacts on these impaired marshes (which cannot as efficiently transform or release N) by directly diminishing their ability to resist SLR via organic matter accretion. In summary, we predict that SLR will cause a decrease in the removal of NO_3^- and NH_4^+ by interior portions of salt marshes, and that this decrease in ecosystem function will be most pronounced in locations where groundwater discharge has been significantly diminished.

3C. Predictions for salt or brackish marshes: Tidal creek channels and tidal creek vicinity—Physical and biogeochemical environment: A major effect of SLR could be increased dissection of tidal marshes by an expanding tidal channel network (Kirwan et al. 2008), resulting in an increased marsh/channel interface area. Presently, tidal creek banks are among the most aerated (Gribsholt et al. 2005; Wilson and Gardner 2005) well-flushed (Howes and Goehringer 1994; Wilson and Gardner 2006), and productive (Howes and Goehringer 1994; Wilson and Gardner 2006) parts of tidal marshes. Rhizopsheres of tall-form *Spartina alterniflora* and fiddler crab burrows support high rates of N cycling across coupled oxic and anoxic sediments. As a result, the portions of marshes fringing tidal channels have been reported to be net sinks for inorganic N species from tidal marshes (Whiting et al. 1989; Anderson et al. 1997), and a whole-ecosystem ^{15}N tracer enrichment study provides preliminary evidence of denitrification in creek banks during drainage (Gribsholt et al. 2005). Tidal creek bottoms are also important sites for denitrification, accounting for 60% of total marsh denitrification measured in a New England salt marsh (Kaplan et al. 1979).

Synergistic effects: Given that the tidal creek/marsh interface is a current hotspot for N transformations, we expect that an expansion in the total area of this interface will result in greater total NO_3^- reduction in portions of the marsh that abut tidal creeks. Examination of the more indirect effects of SLR on marsh/creek systems (Fig. 5) leads us to further hypothesize that per unit length of creek bank, nitrification and denitrification may become even more efficient. For example, increased tidal amplitudes lead to larger volumes of drainage through the creek bank and longer flow paths and residence times for porewater flowing from the marsh through the creek bank to the channel (Wilson and Gardner 2006), all of which would be expected to enhance total denitrification (Seitzinger et al. 2006). Increased turbulence intensities and enhanced flocculation of fine material, mediated by increased salinities, would further contribute to the evolution of higher creek banks, due to the relatively high settling velocities of compound, flocculated particles (Larsen et al. 2009a). Higher creek banks would result in a larger volume of water draining through the banks (Howes and Goehringer 1994), further increasing the potential for denitrification. Additionally, larger grain sizes on the creek bank could result in higher porosities, higher redox potentials, and a higher potential for coupled nitrification/denitrification. Furthermore, deposition of relatively large sediment grains on tidal marsh surfaces has been linked to benthic algal colonization (Cahoon et al. 1999; Croft et al. 2006), which could further promote coupled nitrification/denitrification (Krause-Jensen et al. 1999) and stabilize the sediment, while countering the greater erosion potential of a more turbulent tidal creek. Deposition of flocculated particles in the vicinity of creek banks may also provide an additional influx of allochthonous organic carbon to the marsh benthos that could support denitrification. Finally, larger populations of burrowing organisms, pushed further inland by increasing salinity, would further aerate the sediments of marshes fringing tidal channels (Croft et al. 2006), again promoting coupled nitrification/denitrification.

