Chambers, L.G., Davis, S.E., and T.G. Troxler. in press. Sea level rise in the Everglades: plant-soil-microbial feedbacks in response 1 2 3 4 to changing physical conditions. In: J.A. Entry, A.D. Gottlieb, K. Jayachandrahan and A. Ogram (eds.) Microbiology of the Everglades Ecosystem. CRC Press, Boca Raton. 5 Sea Level Rise in the Everglades: Plant-Soil-Microbial Feedbacks in Response to 6 **Changing Physical Conditions** Lisa G. Chambers^{*1}, Stephen E. Davis² and Tiffany G. Troxler³ 7 8 9 ¹Department of Earth and Atmospheric Science, Saint Louis University, 3642 Lindell Blvd., St. Louis, MO 63108. Email: chamberslg@slu.edu, phone: 314-977-3276, fax: 314-977-3117 10 ²Everglades Foundation, 18001 Old Cutler Rd. suite 625, Palmetto Bay, FL 33157. Email: 11 12 sdavis@evergladesfoundation.org, phone: 786-249-4460 ³Southeast Environmental Research Center, Florida International University, 11200 SW 8th Street, 13 Miami, FL 33199. Email: troxlert@fiu.edu, phone: 305-348-1453 14 15 *corresponding author 16 Introduction Coastal wetlands occupy the intertidal zone between the freshwater Everglades and the Gulf of 17 Mexico. At the interface with the marine environment, these wetlands are dominated by mangrove 18 forests, tidal creeks, and mudflats. Behind the coastal fringe zone is an ecotone that transitions into a 19 20 freshwater/upland community characterized by an increasing diversity of halophytic to glycophytic trees, 21 shrubs, and herbaceous vegetation. These productive coastal wetlands provide numerous, important ecosystem services. Directly benefiting humans, coastal wetlands function as habitat and nursery grounds 22 23 for shellfish and other commercially important fisheries, stabilize the coastline, and lessen the impact of 24 storm surges (Aburto-Oropeza et al. 2008, Costanza et al. 2008, Gedan et al. 2011). Moreover, some of 25 the most important functions of coastal wetlands are less tangible processes, including nutrient cycling, 26 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 27 28 significant threat to their global distribution and extent. In order to persist, the soil platform of a coastal 29 wetland must maintain a specific elevation niche relative to the ocean, normally between mean sea level 30 and mean high tide (Morris et al. 2002).

31 This chapter addresses the connections between sea level rise and Everglades soil microbial 32 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, 33 34 hydrologic drivers that are known to alter the structure and productivity of coastal wetland plant 35 communities (e.g., Williams et al 1999, Donnelly and Bertness 2001, Teh et al. 2008, Smith 2009). Plant 36 community change can thus affect the quality and quantity of organic C inputs to the system, which in 37 turn, can influence soil microorganisms and biogeochemical processes (Neubauer et al. 2013, Morrissey 38 et al. 2014). The feedback between plant and soil microbial dynamics, vegetation change, and evidence 39 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, which promotes vertical accretion and 40 41 resilience to rising sea levels, we will also describe the current understanding of how sea level drivers 42 may directly impact soil microbial activity and diversity. Finally, the chapter will conclude with a 43 discussion of how sea level rise impacts are assessed and the current evidence of sea level rise in the Everglades. 44

45 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 46 47 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 48 49 from the ocean that is recorded in a stratigraphy of alternating freshwater and marine sediments (Willard 50 and Bernhardt 2011). For instance, during the Eemian interglacial period, which began about 120,000 51 years ago, sea levels were at least 6.6 meters higher than present and south Florida was a shallow bay 52 (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 53 54 the last glacial period, sea levels dropped to approximately 120 m lower than today, exposing the 55 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 56

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 $3.1 (\pm 0.7)$ 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).

62 The flat, emergent wetland-dominated landscape of the Everglades has earned it the nickname, 63 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 64 level, and half of Everglades National Park lies below 0.6 m of sea level (Titus and Richman 2001). 65 Further, the slope of the Everglades averages just 5-8 cm (2-3 inches) per mile (Lodge 2010, McVoy et al. 66 67 2011). These geomorphologic conditions make south Florida's natural environments highly vulnerable to 68 increased sea levels. When considering the population that lives immediately adjacent to the Everglades 69 (approximately 6 million people, U.S. Census Bureau), the flat, gently sloping landscape renders the 70 Everglades a virtual "canary in a coal mine" for how both society and the natural environment will 71 respond to sea level rise.

