CHAPTER

5

Sea Level Rise in the Everglades: Plant-Soil-Microbial Feedbacks in Response to Changing Physical Conditions

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Introduction

Coastal wetlands occupy the intertidal zone between the freshwater Everglades and the Gulf of Mexico. At the interface with the marine environment, these wetlands are dominated by mangrove forests, tidal creeks, and mudflats. Behind the coastal fringe zone is an ecotone that transitions into a freshwater/upland community characterized by an increasing diversity of halophytic to glycophytic trees, shrubs, and herbaceous vegetation. These productive coastal wetlands provide numerous, important ecosystem services. Directly benefiting humans, coastal wetlands function as habitat and nursery ground for shellfish and other commercially important fisheries, stabilize the coastline, and lessen the impact of storm surges (Aburto-Oropeza et al. 2008; Costanza et al. 2008; Gedan et al. 2011). Moreover, some of the most important functions of coastal

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wetlands are less tangible processes, including nutrient cycling, pollution removal, and carbon (C) storage (Craft et al. 2009; Gedan et al. 2009; Barbier 2013). Because coastal wetlands are a transitional ecosystem between the land and the ocean, sea level rise represents a significant threat to their global distribution and extent. In order to persist, the soil platform of a coastal wetland must maintain a specific elevation niche relative to the ocean, normally between mean sea level and mean high tide (Morris et al. 2002).

This chapter addresses the connections between sea level rise and Everglades soil microbial processes, with a focus on soil C dynamics and the relationship between vegetation, soil, and microbial ecology. Specifically, salinity and inundation are expected to increase under projected sea level rise, hydrologic drivers that are known to alter the structure and productivity of coastal wetland plant communities (e.g., Williams et al. 1999; Donnelly and Bertness 2001; Teh et al. 2008; Smith 2009). Plant community change can affect the quality and quantity of organic C inputs to the system, which in turn, can influence soil microorganisms and biogeochemical processes (Neubauer et al. 2013; Morrissey et al. 2014a). The feedback between plant and soil microbial dynamics, vegetation change, and evidence of such shifts in the Everglades will be discussed. Because soil microbes play a key role in regulating how much organic matter is buried or stored in coastal wetlands, processes which promote vertical accretion and resilience to rising sea levels, we will also describe the current understanding of how sea level drivers may directly impact soil microbial activity and diversity. Finally, the chapter will conclude with a discussion of how sea level rise impacts are assessed and the current evidence of sea level rise in the Everglades.

South Florida and Sea Level Rise Throughout History

Changes in global sea level are a natural part of the geologic history of the earth and have always been a key abiotic driver of the ecology of Florida. South Florida, in particular, is considered as being “land from sea” because this region has undergone a repeated history of submergence and emergence from the ocean that is recorded in a stratigraphy of alternating freshwater and marine sediments (Willard and Bernhardt 2011). For instance, during the Eemian interglacial period, which began about 120,000 years ago, sea levels were at least 6.6 meters higher than present and south Florida was a shallow bay (Muhs et al. 2011). During this period, the coral reefs formed that would later become the Florida Keys and sediments began to collect on the Florida platform. Approximately 18,000 years ago, at the height of the last glacial period, sea levels dropped to approximately 120 m lower than today, exposing the carbonate platform that includes present-day south Florida (Wanless et al. 1994). This was followed by a period of step-wise rises in sea level that deposited and recycled sediments, allowed for organic matter accumulation, and eventually led to the evolution of the Everglades during a period of relatively stable sea levels, approximately 3,200 years before present (Locker 1996). Sea level began to rise again in approximately 1850 at a rate of ~1.7 mm y^{-1}, and has accelerated since 1993 to a rate of between 2.8 and 3.1 (± 0.7) mm y^{-1}. Half of the current rate of sea level rise is attributed to thermal expansion of the ocean and half to melting land ice (IPCC 2007).

The flat, emergent wetland-dominated landscape of the Everglades has earned it the nickname, The River of Grass. Over its recent geologic history, the size and shape of the Everglades have changed in concert with sea levels. Currently, approximately 1/3 of the greater Everglades are within 1.5 m of sea level, and half of Everglades National Park lies below 0.6 m of sea level (Titus and Richman 2001). Further, the slope of the Everglades averages just 5–8 cm (2–3 inches) per mile (Lodge 2010; McVoy et al. 2011). These geomorphologic conditions make south Florida's natural environments highly vulnerable to increased sea levels. When considering the population that lives immediately adjacent to the Everglades (approximately 6 million people, U.S. Census Bureau), the flat, gently sloping landscape renders the Everglades a virtual "canary in a coal mine" for how both society and the natural environment will respond to sea level rise.

As sea level rises, the coastal zone along the Everglades will be increasingly exposed to salinity and inundation. The general thinking is coastal wetlands may respond by: 1) keeping pace with sea level through vertical accretion, 2) migrating landward to maintain an optimal elevation relative to sea level, or 3) submerging. It has been predicted that if sea level rises between 0.18–0.59 m before the end of this century, 30% of the world's coastal wetlands will be lost, either to submergence or the inability to migrate landward (IPCC 2007). An increase in mean sea level of 1 m will inundate approximately 4,050 km^3 (4 million acres) of wetlands in coastal areas (Neumann et al. 2000). Therefore, understanding the controls over the fate of C stored in coastal soils will be critical in predicting the fate of our coastlines—not to mention the vast reservoir of nutrients (particularly nitrogen (N) and phosphorus (P)) stored in those soils.

In south Florida, sea levels are conservatively predicted to rise 0.60 m by 2060 (Zhang et al. 2011). This will cause salinity and inundation to increase in fresh and brackish water areas of the Florida coastal zone and will increase the risk of storm surge-induced flooding and saltwater exposure in oligohaline areas of the Everglades at the top of the estuarine ecotone (Teh et al. 2008; Pearlstine et al. 2010). The Everglades also has the added risk factor of being a highly modified and managed system with a large number of canals, ditches, and dams used to divert water for flood control, agricultural water supply, and human consumption. For example, the construction of canals on the east and west sides of Lake Okeechobee in the northern Everglades caused a 10-fold increase in the portion of freshwater flowing directly into the Atlantic Ocean and Gulf of Mexico, bypassing the Everglades. Much of this freshwater had previously flowed south through the Everglades and into Florida Bay, effectively countering saltwater along the coastal interface (Nuttle et al. 2000). The change in the quantity, timing, and distribution of freshwater delivery to the coastal zone by this and many other hydrologic alterations throughout the Everglades are believed to be amplifying saltwater intrusion and the rate of the landward migration of coastal habitats, especially in the eastern Everglades (Ross et al. 2000).