Tidal creek channel bottoms serve as the major site of denitrification in some marshes because of relatively large fluxes of nitrate-rich water across the biogeochemically reactive creek bed (e.g., Nowicki et al. 1999). Within creek bottoms, the effect of SLR on the N cycling will likely vary along the estuarine gradient. As in the marsh interior, deeper portions of tidal creeks will experience lower redox potentials that promote denitrification but inhibit coupled nitrification/denitrification, and more saline portions of tidal creeks will likely experience an increase in the importance of DNRA relative to denitrification. However, in contrast to marsh interior zones, denitrification in tidal creek beds is additionally controlled by variations in flow velocity (O'Connor et al. 2006), which is expected to increase with SLR. When flows are slow (shear velocity less than 0.23 cm s^{-1}), further increases in velocity tend to promote denitrification, whereas when flows are fast (shear velocity greater than 0.39 cm s^{-1}), further increases in flow tend to inhibit denitrification (O'Connor and Hondzo 2008). Thus, near the heads of tidal creeks or during slowly flowing portions of the tidal cycle, SLR will likely increase denitrification, whereas seaward portions of the tidal creek will likely experience lower denitrification rates. The portions of the creek channel most effective for denitrification will essentially be likely to shift inland. Because the tidal creek network will likely expand laterally and longitudinally as a result of SLR, we predict that the total amount of nitrate removal occurring in tidal creek bottoms may not substantially change as a direct consequence of SLR. Similarly, total nitrification in tidal creek beds may also change little, with the most effective regions for nitrification shifting inland. However, where human development restricts inland shifts of the tidal creek network, a loss of total N removal in creek beds may occur.

When N loading is combined with SLR, total N removal via denitrification and coupled nitrification/denitrification is likely to increase substantially in both creek beds and creek banks. Fertilization experiments in a Massachusetts, USA, marsh revealed that N loading may increase denitrification by an order of magnitude in tidal creek sediments and coupled nitrification/denitrification 3-fold (Koop-Jakobsen and Giblin 2010). An increase in the total area of creek bed resulting from SLR (e.g., Kirwan et al. 2008) would further increase total creek bed N removal. Moreover, the fertilization experiment increased the productivity of benthic macroalgal production in sparsely shaded creek banks and beds. As a result, bacterial communities in these locations were relieved of limitation by the labile organic carbon supply and were more productive, in contrast to the bacterial communities in the shaded marsh interior (Deegan et al., 2007). Thus, the greatest efficiency gains in total N removal in tidal creek banks and creek beds may result from a combination of SLR and N loading, which highlights the importance of considering interacting multiple stressors.

3D. Predictions for tidal freshwater marshes—Plant community dynamics: In tidal freshwater marshes, the dominant physical effects of SLR will be increasing salt water intrusion and increasing tidal inundation frequency and duration. As a consequence of these changes, SLR can cause different shifts in tidal freshwater marsh plant communities: salt-intolerant to salt-tolerant species, and/or a shift of dominant life forms in which a community codominated by annuals and perennials shifts to a plant community dominated by perennial species. Both of these shifts in community structure will result in a community that is less diverse and less resistant to invasion than the former freshwater marsh ecosystem. These plant community changes will have a dramatic impact on organic carbon quality given the substantially higher C:N ratios of salt marsh (Craft et al. 2009) and perennial plant tissues (Hopfensperger et al. 2009a). Thus, when freshwater marsh species shift to more halophytic and perennial species, detrital organic matter becomes more refractory, which leads to a decrease in organic matter decomposition rates and an increase in soil surface elevation (Morris and Bowden 1986) that could compensate for an increase in tidal amplitude. However, N loading may compensate for the effects of species shifts on organic matter quality by increasing tissue N content (Drake et al. 2008).

The plant community shifts associated with SLR would also decrease porewater concentrations of dissolved inorganic nitrogen through massive plant uptake compared to the native, heterogeneous, freshwater marsh community (Findlay et al. 2002; Windham and Meyerson 2003; Windham-Myers 2005). The shift from a mixed community to one dominated by perennials may lead to increased nutrient retention, as perennial species store nutrients that are not recycled each year in their below-ground vegetative structures. Moreover, through time a shift to perennial dominance could diminish the density and diversity of the seed bank since it will not be replenished year after year by annual species (Hopfensperger et al. 2009b), thereby perpetuating the dominance of perennial and/or invasive species.