72 As sea level rises, the coastal zone along the Everglades will be increasingly exposed to salinity 73 and inundation. The general thinking is coastal wetlands may respond by: 1) keeping pace with sea level 74 through vertical accretion, 2) migrating landward to maintain an optimal elevation relative to sea level, or 75 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 76 landward (IPCC 2007). An increase in mean sea level of 1 m will inundate approximately 4,050 km³ (4 77 78 million acres) of wetlands in coastal areas (Neumann et al. 2000). Therefore, understanding the controls 79 over the fate of C stored in coastal soils will be critical in predicting the fate of our coastlines—not to 80 mention the vast reservoir of nutrients (particularly nitrogen (N) and phosphorus (P)) stored in those soils. 81 In south Florida, sea levels are conservatively predicted to rise 0.60 m by 2060 (Zhang et al. 82 2011). This will cause salinity and inundation to increase in fresh and brackish water areas of the Florida

83 coastal zone and will increase the risk of storm surge-induced flooding and saltwater exposure in 84 oligohline 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 85 86 with a large number of canals, ditches, and dams used to divert water for flood control, agricultural water 87 supply, and human consumption. For example, the construction of canals on the east and west sides of 88 Lake Okeechobee in the northern Everglades caused a 10-fold increase in the portion of freshwater 89 flowing directly into the Atlantic Ocean and Gulf of Mexico, bypassing the Everglades. Much of this 90 freshwater had previously flowed south through the Everglades and into Florida Bay, effectively 91 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 92 93 throughout the Everglades are believed to be amplifying saltwater intrusion and the rate of the landward 94 migration of coastal habitats, especially in the eastern Everglades (Ross et al. 2000).

95 Soil Elevation and the Carbon Cycle

96 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 97 98 predominately histosols and entisols. Histosols, or peat soils, found in the Everglades coastal zone can be 99 up to 5.5 m deep with total C contents of 15-42% and organic matter contents of 32-89% (Whelan et al. 100 2005, Castaneda 2010, Chambers et al. 2014). These areas often support riverine and fringe mangroves. 101 Everglades enitsols are typically either of a marl-type, derived from dry-down and deposition of calcitic 102 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, 103 104 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

109 contributions to soil elevation (i.e., belowground production and litter accumulation) and deposition of 110 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 111 112 inorganic C) through the slowing of water velocities by aboveground biomass. Studies indicate both 113 organic and inorganic C are important to vertical marsh accretion (Day et al. 2000), with the latter 114 generally comprising a greater percentage of the soil as the proximity to the ocean or rivers increases. 115 Soil C accumulation in coastal wetlands is a balance between the C inputs (i.e., imports and CO₂ fixation) and outputs (i.e., exports, CO₂, and CH₄ flux) from the system. Major C reservoirs include plant biomass, 116 117 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/retention must exceed losses on a magnitude that 118 119 mimics or exceeds the current rate of sea level rise (Morris et al. 2002, Day et al. 2011).

120 Several lines of evidence suggest that conditions are generally met for coastal wetland 121 elevations to be sustainable in the context of current rates of sea-level rise. For example, a meta-analysis 122 of the accretion rates from 15 mangrove forests throughout the world indicates approximately 80% of the 123 systems studied are currently accreting at, or faster than, the rate of global sea level rise (Alongi 2008). 124 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 125 level was rising at a rate of 2.2 mm y⁻¹ (Smoak et al. 2013). However, rates of sea level rise are not 126 127 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 128 129 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

135 sediment supplies are low, as is the case in many areas of the coastal Everglades, root biomass and 136 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 137 138 account for 1-12 mm of surface elevation increase per year—equivalent to as much as 55% of the annual 139 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 140 141 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 142 143 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 144 Slough mangroves found that both resource limitations and greater inundation were correlated with 145 increased fine root production, which was a primary driver of soil formation and accretion (Castaneda-146 147 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 148 149 response of mangrove root productivity to nutrient addition is especially important in the coastal 150 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. 151