Soil Elevation and the Carbon Cycle

Carbon storage and accumulation is vital to the health of the coastal Everglades because it is a major component of the soils and sediments that serve as the wetland platform.

Everglades soils are predominately histosols and entisols. Histosols, or peat soils, found in the Everglades coastal zone can be up to 5.5 m deep with total C contents of 15–42% and organic matter contents of 32–89% (Whelan et al. 2005; Castaneda 2010; Chambers et al. 2014). These areas often support riverine and fringe mangroves. Everglades enitsols are typically either of a marl-type, derived from dry-down and deposition of calcitic periphyton mats, or derived from marine sediments resulting from storm and tidal influences in the coastal zone. These inorganic C-dominated soils are typically shallower and support "dwarf" mangroves, sawgrass, or may be unvegetated.

Many coastal wetlands have persisted through centuries of sea level fluctuations due to the natural feedback mechanism of vertical marsh accretion: the accumulation of soil C that leads to an increase in the elevation of the wetland platform (Morris et al. 2002; McKee et al. 2007). This process is a dynamic interplay between sea level and primary production governed by both autochthonous contributions to soil elevation (i.e., belowground production and litter accumulation) and deposition of allochthonous mineral sediments on the soil surface (Morris et al. 2002). The vegetation directly adds organic C to the soil, while also enhancing further sediment deposition (containing both organic and inorganic C) through the slowing of water velocities by aboveground biomass. Studies indicate both organic and inorganic C are important to vertical marsh accretion (Day et al. 2000), with the latter generally comprising a greater percentage of the soil as the proximity to the ocean or rivers increases. Soil C accumulation in coastal wetlands is a balance between the C inputs (i.e., imports and CO_2 fixation) and outputs (i.e., exports, CO_2, and CH_4 flux) from the system. Major C reservoirs include plant biomass, detritus, peat, microbial biomass, and dissolved C (Fig. 1). In order for coastal wetlands to "keep pace" with sea level rise, production and sediment input/

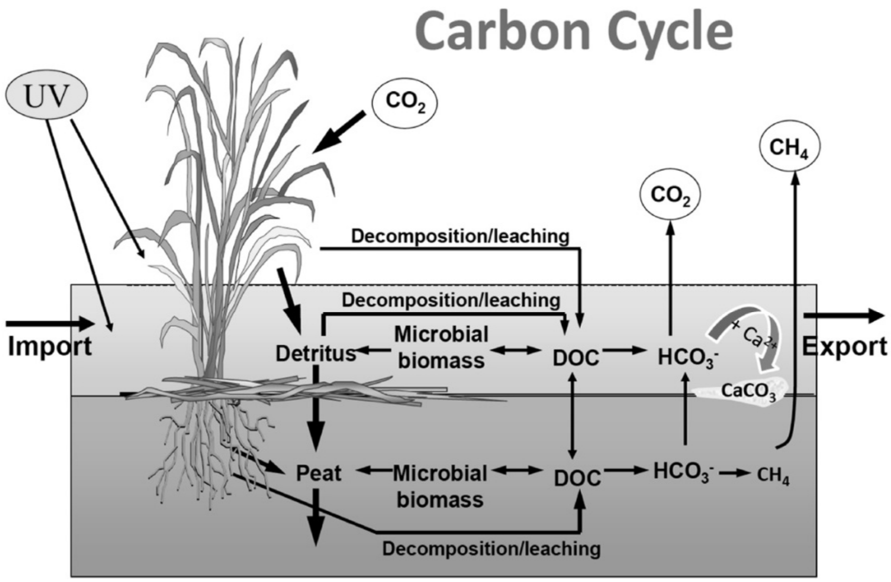

Figure 1. A generalized depiction of the carbon cycle in wetlands, including the major storage reservoirs and transformations. Modified from: Reddy and R. Delaune 2008.

retention must exceed losses on a magnitude that mimics or exceeds the current rate of sea level rise (Morris et al. 2002; Day et al. 2011).

Several lines of evidence suggest that conditions are generally met for coastal wetland elevations to be sustainable in the context of current rates of sea level rise. For example, a meta-analysis of the accretion rates from 15 mangrove forests throughout the world indicates approximately 80% of the systems studied are currently accreting at, or faster than, the rate of global sea level rise (Alongi 2008). At least one area of the Everglades is responding in a similar manner. In the coastal fringe mangroves of Shark River Slough, average accretion rates between 1924 and 2009 were 2.5 to 3.6 mm y^{-1}, while sea level was rising at a rate of 2.2 mm y^{-1} (Smoak et al. 2013). However, rates of sea level rise are not uniform across our coasts, coastal vegetation is not restricted to mangrove forests, and human impacts in the coastal zone, such as freshwater diversion, alter dynamics that may otherwise lead to accretion rates that exceeds rates of sea level rise.

The relative importance of organic versus inorganic sediment accumulation necessary to combat coastal submergence has been studied extensively elsewhere (e.g., Nyman et al. 1990; Day et al. 2011), but little information is available for the Everglades. Often, allochthonous deposition is the critical factor for wetland accretion in meso-tidal systems characterized by high sediment loads; these types of coastal wetlands are thought to be the most stable during periods of sea level rise (Morris et al. 2002). Where sediment supplies are low, as is the case in many areas of the coastal Everglades, root biomass and productivity likely become the major contributor to soil accretion. A recent study of mangroves in Belize and Florida showed approximately 50% of production occurs belowground and mangrove roots can account for 1–12 mm of surface elevation increase per year—equivalent to as much as 55% of the annual vertical change in soil elevation (McKee 2011). Furthermore, mangrove roots are fairly refractory and have slow rates of decomposition in the field, especially relative to mangrove leaves (Middleton and McKee 2001). Root decomposition studies by Huxham et al. (2010) and McKee et al. (2007) found about 24–60% of root material remained after 1-year of decomposition in the field, depending on species and tidal position. However, root accumulation rates differ by mangrove forest types (e.g., fringe, dwarf, etc.) and are sensitive to variations in the supply of N or P (McKee et al. 2007). A study conducted in Taylor Slough mangroves found that both resource limitations and greater inundation were correlated with increased fine root production, which was a primary driver of soil formation and accretion (Castaneda-Moya et al. 2011). This suggests that differential plant growth responses to nutrient availability or sea level rise stressors, such as inundation, may be key determinants of coastal wetland resilience. The response of mangrove root productivity to nutrient addition is especially important in the coastal Everglades because Florida Bay tends to be the primary source of nutrients (Childers et al. 2006), making increased nutrient supply a possible indirect effect of sea level rise.