N biogeochemistry: Increasing soil salinities and H_2S concentrations will have many of the same repercussions as discussed above for salt marshes, including an increase in the importance of DNRA relative to denitrification and anammox, subsequently resulting in less effective removal of N to the atmosphere. In addition, the decrease in organic matter quality due to changes in the plant community may cause a shift from N mineralization to bacterial immobilization, and provide further support for a shift from denitrification to DNRA. Potential denitrification rates and N_2O production are significantly greater in tidal freshwater marshes than in salt marshes (Dodla et al. 2008), suggesting that upriver shifts in vegetation zonation resulting from SLR will reduce denitrification and reduce N_2O emissions to the atmosphere. Similarly, lower soil NO_3^- concentrations have been found in homogenous areas dominated by perennials, which may lead to lower denitrification rates (Hopfensperger et al. 2009a). The extent to which N_2O emissions will be altered in response to changing marsh distributions is an area in need of assessment through further contrasts of these ecosystems.

Synergistic effects: Similar to interior salt marshes, the predicted response of tidal freshwater marshes to multiple perturbations is different from the response to one stressor acting alone. An increase in H_2S concentration, due to increased salt water, will inhibit plant uptake of N and reduce plant productivity, leading to a deepening of the marsh surface, though salinity-induced species shifts accompanied by higher organic matter C:N ratios, will, to some degree, counteract this effect. Additionally, when significant N loading is coupled with an increase in H_2S concentration, the inhibitory effects of H_2S on macrophytes may be overcome by the abundantly available N, further increasing rates of soil accretion. Overall, we predict that SLR-induced inundation coupled with plant community shifts will result in an increased importance of DNRA and bacterial N immobilization, ultimately resulting in an ecosystem that retains more N and is less effective at permanent N removal from the watershed. In areas experiencing both SLR and N loading, we predict the additional N will lead to a shift from fermentative DNRA to sulfur-driven DNRA, but still result in a system that retains more N than the previous freshwater marsh.

CONCLUSIONS

The main ecological effect of climate change is often viewed as inducing unidirectional shifts in community zonation and associated ecosystem functioning along gradients (e.g., low-elevation communities will replace high-elevation communities), with the structure and function at the end of the gradient being lost. To some extent, this general pattern is consistent with predicted responses of tidal marshes to SLR; increased salinities and depths may cause an upriver shift in macrophyte zonation and N cycling. However, this simplified view does not account for cross-scale interactions and synergistic feedbacks that can significantly alter the value of the N-related ecosystem services provided by tidal marshes.

We hypothesize that cross-scale interactions and feedbacks in wetlands responding to SLR will either enhance or diminish N removal mainly through impacts on NO_3^- reduction (denitrification and DNRA) or coupled nitrification/denitrification. On one hand, sediment accretion feedbacks can reduce the loss of tidal marsh area and upriver translation of marsh structure and function by compensating for increased surface-water elevations. On the other hand, diminished freshwater flushing by groundwater discharge could shift patterns of salinity, H_2S, and water depth, resulting in shifting patterns in dominant N cycling processes in tidal marshes, with likely adverse consequences for N removal. We predict these changes will lead to decreased N removal from salt- and freshwater tidal marsh interiors, where increases in DNRA relative to denitrification are expected. In contrast, positive feedbacks between SLR, turbulence, disturbance, and vegetation dynamics will likely lead to enhanced dissection of tidal marshes by tidal creeks, which, despite the loss of rooted vegetation, will likely lead to local enhancement of rates of nitrification and denitrification.

Whether the overall N-removal function of a particular tidal marsh increases or decreases under SLR depends on several site-specific factors, including sediment, microbial, macrophyte, and hydrologic characteristics, and whether primary sources of NO_3^- and NH_4^+ to the receiving estuary are groundwater or other sources. In estuaries receiving nutrients predominantly from surface-water, the increase in hydrologic exchange between surface-water and porewater through tidal creek banks and the accompanying N reduction may be sufficient to overcome a decrease in N removal from the marsh interior. In contrast, in estuaries where groundwater is the primary source of nutrients, the loss of denitrification along groundwater discharge flow paths may dominate the whole-marsh N removal response to SLR. The site-specificity of the response of tidal marsh ecosystem functions to SLR underscores the need for combinations of experimental field studies and process-based numerical models (French 2006).