152 While root dynamics are thought to be important drivers of soil elevation in the coastal 153 Everglades, storm events that deliver large quantities of inorganic sediment can be significant in localized 154 areas (Castañeda-Moya et al. 2010), as well as seasonal groundwater dynamics that may affect the shrinkswell dynamics of the peat soils (Whelan et al., 2005). For example, a single hurricane (Wilma, 2005) 155 deposited between 0.5 and 4.5 cm of sediment across Shark River Slough and exceeded and annual 156 vertical accretion rate by 8-17 times (Castañeda-Moya et al. 2010). Benthic mats (dominated by algae 157 158 and cyanobacteria) can also contribute as much as 0.5-5 mm in soil elevation each year, accounting for 9-159 35% of the total increase in soil elevation (McKee 2011). In addition to the direct contributions benthic

160 mats and inorganic sediments make to soil accretion, their contributions may also increase nutrient 161 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 162 of organic matter by utilizing C in senescing leaves and roots, as well as organic exudates from roots, as 163 164 energy sources. These organisms assist in the break-down of organic polymers into monomers, which can 165 then be assimilated by bacteria and function as electron donors during respiration. The process of organic matter mineralization can result in the release of organic C in a particulate (POC) or dissolved (DOC) 166 form, or as dissolved carbon dioxide (CO_2) or methane (CH_4) gas (Schlesinger 1997). This C may be 167 168 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 169 170 core studies (excluding vegetation) indicate organic C loss from coastal wetland soils predominately 171 occurs through microbial respiration and the subsequent release of CO₂ back to the atmosphere. Across a 172 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, 173 174 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 175 176 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 177 178 and may exceed DOC export by a factor of 3 to 10 (Bouillon et al. 2008). Finally, a large portion of 179 mangrove organic C remains buried in the soil, with a global average burial rate of 26.1 Tg OC 180 (Breithaupt et al. 2012).

Depending on the influence of tides and 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.

190 Considering all of this, it remains unclear if the necessary soil accretion rates can be maintained 191 under the accelerated rate of sea level rise scientists are predicting (e.g., Church and White 2006, Haigh et 192 al. 2014), and what the consequences will be of the water management activities and human development 193 within the greater Everglades watershed. Despite pole-ward expansion of mangroves with global 194 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 195 196 wetlands world-wide will be out-paced by rising sea levels, leading to submergence and land loss. This 197 fate can be driven by physical constraints, such as a small tidal range or low sediment supply in the 198 coastal zone (Nicholls et al. 1999), or a biological feedback. For example, submergence is often observed 199 when areas of salt-sensitive coastal vegetation are not colonized by more salinity tolerant species quickly 200 enough. The existing vegetation becomes stunted or dies as a result of water-logging, osmotic stress, the 201 accumulation of toxic hydrogen sulfide (HS⁻) from intruding seawater, or salinity induced nutrient 202 inhibition (Koch et al. 1990, Bradley and Morris 1991, Batzer and Shartiz, 2006). Because live plants 203 play a vital function in maintaining soil structure, slowing water velocities to allow for sediment 204 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. 205 206 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). 207

208 *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

212 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 213 material to cave-in upon the subsurface soil, resulting in a rapid loss of elevation (DeLaune et al. 1994). 214 215 Recent geological research in the Everglades has shed light on the potential for collapse of freshwater 216 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 217 218 Cape Sable and Whitewater Bay that they attributed to disturbance caused by channelization, storm surge, 219 sea level rise, and freshwater diversion. These collapse events have led to the exposure of previously 220 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 221 222 similar to general "submergence," in which the depth of inundation increases without a comparable 223 response in vertical accretion and the system slowly converts to open water, peat collapse results in a 224 more rapid transition to open water conditions and can occur away from the aquatic edge, such as near the 225 inland ecotonal boundary of salt-tolerant vegetation, as observed in the Everglades.

Freshwater peat collapse could limit the landward colonization of mangrove propagules in 226 response to sea level rise by reducing the soil elevation to a point that it is too deep for new vegetation to 227 228 become established; this occurrence may be spatially heterogeneous, based on the location of freshwater 229 peat deposits throughout the Everglades. Shallow open water habitat or embayments may develop 230 instead, potentially interrupting the dispersal mechanisms for more salt-tolerant mangrove vegetation to 231 migrate landward. Alternatively, successfully colonization of peat collapse areas would hinge upon the 232 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 diversion have been extensive 233 234 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.

244 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 245 246 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 247 248 sign of impending collapse (Turner et al. 2004). However, accelerated soil mineralization may already be 249 underway while the vegetation is still in place. Additionally, some areas of the coastal Everglades are 250 composed of mineral sediments and soils that developed under the influence of marl-forming periphyton. 251 The response of these types of soils to sea level rise, de-watering, and accelerated mineralization are not 252 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 253 254 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 255 more light on the validity of the peat collapse concept and provide us with better predictive capability as 256 257 to how Everglades peat soils will respond to sea-level rise.