While root dynamics are thought to be important drivers of soil elevation in the coastal Everglades, storm events that deliver large quantities of inorganic sediment can be significant in localized areas (Castañeda-Moya et al. 2010), as well as seasonal groundwater dynamics that may affect the shrink-swell dynamics of the peat soils (Whelan et al. 2005). For example, a single hurricane (Wilma 2005) deposited between

0.5 and 4.5 cm of sediment across Shark River Slough and exceeded the annual vertical accretion rate by 8–17 times (Castañeda-Moya et al. 2010). Benthic mats (dominated by algae and cyanobacteria) can also contribute as much as 0.5–5 mm in soil elevation each year, accounting for 9–35% of the total increase in soil elevation (McKee 2011). In addition to the direct contributions benthic mats and inorganic sediments make to soil accretion, their presence may also increase nutrient availability in the wetland (Castañeda-Moya et al. 2010), which will feed back into primary production.

Heterotrophic soil microbes, on the other hand, continually act in opposition to the accumulation of organic matter by utilizing C in senescing leaves and roots, as well as organic exudates from roots, as energy sources. These organisms assist in the break-down of organic polymers into monomers, which can then be assimilated by bacteria and function as electron donors during respiration. The process of organic matter mineralization results in the release of organic C in a particulate (POC) or dissolved (DOC) form, or as carbon dioxide (CO_2) or methane (CH_4) gas (Schlesinger 1997). This C may be exported via aquatic transport during the ebb tide, or lost to the atmosphere via soil efflux or diffusion and ebullition through the water column (Dittmar et al. 2006; Bouillon et al. 2008). Laboratory intact soil core studies (excluding vegetation) indicate organic C loss from coastal wetland soils predominately occurs through microbial respiration and the subsequent release of CO_2 back to the atmosphere. Across a salinity gradient of tidal freshwater, brackish, and salt marsh soils, an average of $> 96\%$ of C lost was emitted as CO_2, $\leq 3\%$ as CH_4, and $< 1\%$ as DOC (Chambers et al. 2013). At the ecosystem scale, mangrove research has found a significant portion of C (up to 50% of litter production) is exported as leaves, detrital material, and dissolved C, with the contribution of C to the coastal zone dependent upon the tidal amplitude, season, geomorphology, and productivity (Jennerjahn and Ittekkot 2002; and references therein). Dissolved inorganic C (DIC) export appears to be important in mangrove systems and may exceed DOC export by a factor of 3 to 10 (Bouillon et al. 2008). Finally, a large portion of mangrove organic C remains buried in the soil, with a global average burial rate of 26.1 Tg OC (Breithaupt et al. 2012).

Depending on the influence of tides and the presence of litter consumers (e.g., crabs), other internal pathways contributing to C loss may prevail. Early work by Robertson et al. (1992) showed that sesarmid crabs can account for the consumption or burial of up to 28% of the total annual litterfall in a mangrove forest, making it easier for by-products to be mineralized by microorganisms or to be exported tidally. Other studies tracking the fate of leaf litter have shown that > 30% of the dry mass of leaf litter is leachable, contributing to C loss but also representing a source of nutrients that can facilitate bacterial colonization and increased palatability of the leaf detritus (Davis et al. 2003; Davis et al. 2006). Increased exposure of coastal wetlands to tidal flushing due to sea level rise could affect the relative importance of this type of internal cycling, thus affecting net soil accretion.

Considering all of this, it remains unclear if the necessary soil accretion rates can be maintained under the accelerated rate of sea level rise scientists are predicting (e.g., Church and White 2006; Haigh et al. 2014), and what the consequences will be of the water management activities and human development within the greater Everglades watershed. Despite pole-ward expansion of mangroves with global warming and the ability to migrate landward, Alongi (2008) predicts a 10–15% global loss of mangroves under accelerated rates of sea level rise by 2100. Some research forecasts accretion in many coastal wetlands world-wide will be out-paced by rising sea levels, leading to submergence and land loss. This fate can be driven by physical constraints, such as a small tidal range or low sediment supply in the coastal zone (Nicholls et al. 1999), or a biological feedback. For example, submergence is often observed when areas of salt-sensitive coastal vegetation are not colonized by more salinity tolerant species quickly enough. The existing vegetation becomes stunted or dies as a result of water-logging, osmotic stress, the accumulation of toxic hydrogen sulfide (HS^-) from intruding seawater, or salinity induced nutrient inhibition (Koch et al. 1990; Bradley and Morris 1991; Batzer and Shartiz 2006). Because live plants play a vital function in maintaining soil structure, slowing water velocities to allow for sediment deposition, and providing a source of soil organic matter, a decrease in vegetation health can rapidly cascade into peat collapse, ponding, and accelerated submergence (Nyman et al. 1990; DeLaune et al. 1994). There is also speculation that rising sea levels could exacerbate erosion along the coastline of the Everglades, which also contributes to submergence (Wanless et al. 1994).

Peat Collapse in the Everglades?

Much of the coastal Everglades include peat soils (Craft and Richardson 2008), which have a very low bulk density (often exceeding 85% pore space by volume; Nyman et al. 1990), making them susceptible to collapse. Peat collapse can occur in a variety of systems under varying circumstances (Day et al. 2011), but is typically initiated by a loss of soil structure, such as by de-watering, accelerated decomposition, or root death. This reduces the strength of the soil matrix and causes the surface soil material to cave-in upon the subsurface soil, resulting in a rapid loss of elevation (DeLaune et al. 1994). Recent geological research in the Everglades has shed light on the potential for collapse of freshwater organic peat soils as they are exposed to increasingly saline conditions (Fig. 2). In a report for Everglades National Park, Wanless and Vlaswinkel (2005) describe a series of "collapse" events that occurred in Cape Sable and Whitewater Bay that they attributed to disturbance caused by channelization, storm surge, sea level rise, and freshwater diversion. These collapse events have led to the exposure of previously freshwater wetlands to more inundated and saline conditions, often converting emergent freshwater marsh areas to open water before mangroves have time to become established and stabilize the soil. Although similar to general "submergence," in which the depth of inundation increases without a comparable response in vertical accretion and the system slowly converts to open water, peat collapse results in a more rapid transition to open water conditions and can occur away from the aquatic edge, such as near the inland ecotonal boundary of salt-tolerant vegetation, as observed in the Everglades.