The growing awareness of how cross-scale interactions and feedbacks will affect the ecosystem services provided by tidal marshes will promote more realistic valuation of these drivers in cost-benefit analyses and will improve coastal management. For example, this review argues against actions that draw down upland coastal aquifers and further reduce groundwater discharge to tidal marshes. It also makes a case against new dam construction that would reduce the sediment loads carried by rivers feeding into tidal marshes and further contribute to marsh deepening. Likewise, it suggests that incision of tidal creeks might not decrease a marsh's capacity for nitrate removal, and thus that management to curtail creek incision may not be necessary. Finally, in synthesizing this conceptual model, we have identified several new hypotheses that should be tested to fully understand how SLR will impact

N removal ecosystem services. This synergistic understanding will lead to improved holistic forecasting of marsh response to climate change.

Glossary

Aerenchymous tissue. Plant tissue with large air spaces that facilitates delivery of oxygen to the sediment.
Aerobic. Requiring oxygen to occur.
Allochthonous. Found in a place other than where formation occurred.
Anaerobic. Occurring in the absence of oxygen.
Anammox. The anaerobic oxidation of ammonia by microorganisms that use NO_2^- as an electron acceptor and NH_4^+ as an electron donor in a chemolithotrophic metabolism.
Annuals. Plants that complete their life cycle within 1 year.
Anoxia. The absence of oxygen.
Aquifer. Porous rock or sediment that is permeable and saturated with water.
Autochthonous. Local; found at the same location as formation.
Basin of attraction. The set of initial conditions leading to long-term behavior that approaches a particular equilibrium.
Bed shear stress. The area-normalized force of flowing water on the underlying surface/sediment.
Chemolithoautotrophic. Obtaining the necessary carbon for metabolic processes from carbon dioxide fixation, while using inorganic compounds such as nitrogen, iron, or sulfur as an energy source.
Dead zones. Areas of the coastal ocean that cannot support life owing to depleted oxygen levels, thought to be caused by increased nutrients that cause harmful algal blooms.
Denitrification, respiratory: a form of anaerobic respiration in which microbes convert nitrate (NO_3^-) to increasingly reduced N forms (nitrite, gaseous NO, N_2O, or N_2). The full reduction to N_2 is of particular importance because N_2 is much less biologically available and reactive.
Denitrifiers. Organisms that perform denitrification.
Dispersion. A bidirectional movement of water and solutes due to diffusion and nonuniform flow.
Dissimilatory nitrate reduction to ammonium (*DNRA*). An energy-generating microbially catalyzed conversion of nitrate (NO_3^-) to ammonium (NH_4^+) under anaerobic conditions.
    Fermentative: DNRA that is thought to occur under conditions of high labile organic carbon availability.
    Sulfur-driven: DNRA that is thought to occur where sulfur-oxidizing bacteria have access to NO_3^-. Sulfide (H_2S) is thought to be the electron donor in the process.
Distal. Characterizing an indirect or several-steps-removed effect.
Distichlis spicata. A perennial marsh grass widespread throughout the Americas.
Dynamic equilibrium. The condition under which different components of the system, although often changing, continually reach a balance in which system inputs are roughly equal to outputs.
Ecogeomorphic. Pertaining to interactions between ecology and geomorphology.
Eddy. A vortex, or circular motion of water.
Emergent vegetation. Vegetation that fully protrudes through the water column.
Entrainment, sediment. The suspension of particles by flowing water.
Estuarine gradient. The continuum of salinities and associated landscape features along the mixing zone between the coastal ocean and freshwater rivers.
Evapotranspiration. The combination of evaporation and transpiration that converts water from a liquid to a vapor and releases it to the atmosphere.
Feedback. The process of a system's output affecting an input.
Feedback, positive. A signal amplification process, whereby the output signal intensifies the input signal.
Feedback, negative. A signal-damping process, whereby the output signal diminishes the input signal.
Fermentation. The metabolic processes conducted by microbes whereby organic carbon compounds are used as both electron donor and acceptor in low-oxygen conditions to yield energy.
Fetch. A length of water over which wind blows.
Flocculation. The aggregation of particles suspended in water.
Flocs. Compound particles/aggregates that form through the process of flocculation.
Glycine betaine. A nitrogen-rich compound used by salt-tolerant plants
Groundwater discharge. The flow of groundwater into surface water.
Halophytes. Plants that thrive under highly saline conditions.
Hydraulic head. The total pressure caused by water above a given point in an aquifer, which results from a combination of the water table's elevation, velocity, and confining pressure of the aquifer.
Hypoxia. Oxygen depletion to a level that is between 1% and 30% saturation.
Impatiens capensis. Also known as jewelweed, an annual plant native to North America.
Juncus gerardi. A tidal marsh plant species common in northern North America and Greenland.
Labile. Readily undergoing change through uptake or decomposition.
Leaf area index. The total upper leaf surface of vegetation divided by the surface area of the land occupied by the vegetation.
Macrophytes. Aquatic plants.
Methanogenesis. The production of methane gas (CH_4) by archaea that ferment simple organic carbon compounds or oxidize H_2 under anaerobic conditions, with co-production of CO_2.
Nitrification. The energy-yielding, microbially mediated oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and subsequently nitrate (NO_3^-).
Nitrifiers. Organisms that perform nitrification.