258 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

264 (*Rhizophora mangle*), followed by black mangrove (*Avicennia germinans*) and white mangroves (Laguncularia racemosa) as you move landward. Mangroves are typically able to tolerate high salinities 265 $(\sim 30+ \text{ ppt})$ and are adapted to wide fluctuations in both water level and salinity. A sharp ecotone often 266 separates mangroves from the less salinity tolerant communities, such as hardwood hammocks, that are 267 268 located further inland. This boundary is maintained by a combination of the salinity gradient and a 269 positive feedback mechanism by which each species modifies its' own environment to promote its 270 permanence (Jiang et al. 2011). In some areas of the coastal Everglades, particularly the southeastern 271 region near Taylor Slough, the mangroves have a less abrupt inland ecotone, first becoming interspersed 272 with herbaceous and succulent halophytes (e.g., Batis maritima, Borrichia frutescens and Juncus romoerianus), then giving way to Gulf Coast spikerush (Elecocharis cellulosa) and less salt tolerant 273 274 sawgrass (Cladium jamaicense) communities (Ross et al. 2000). There are also areas of unvegetated mud 275 flats and limestone pinnacles (Smith et al. 2013). If the coastal Everglades follow the typical model for 276 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 277 278 way to mangroves. However, the risk of soil collapse in predominantly peat-based oligohaline or 279 freshwater areas needs to be considered; this could lead to the establishment of open water conditions 280 prior to mangrove establishment (Wanless and Vlaswinkel 2005).

281 Salinity as a driver of vegetation change

282 Across the coastal Everglades landscape, salinity is a key driver of primary productivity and composition (Castañeda-Moya et al. 2011, 2013, Troxler et al. 2013). However, the salinity gradient is 283 284 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 285 Everglades penetrates well into the mangrove zone, while reduced flows during the dry season 286 287 (December-April) allow tidal water to penetrate further upstream. For example, under dry season 288 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). 289

290 During the wet season, the surface water of these same areas is typically fresh (<0.5 ppt). Sawgrass is 291 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 292 293 drought in Taylor Slough, the replacement of sawgrass by more salt-loving species such as mangroves has 294 been observed (Ross et al. 2000). Mangrove expansion in other areas of the Everglades has also been 295 noted and thought to be correlated with increased water levels associated with sea level rise (Smith et al. 296 2013). Extended droughts, managed flow reductions, and the construction of canals and ditches can all 297 initiate inland mangrove expansion by allowing the tidal prism to migrate upstream and carry with it 298 mangrove propagules to facilitate mangrove expansion (Fig. 4; Ross et al. 2000).

The observed expansion of mangroves can have numerous implications for soil microbiology, 299 300 although, to our knowledge, this area of research has received little attention in the literature. For 301 example, while both mangroves and sawgrass conservatively store nutrients in tissues of leaves, resulting 302 in high C to nutrient ratios, the quantity and quality of organic matter provided by mangrove wood and 303 leaf litter may be less labile than sawgrass litter. This consideration led Bianchi et al. (2013) to 304 hypothesize that an increased C storage capacity of wetlands would ensue with continued pole-ward 305 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 306 307 disturbance events such as fire, lightning strikes, and hurricanes on light penetration and soil temperature, 308 and could also alter the rate of vegetation-induced sediment deposition. Finally, soil redox potential may be differ under cover of these different plant communities, which affects the utilization of various electron 309 acceptors by soil microbes and influences the overall rate of C mineralization (Reddy and DeLaune 310 311 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 312 313 of nutrients, rates of soil respiration, and other physio-chemical conditions in the soil (Alongi et al. 2000). 314 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 317 318 vegetation and conditions in the soil. In the Everglades, studies have found a linear decrease in the lightuse efficiency of mangroves as salinity increases, suggesting decreased productivity with saltwater 319 320 intrusion (Barr et al. 2010). Sawgrass (C. jamaicense) aboveground net primary production has also been 321 reported to be negatively correlated with surface water salinity, especially periods of high maximum 322 salinities, which primary production rates seem slow to recover from (Childers et al. 2006, Troxler et al. 323 2013). Increasing root phosphatase activity has been detected for sawgrass plants associated with relatively low salinity levels (0.5-5ppt), indicating a strong demand for P (Rejmankova and Macek 2008). 324 325 Field and laboratory studies conducted elsewhere on marsh vegetation have documented plant mortality 326 and reduced growth in several other common Gulf of Mexico species (e.g., Sagittaria lancifolia, Panicum 327 *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 328 329 suffers from osmotic stress (Batzer and Shartiz 2006) and an accumulation of hydrogen sulfide (HS⁻) in 330 the soil porewater. Hydrogen sulfide, a by-product of sulfate reduction, acts as a phytotoxin and 331 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 332 333 storm surges. Even if the intensity and frequency of storm surges is not affected by climate change, sea 334 level rise will still result in an increase in the height of the surge, and thus increase the area of land 335 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 336 storm surges throughout Florida is expected to be condensed, such that a 1-in-50 year surge will be 337 338 experienced roughly every 5 years (Park et al. 2011). This coincides with evidence that the number of 339 maximum water level events (meteorological and storm related) has increased in frequency in south Florida since 1961 (Obeysekera et al. 2011). 340