Freshwater peat collapse could limit the landward colonization of mangrove propagules in response to sea level rise by reducing the soil elevation to a point that it is too deep for new vegetation to become established; this occurrence may be spatially heterogeneous, based on the location of freshwater peat deposits throughout the Everglades. Shallow open water habitat or embayments may develop instead, potentially interrupting the dispersal mechanisms for more salt-tolerant mangrove

Figure 2. Photographs showing evidence of peat collapse in a sawgrass (*Cladium jamaicense*) marsh surrounded by an expanding mangrove forest in lower Shark River Slough, Everglades National Park. [Photo credit: South Florida Water Management District.]

vegetation to migrate landward. Alternatively, successfully colonization of peat collapse areas would hinge upon the ability of vegetation to rapidly accrete new peat soil or mineral sediment, as described earlier, to keep pace with increasing sea level. Areas of south Florida where freshwater diversions have been extensive may be especially vulnerable to wetland loss via peat collapse as sea level rises.

Wanless and Vlaswinkel (2005) describe a few plausible explanations for the observed peat collapse in the Everglades. First, over-drainage of some areas may lead to soil drying, organic matter oxidation, and compaction. Next, hurricanes, which occur frequently in south Florida on geological timescales, physically damage vegetation, leading to soil exposure. These soils are then vulnerable to oxidation and collapse until vegetation is reestablished and organic soils are re-stabilized. Finally, Wanless and Vlaswinkel (2005) describe a second scenario where increasing salinity (from sea-level rise or storm surge) stresses, and then kills obligate freshwater vegetation at the top of the estuarine ecotone. Until more salt-tolerant vegetation is reestablished, the organic peats are also vulnerable to oxidation and collapse.

The scenarios posed by Wanless and Vlaswinkel (2005) rely on vegetation reestablishment in order to protect peat soils from oxidizing and "collapsing", as it is the establishment of plants and their investment of belowground biomass (i.e., roots) that serve to stabilize the soils. Studies of peat collapse events in coastal Louisiana also indicate death of belowground biomass is a key instigator and warning sign of impending collapse (Turner et al. 2004). However, accelerated soil mineralization may already be underway while the vegetation is still in place. Additionally, some areas of the coastal Everglades are composed of mineral sediments and soils that developed under the influence of marl-forming periphyton. The response of these types of soils to sea level rise, de-watering, and accelerated mineralization are not understood. In this chapter, we propose a slightly different alternative that considers changes in both the plant-mediated control over peat soil formation and maintenance, as well as the underlying biogeochemical mechanisms behind peat degradation, compaction, and collapse. Recent experimental data combined with concepts in wetland soil biogeochemistry (described later in this chapter) may shed more light on the validity of the peat collapse concept and provide us with better predictive capability as to how Everglades peat soils will respond to sea-level rise.

Vegetation Change

The distribution of vegetation communities across the Everglades is a function of salinity, depth, hydroperiod, and nutrient availability (Daoust and Childers 2004; Barr et al. 2010; Castaneda-Moya et al. 2013; Troxler et al. 2013). In the coastal zone, vegetation species typically orient in identifiable zones parallel to the shoreline or tidal creeks; these zones are dictated mainly by each species' tolerance to salt and water-logging (Fig. 3). In general, the Everglades coastal fringe is dominated by red mangrove (*Rhizophora mangle*), followed by black mangrove (*Avicennia germinans*) and white mangrove (*Laguncularia racemosa*) as you move landward. Mangroves are typically able to tolerate high salinities (~30 + ppt) and are adapted to wide fluctuations in both water level and salinity. A sharp ecotone often separates mangroves from the less salinity tolerant communities, such as hardwood hammocks, that are located further inland. This boundary is maintained by a combination of the salinity gradient and a positive feedback mechanism by which each species modifies its' own environment to promote its permanence (Jiang et al. 2011). In some areas of the coastal Everglades, particularly the southeastern region near Taylor Slough, the mangroves have a less abrupt inland ecotone, first becoming interspersed with herbaceous and succulent

Figure 3. Typical vegetation zonation patterns observed in the coastal Everglades, with mangroves occupying the land fringe, followed by one or more ecotonal boundaries into less salt tolerant vegetation [Photo credit: Lisa G. Chambers].

halophytes (e.g., *Batis maritima, Borrichia frutescens* and *Juncus romoerianus*), then giving way to Gulf Coast spikerush (*Elecocharis cellulosa*) and less salt tolerant sawgrass (*Cladium jamaicense*) communities (Ross et al. 2000). There are also areas of unvegetated mud flats and limestone pinnacles (Smith et al. 2013). If the coastal Everglades follow the typical model for landward migration, the seaward edge of the mangrove forests will submerge and give-way to subtidal habitats such as tidal flats and seagrass beds. Upstream, oligohaline and freshwater marshes will give way to mangroves. However, the risk of soil collapse in predominantly peat-based oligohaline or freshwater areas needs to be considered; this could lead to the establishment of open water conditions prior to mangrove establishment (Wanless and Vlaswinkel 2005).

Salinity as a Driver of Vegetation Change

Across the coastal Everglades landscape, salinity is a key driver of primary productivity and species composition (Castañeda-Moya et al. 2011; 2013; Troxler et al. 2013). However, the salinity gradient is highly dynamic, varying daily (with tides), seasonally (wet and dry season), and over the longer term (e.g., drought periods). During the wet season (May–November), freshwater flow from the northern Everglades penetrates well into the mangrove zone, while reduced flows during the dry season (December–April) allow tidal water to penetrate further upstream. For example, under dry season conditions in lower Taylor Slough, surface water salinity can exceed 40 ppt, and porewater salinity levels in some sawgrass (*C. jamaicense*) marshes can exceed 30 ppt (McIvor et al. 1994; Troxler et al. 2012). During the wet season, the surface water of these same areas is typically fresh (< 0.5 ppt). Sawgrass is only weakly salt-tolerant and can be negatively affected by even small increases in salinity, showing signs of physiological stress at salinities as low as 5 ppt (Rejmankova and Macek 2008). During periods of drought in Taylor Slough, the replacement of sawgrass by more salt-loving species such as mangroves has been observed (Ross et al. 2000). Mangrove expansion in other areas of the Everglades has also been noted and thought to be correlated with increased water levels associated with sea level rise (Smith et al. 2013). Extended droughts, managed flow reductions, and the construction of canals and ditches can all initiate inland mangrove expansion by allowing the tidal prism to migrate upstream and carry with it mangrove propagules to facilitate mangrove expansion (Fig. 4; Ross et al. 2000).