Nitrogen fixation. The microbially mediated conversion of gaseous N_2 into ammonium (NH_4^+), a “fixed” or bioavailable form of nitrogen.

Osmotic regulation. Maintenance of an optimal osmotic pressure (the pressure on cell membranes exerted by solvent molecules) within an organism.

Oxidation. The loss of an electron by an atom, molecule, or ion.

Perennials. Plants that persist in the environment for more than 1 year.

Photosynthesis. The generation of carbohydrates from carbon dioxide and water using radiant energy.

Phragmites australis. Also known as the common reed, a large perennial grass found in wetlands throughout temperate and tropical regions of the world.

Pilea pumila. Also known as Canadian clearweed, an annual plant found in the Eastern and Gulf Coast portions of North America.

Porewater. Shallow subsurface water found within the pores of sediment.

Proline. A nitrogen-rich amino acid used by salt-tolerant plants.

Proximal. Characterizing an immediate, direct effect.

Recharge. The flow of surface water into the aquifer.

Redox. A descriptor of chemical reactions in which the oxidation state of participating atoms or molecules changes.

Reductase. The catalyst of a reduction reaction.

Reduction. The gain of an electron by an atom, molecule, or ion.

Respiration. The set of metabolic processes through which organisms obtain energy.

Rhizosphere. The zone of soil containing and surrounding plant roots.

Saltwater intrusion. The movement of saline water into freshwater aquifers.

Sarcocornia. A genus of succulent salt-tolerant coastal plants that is widely distributed throughout North America.

Seepage face. A location along a slope where water from an aquifer emerges at atmospheric pressure.

Spartina alterniflora. Also known as saltmarsh cordgrass, a perennial deciduous grass found in salt marshes and native to North America.

Spartina maritima. A tidal marsh plant species found along the Gulf Coast of North America.

Spartina patens. Also known as saltmeadow cordgrass, a perennial grass native to the Atlantic coast of North America that is found in the upper portions of brackish marshes.

Stomatal conductance. A measure of the rate of passage of water vapor and/or carbon dioxide through the pores in plant tissue.

Stressor. Any agent that causes stress to an organism.

Suaeda. A genus of salt-tolerant coastal plants that is widely distributed throughout North America and can often tolerate alkaline soils.

Surface/subsurface exchange. The bidirectional flow of water between the surface and below-ground aquifers and porewater.

Synergistic. Pertaining to the situation whereby the total effect of multiple factors is greater than the sum of individual effects.

Tidal wedge. An intrusion of seawater into a tidal estuary in the form of a vertical wedge, in which lighter freshwater from a river rests atop dense saltwater.

Transgression. The upslope movement of tidal marsh vegetation.

Transpiration. The emission of water vapor from the leaves of plants.

Turbulence intensity. A mathematical measure of the level of turbulence, or unstable flow, within a parcel of water.

Turbulent wakes. The pattern of turbulence, or unstable flow, in the lee of an object that protrudes into the flow.

Zonation. The distribution of plants in biogeographic zones.

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