The observed expansion of mangroves can have numerous implications for soil microbiology, although, to our knowledge, this area of research has received little attention in the literature. For example, while both mangroves and sawgrass conservatively store nutrients in tissues of leaves, resulting in high C to nutrient ratios, the quantity and quality of organic matter provided by mangrove wood and leaf litter may be less labile than sawgrass litter. This consideration led Bianchi et al. (2013) to hypothesize that an increased C storage capacity of wetlands would ensue with continued pole-ward expansion of mangroves into coastal zones previously dominated by graminoids (e.g., *Spartina alterniflora*). The landward migration of mangroves in the Everglades could alter the impact of disturbance events such as fire, lightning strikes, and hurricanes on light penetration and soil temperature, and could also alter the rate of vegetation-induced sediment deposition. Finally, soil redox potential may

Figure 4. Mangroves expanding landward along tidal creeks in the coastal Everglades, likely facilitated by saltwater intrusion and propagule dispersal [Photo credit: Lisa G. Chambers].

be differ under cover of these different plant communities, which affects the utilization of various electron acceptors by soil microbes and influences the overall rate of C mineralization (Reddy and DeLaune 2008). Within mangrove forests themselves, there can be species zonation and spatial heterogeneity that produce differences in rhizosphere oxidation, which can affect C mineralization pathways, the availability of nutrients, rates of soil respiration, and other physio-chemical conditions in the soil (Alongi et al. 2000). In contrast to mangroves, soil redox potential in monotypic sawgrass communities seem to vary with water level, but otherwise remain fairly consistent throughout the surficial (0–25 cm) soil and are not significantly affected by nutrient gradients (Qualls et al. 2001).

In addition to shifting species composition, salinity can also have a direct physiological effect on vegetation and conditions in the soil. In the Everglades, studies have found a linear decrease in the light-use efficiency of mangroves as salinity increases, suggesting decreased productivity with saltwater intrusion (Barr et al. 2010). Sawgrass (*C. jamaicense*) aboveground net primary production has also been reported to be negatively correlated with surface water salinity, especially periods of high maximum salinities, which primary production rates seem slow to recover from (Childers et al. 2006; Troxler et al. 2013). Increasing root phosphatase activity has been detected for sawgrass plants associated with relatively low salinity levels (0.5–5 ppt), indicating a strong demand for P (Rejmankova and Macek 2008). Field and laboratory studies conducted elsewhere on marsh vegetation have documented plant mortality and reduced growth in several other common Gulf of Mexico species (e.g., *Sagittaria lancifolia, Panicum hemitomon, Leersia oryzoides*) as salinity increases, with each species having slightly different levels of salt-sensitivity (McKee and Mendelssohn 1989). Wetland vegetation that is not adapted to saltwater often suffers from osmotic stress (Batzer and Shartiz 2006) and an accumulation of hydrogen sulfide (HS^-) in the soil porewater. Hydrogen sulfide, a by-product of sulfate reduction, acts as a phytotoxin and suppresses plant metabolism, reduces growth, and inhibits nutrient uptake (Koch et al. 1990).

In some cases, vegetation shifts are thought to be initiated by extreme salinity events, such as storm surges. Even if the intensity and frequency of storm surges is not affected by climate change, sea level rise will still result in an increase in the height of the surge, and thus increase the area of land inundated by a high water event. However, studies suggest episodes of coastal flooding will increase in the coming decades (Najjar et al. 2000). Based on historic data and predictive models, the return period of storm surges throughout Florida is expected to be condensed, such that a 1-in-50 year surge will be experienced roughly every 5 years (Park et al. 2011). This coincides with evidence that the number of maximum water level events (meteorological and storm related) has increased in frequency in south Florida since 1961 (Obeysekera et al. 2011).

It is thought that much of the current distribution of mangroves is a product of past hurricanes (Doyle et al. 2003). Storm surges, like droughts, can accelerate the landward migration of the mangrove ecotone by carrying and depositing propagules further inland. The sharp vegetation boundary between the coastal mangroves and hardwood hammocks seems especially vulnerable to saltwater intrusion events. Models predict that just a 1-day saltwater intrusion event of salinities > 15 ppt could initiate a transition to a mangrove dominated system within a previously hammock community as a result of salinity stress (Teh et al. 2008). Meanwhile, other research in the Everglades has documented catastrophic damage to mangroves as a result of hurricanes (e.g., wind throws, defoliation, smothering by sediments), leading to a transition to mudflats near the coastline (Smith et al. 2009).

Phosphorus as a Driver of Vegetation Change

Because of the Everglades' legacy as a nutrient-limited system, differentiating between the impacts of sea level rise (salinity and inundation), and the associated increase in nutrient supply (especially P) accompanying saltwater intrusion, can be challenging. Most estuarine wetlands tend to be N-limited, meaning plant productivity is constrained by the availability of N needed for biomass synthesis (Vitousek and Howarth 1991). While N is still an important element for growth and production in the Everglades, P typically regulates the species composition and trophic state of the greater ecosystem (Noe et al. 2001). In its pristine, pre-drainage state, P in the Everglades was naturally low (< 10 ug L^{-1}), with much of it being derived from the atmosphere (Belanger et al. 1989). The P limitation was a key driver in evolution of Everglades ecology, favoring the establishment of a unique assemblage of species with low P requirements (e.g., periphyton, sawgrass). Today, the northern Everglades are subject to P loading, mostly from agricultural sources, which has led to a shift in plant communities. This is especially evident in the Water Conservation Areas where periphyton biomass has declined and areas previously occupied almost exclusively by *C. jamaicense* are now monotypic stands of *Typha domingesis* (Davis 1991; McCormick et al. 1998).

Understanding the implications of P loading in the northern Everglades is relevant to a discussion of sea level rise because P concentrations in Florida Bay are naturally higher than the un-impacted areas of the Everglades, making the ocean the primary source of P in the coastal zone (Childers et al. 2006; Rivera-Monroy et al. 2007). There is increasing evidence of the importance of marine-derived P in shaping mangrove forest structure and productivity in the Everglades. For example, the reestablishment of a mangrove community damaged by Hurricane Donna (1960) was evaluated to determine the driving forces of structural development. The study found that neither soil salinity nor sulfide concentrations reached levels known to influence species composition, but concentrations of N and P mirrored productivity rates. Both basal area and wood production were highest at the coast (where N and P availability was greatest) and decreased further inland (Chen and Twilley 1999). Research also indicates the importance of marine-derived P in the partitioning of C within mangroves. Trees growing in upstream portions of the estuary and regions with low tidal exchange allocated more biomass belowground, rather than aboveground, in response to the P gradient (Castañeda-Moya et al. 2013). Belowground productivity contributes significantly to soil accretion and preserves soil structure to combat peat collapse (DeLaune et al. 1994; Turner et al. 2004). How an influx of P with saltwater intrusion might affect accretion rates, belowground productivity, and soil stability in the coastal Everglades has not been investigated.

Vegetation-Microbial Interactions

Vegetation change directly impacts soil microbiology by altering the amount and timing of C available to microbes, the lability of the C substrate, and the structural habitat for microbes. This is in addition to the direct impact of the physical changes caused by sea level rise (e.g., increasing salinity, altered nutrient availability, and changing depth and duration of flooding). In general, plant species richness and diversity tend to decrease with increasing salinity (e.g., Odum 1988; Wieski et al. 2010; Sharpe and Baldwin 2012). In the Everglades, sea level rise threatens the future of as many as 21 species of rare, low-lying coastal plants that lack adjacent suitable habitat for species migration (Saha et al. 2011). The decrease in wetland structural complexity caused by salinity also reduces the variety of terrestrial organic matter to serve as a microbial substrate, and could prompt a similar decline in the diversity of the microorganisms that rely on them. Indeed, a variety of studies have shown different plant species and functional guilds support unique microbial assemblages (e.g., Grayston et al. 1998; Troxler et al. 2012), suggesting changes in coastal plant community distribution driven by sea level rise will likely cascade into an alteration of soil microbial ecology. However, no studies to date have directly studied the effect of reduced plant species diversity due to sea level rise on soil microbial diversity.

Shifts in vegetation composition can also impact microbes due to differences in the bioavailability of their litter material. For example, polyphenolic compounds such as condensed tannins and lignins, reduce the ability of microbes to degrade those tissues, creating the need for expensive exoenzyme production to break-down these refractory materials (Field and Lettinga 1992; Berg et al. 1996). Leached, plant-derived polyphenolic compounds may also have an inhibitory effect on microbial activity (Field and Lettinga 1992). In general, species with high lignin content, high leaf dry matter content, and greater specific leaf area (common characteristics of woody species) have slower decay rates (Prescott 2011). Inputs of organic matter from plants occur as leaf and root litter, and dissolved organic matter (DOM) from litter leaching. While components of freshly leached DOM can be easily degraded and stimulate microbial respiration, litter DOM can also contain less labile components that reflect those chemically-complex compounds found in litter tissue (see Cornwell et al. 2008 for overview). While both the complexity and nutritional composition (structure of C-C bonds and C:N:P) of plants either in leaves or roots are important for soil organic matter (SOM) dynamics, microbial community composition also has a proximate control on SOM (Melillo et al. 1982). For instance, fungal and actinomycete bacterial species are among the most efficient in degrading more complex C compounds, but are associated with degradation in aerobic, low nutrient environments (Goodfellow and Williams 1983; McCarthy et al. 1987; Güsewell and Gessner 2009; Peltoniemi et al. 2009). With adequate nutrient supply, microbes may also synthesize metabolically expensive enzymes to acquire complex C molecules of recalcitrant tissues (Moorehead and Sinsabaugh 2006). Recent research suggests SOM quantity and quality (as indicated by C:N) is inversely related to salinity in oligohaline wetlands (Morrissey et al. 2014b). In the Everglades, the expansion of mangroves into areas previously dominated by hardwood hammocks or graminoid is expected to result in significant changes in the quality of liter material and alter SOM dynamics in the coastal zone.

Microbial Ecology and Biogeochemistry

The connection between sea level rise and microbiology is an emerging area of research with broad implications given the strong connection between hydrology, plant production, soil microbes, and soil C storage. Soil microbes are often the first organisms in a wetland to respond to environmental changes due to their large surface-to-volume ratio and rapid turnover rate. Although microbial changes are less visible than vegetation shifts, they often occur within a matter of hours or days following an event and could involve alterations in community function, composition, and diversity. For example, periphyton mats in the Everglades (a mixture of cyanobacteria, algae, and microinvertbrates), are highly sensitive to changes in P concentrations and begin to show changes in species composition within a few weeks—long before changes can be observed in the soil or vegetation (McCormick et al. 2001). In coastal wetlands, saltwater intrusion, increased inundation, and storm surge events linked to sea level rise could all directly alter soil microbial community structure, activity, and subsequently the balance of soil C that controls how resilient a wetland is to sea level rise (e.g., Chambers et al. 2011; 2013; Neubauer et al. 2013).

From the most fundamental perspective, salinity increases the ionic strength and conductivity of the microbial environment in coastal wetlands. In order to survive in saline conditions, microorganisms must be capable of osmoregulation, which can involve either the accumulation of potassium chloride in the cytoplasm, or the biosynthesis and/or accumulation of compatible solutes (Oren 2008). Salt intolerant species without these capabilities will experience osmotic stress, disruptions in metabolic function, or even cell lysis upon exposure to salinity (e.g., Reitz and Haynes 2003; Wichern et al. 2006). There is a long history of research pertaining to the effects of salt accumulation in upland soils that demonstrates salt can reduce the size of the soil microbial community and microbial activity, as indicated by lower rates of CO_2 and CH_4 production (Pattnaik et al. 2000; Muhammad et al. 2006; Gennari et al. 2007). It is believed the higher conductivity in the soil-water environment causes osmotic/ionic stress to the organisms and leads to an overall decrease in the rate of C cycling in these systems (Frankenberger and Bingham 1982; Gennari et al. 2007). Few studies have investigated the direct impacts of ionic strength on soil microbiology in wetlands or aquatic systems. A laboratory study where a freshwater wetland soil was exposed to an increase in conductivity from 0 to ~28 mS cm^{-1} through the addition of NaCl demonstrated a 30% decline in microbial respiration over a period of 3 weeks (Chambers et al. 2011). Whether this decline resulted from a general reduction in microbial activity or a shift in community structure remains unclear.

When addressing the impact of sea level rise on wetland soil microbiology, another environmental change may be even more critical than the increase in ionic strength—an increase in the sulfate, SO_4^{2-}, concentration. Unlike inland salinity discussed above, seawater contains a consistent ratio of ions, of which SO_4^{2-} is the third most abundant. Sulfate functions as a terminal electron acceptor (TEA) that soil microbes can utilize for anaerobic respiration. In most terrestrial ecosystems, the presence of SO_4^{2-} is of little consequence to the microbial biota because TEAs are plentiful. The most commonly used TEA by heterotrophic bacteria is oxygen, which utilizes C as an energy source (electron donor) and produces energy in a relatively efficient manner. The presence of water reduces the diffusion of oxygen into the soil by 10,000 times, requiring microbes in wetlands and coastal ecosystems to rely on alternative TEAs, which they utilize in a specific sequence based on their availability and potential energy yield (Patrick and DeLaune 1977; Table 1). Sulfate is near the bottom of the energy cascade and is used only when the environment becomes sufficiently reduced (as indicated by an oxidation reduction potential (Eh) of < –100 mV) and produces only -0.7×10^{-3} kJ mol^{-1} of energy.

Sulfate reduction is typically the dominant pathway of microbial respiration in brackish and saline marshes and mangroves (Howarth 1984; Weston et al. 2006; Kristensen et al. 2008). This suggests that although an increase in ionic strength from seawater intrusion may slightly suppress microbial activity by causing osmotic stress, there will also be a stimulatory effect from the influx of SO_4^{2-} providing an abundance of new TEAs for anaerobic respiration. This was demonstrated under laboratory conditions where CO_2 production rates showed a short-term increase (20–32%) in proportion to the concentration of sulfate added to a freshwater wetland

Table 1. Theoretical energy yields (the more negative the value, the greater the net energy gain) calculated as reactions coupled with glucose oxidation ($C_6H_{12}O_6 \rightarrow CO_2$) and H_2 oxidation ($H_2 \rightarrow H^+$).

Alternative Electron Acceptor	Dominant C End-Product	Eh Range (@ pH 7)	Theoretical Energy Yield (ΔG^o_R)
NO_3^-	CO_2	250 to 350 mV	-14.5×10^{-3} kJ mol^{-1}
Mn^{4+}	CO_2	220 to 300 mV	-3.0×10^{-3} kJ mol^{-1}
Fe^{3+}	CO_2	120 to 180 mV	-1.7×10^{-3} kJ mol^{-1}
SO_4^{2-}	CO_2	–100 to –250 mV	-0.7×10^{-3} kJ mol^{-1}
CO_2	CH_4	< –250 mV	-0.1×10^{-3} kJ mol^{-1}

soil (Chambers et al. 2011). Additions of 10 ppt seawater to freshwater sediment cores can cause SO_4^{2-} reduction to become the dominant pathway for microbial respiration after only 12 days, and account for 95% of all organic C oxidation after 35 days of exposure (Weston et al. 2006). However, the stimulation in the overall rate of C loss through respiration may be short-lived as other factors, such as the availability of labile C substrates or nutrients, become limiting (Chambers et al. 2011). A longer-term manipulative field study in a freshwater tidal marsh found CO_2 flux actually declined in treatments exposed to increased salinity for 3.5 years; this decline was correlated with a reduction in the quality of the SOM, further demonstrating the importance of plant-microbial interactions (Neubauer et al. 2013). Interestingly, while the stimulatory effect of SO_4^{2-} on respiration appears to be somewhat transient, the suppression of methanogensis through competitive inhibition by sulfate reducers appears to persist over time (Chambers et al. 2011; Neubauer et al. 2013). In the laboratory, a pulse of brackish water (13 ppt) in a freshwater wetland soil reduced CH_4 flux by 97% in just 5 days (Chambers et al. 2013). In the field, oligohaline water additions to a freshwater wetland soil caused a 2 to 3-fold decrease in CH_4 production that persisted for 3.5 y (Neubauer et al. 2013).

Hydroperiod is another environmental driver of soil microbial processes. In the coastal Everglades, hydroperiod fluctuates seasonally based on rainfall, and daily, based on semi-diurnal tides. During low water (low tide) conditions, more oxygen can diffuse into the soil to promote aerobic respiration. For this reason, low tide CO_2 production rates can be between 50–300% higher in coastal wetlands than high tide CO_2 production rates, with the variability attributed to differences in the hydraulic conductivity of the soil (Chambers et al. 2013). However, as sea level rises, we can expect deeper, more prolonged periods of inundation. Even wetlands that are accreting vertically at a pace comparable to sea level rise tend to do so in a step-wise manner, creating a lag phase in which inundation is greater than under static sea level conditions (Kirwan and Temmerman 2009). Longer periods of water-logging generally slow down microbial activity because organisms must rely exclusively on anaerobic pathways, which tend to be slower and less efficient than aerobic respiration. In a mesocosm study that simulated sea level rise in an Everglades mangrove peat soil, soil organic C loss was 90% higher under control water levels, as compared increased inundation, when combined with elevated salinities (Chambers et al. 2014). This may reduce the amount of organic C lost through the microbial pathway as hydroperiod increases, promoting soil C storage and accretion. However, the same study also demonstrated that prolonged inundation may actually result in a loss of soil material, as seen by a decrease in surface (0–5 cm) soil bulk density (Chambers et al. 2014). While the mechanism for this reduction in bulk density is not known, it was correlated with an increase in porewater dissolved organic C, causing speculation it may be a product of excessive leaching during water-logging or increased shear stress due to the deeper water column above the soil (Chambers et al. 2014).

It is generally thought microbial density and diversity is comparable in freshwater and saltwater systems, but the identity of the individual organisms themselves differs with salinity (Capone and Kiene 1988). However, new evidence contradicts this axiom, finding higher microbial biomass-associated C in salt marsh soils, compared to freshwater and brackish marsh soils (Chambers et al. 2013). Other research has found a direct correlation between bacterial abundance and salinity in freshwater tidal marshes (Morrissey et al. 2014b). Only one study of microbial community composition has been performed in the Everglades along a salinity transect from 0 to 49 ppt. Here, the diversity of the microbial community remained similar, but the identity of the microbes diverged significantly, based primarily on salinity, and secondarily on P availability (Ikenaga et al. 2010).

Ultimately, while soil microbial communities may be rapid indicators of wetland ecosystem response, the feedback between plant and microbial communities will modulate this response. For example, the presence or absence of plants will have significant influences on soil redox potential (i.e., the size of the oxidized rhizosphere), quantity and quality of organic C, and will interact with enzyme synthesis. Under conditions in which salinity drives a decline of plant productivity, vegetation death, or vegetation community shifts, diversity and function of soil microbial communities will be fundamentally altered. Unfortunately, plant-microbial interactions are not well understood in wetlands, especially in coastal peatlands.

The Future of the Coastal Everglades

As salinity and inundation patterns in the Everglades change in response to sea level rise and human-driven alterations in hydrology, coastal zone ecology is changing as well. The movement of ecotones (regions bridging two distinct community types) is often a reliable way of monitoring environmental change because ecotones develop and migrate in response to specific environmental gradients. Several studies have used historic aerial photography and various bio-indicators to document shifts in the location of coastal ecotones in the Everglades over time. This provides a glimpse of how the ecosystem has responded to past sea level changes and a basis for predicting future ecosystem responses.

The land boundary of the Everglades, and all of Florida, has changed significantly throughout geologic time in response to sea level. Soil cores indicate the current seaward edge of the Everglades formed from red mangrove (*R. mangle*) derived peats that began accumulating approximately 3,500 years B.P. (Parkinson et al. 1989). As sea level rose, the mangrove soil platform accreted vertically and expanded landward. Meanwhile, the establishment and growth of oyster reefs off the coast also allowed mangroves to expand in the seaward direction, creating mangrove islands (Parkinson et al. 1989). The distribution of mangroves, and peat accumulation from relic mangrove forests, are considered good indicators of historic sea level because they always occupy the upper portion of the tidal range (Scholl 1964).

Current research shows that mangroves within the Everglades are continuing to respond to changing sea levels, mainly through the expansion of their coverage at the expanse of inland marsh habitat (Doyle et al. 2003). A look at aerial photographs of the Ten Thousand Islands National Wildlife Refuge on the western edge of the Everglades has shown a 35% increase in mangrove coverage in the past 78 years. The construction of canals near the coast is a driving force in the expansion of mangroves within previously low salinity marshes because they provide a conduit for saltwater intrusion and propagule dispersal (Krauss et al. 2011). In a region near Taylor Slough, known as the Southeast Saline Everglades, researchers have documented the movement of inland ecotones since the 1940s. Here the boundary between the mangrove-graminoid community and the interior sawgrass marsh has shifted inland 3.3 km, which is believed to be in response to a combination of reduced freshwater flows and encroaching seas (Ross et al. 2000; Troxler 2012). In the southeast Everglades, extensive water diversions and flow alterations are accelerating saltwater intrusion and may be a useful model for predicting sea level rise effects elsewhere. According to mollusk records in the coastal soils near Biscayne Bay, prior to local drainage efforts that began ~70 years ago, the marsh/mangrove ecotone was migrating landward at a rate of 0.14 m y^{-1}, but since drainage, the rate has increased to 3.1 m y^{-1} (Gaiser et al. 2006). This migration is correlated with an increase in salinity from 2 ppt to 13.2 ppt. In addition to general mangrove expansion, models also predict the mangroves themselves will have reduced height and contain a greater proportion of red mangroves as sea level rises (Doyle et al. 2003).

While there has been significant research demonstrating that the inland ecotones of the coastal Everglades are migrating landward with rising sea levels, there are large uncertainties about how the balance of coastal erosion and soil accretion will determine the position of the land boundary as sea level rises. Some studies suggest that coastal erosion directly resulting from sea level rise is low, with most documented erosional events accompanying hurricanes (Doyle et al. 2003; Wanless et al. 1994). At present, mangrove soil accretion rates are exceeding sea level rise rates in at least one area of the Everglades (Smoak et al. 2012), but more research is needed to understand how accretion may vary spatially. The fact that seawater serves as the primary source of nutrients to the coastal zone (Childers et al. 2006) suggests that saltwater intrusion could increase productivity (Chen and Twilley 1999), and subsequently soil accretion. However, increasing salinity may have the opposite effect due to the complicated relationship with concomitant physical forcings such as inundation depth, sediment supply, and disturbances (e.g., fire, wind, storm surge). The interaction of salinity-induced collapse of freshwater peats and mangrove expansion is also worth considering as a driver shaping the coastal Everglades of the future.

As discussed earlier, Wanless and Vlaswinkel (2005) suggest that collapsed areas of freshwater peat—as observed in the Cape Sable area of Everglades National Park—may coalesce through time, resulting in larger open water areas. In fact, it is believed that this phenomenon contributed to the formation of Whitewater Bay in Everglades National Park (Wanless and Vlaswinkel 2005). One could hypothesize that unless collapsed areas receive new sediment or are colonized by mangroves that can re-stabilize the soil, they may continue to grow larger and transition directly into subtidal habitat as sea levels continue to rise. With 8,744 km^2 of south and southwest Florida being located below the 1.5 m elevation contour (Titus and Richman 2001) and rates of sea level rise thought to be accelerating (Church and White 2006), the fate of the seaward boundary of the Everglades remains highly uncertain.

Conclusion

Overall, there is ample evidence to support the idea that coastal ecology in the Everglades is changing in concert with rising sea levels. In the southeast Everglades, the signature of sea level rise has been blurred with significant hydrologic modifications that are decreasing freshwater flows and accelerating saltwater intrusion (Ross et al. 2000). However, ecotone shifts and elevated salinities are being documented across the entire ecosystem. Changes in vegetation communities are often the most apparent manifestation of migrating environmental gradients and directly impact soil microbiology by altering the physical and chemical environment. However, the structure and function of microbial communities will likely respond far in advance of vegetation shifts. Few studies have addressed the direct impacts of sea level rise on soil micro-biota, but evidence such as changes in soil respiration rates (CO_2 production) suggest seawater intrusion can accelerate heterotrophic microbial activity for the short-term and suppress methanogenesis for the long-term. The important question is how changes in vegetation type, productivity, and microbial activity will affect the overall balance of C in coastal wetlands. An increase in C inputs and net decrease in microbial respiration would create a positive feedback to promote vertical accretion and increase wetland resilience. In the most likely scenario, different regions of the Everglades will have unique responses to sea level based on the current health of the ecosystem, the supply of inorganic sediments, nutrient availability, topography, and occurrence of extreme events. Future research should focus on quantifying the impact to microbial populations and vital microbial processes such as nutrient cycling, C storage, and the plant-soil interactions that modulate the stability of coastal peatlands vulnerable to sea-level rise, such as the Everglades.

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