341 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 342 ecotone by carrying and depositing propagules further inland. The sharp vegetation boundary between 343 344 the coastal mangroves and hardwood hammocks seems especially vulnerable to saltwater intrusion 345 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 346 347 salinity stress (Teh et al. 2008). Meanwhile, other research in the Everglades has documented 348 catastrophic damage to mangroves as a result of hurricanes (e.g., wind throws, defoliation, smothering by 349 sediments), leading to a transition to mudflats near the coastline (Smith et al. 2009).

350 Phosphorus as a driver of vegetation change

351 Because of the Everglades' legacy as a nutrient-limited system, differentiating between the 352 impacts of sea level rise (salinity and inundation), and the associated increase in nutrient supply 353 (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 354 355 (Vitousek and Howarth 1991). While N is still an important element for growth and production in the 356 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 ($<10 \text{ ug L}^{-1}$), with 357 much of it being derived from the atmosphere (Belanger et al. 1989). The P limitation was a key driver in 358 359 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 360 from agricultural sources, which has led to a shift in plant communities. This is especially evident in the 361 Water Conservation Areas where periphyton biomass has declined and areas previously occupied almost 362 exclusively by C. jamaicense are now monotypic stands of Typha domingesis (Davis 1991, McCormick et 363 364 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, 367 368 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 369 370 of a mangrove community damaged by Hurricane Donna (1960) was evaluated to determine the driving 371 forces of structural development. The study found that neither soil salinity nor sulfide concentrations 372 reached levels known to influence species composition, but concentrations of N and P mirrored 373 productivity rates. Both basal area and wood production were highest at the coast (where N and P 374 availability was greatest) and decreased further inland (Chen and Twilley 1999). Research also indicates 375 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 376 377 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 378 379 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. 380

381 Vegetation-Microbial Interactions

Vegetation change directly impacts soil microbiology by altering the amount and timing of C 382 383 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, 384 385 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, 386 387 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). 388 The decrease in wetland structural complexity caused by salinity also reduces the variety of terrestrial 389 390 organic matter to serve as a microbial substrate, and could prompt a similar decline in the diversity of the 391 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), 392

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.

396 Shifts in vegetation composition can also impact microbes due to differences in the 397 bioavailability of their litter material. For example, polyphenolic compounds such as condensed tannins 398 and lignins, reduce the ability of microbes to degrade those tissues, creating the need for expensive 399 exoenzyme production to break-down these refractory materials (Field and Lettinga 1992, Berg et al. 400 1996). Leached, plant-derived polyphenolic compounds may also have an inhibitory effect on microbial 401 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 402 403 (Prescott 2011). Inputs of organic matter from plants occur as leaf and root litter, and dissolved organic 404 matter (DOM) from litter leaching. While components of freshly leached DOM can be easily degraded 405 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 406 407 the complexity and nutritional composition (structure or C-C bonds and C:N:P) of plants either in leaves 408 or roots are important for soil organic matter (SOM) dynamics, microbial community composition also 409 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 410 411 degradation in aerobic, low nutrient environments (Goodfellow and Williams 1983, McCarthy et al. 1987, 412 Güsewell and Gessner 2009, Peltoniemi et al. 2009). With adequate nutrient supply, microbes may also 413 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 414 415 C:N) is inversely related to salinity in oligonaline wetlands (Morrissey et al. 2014b). In the Everglades, 416 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 417 418 coastal zone.

419 Microbial Ecology and Biogeochemistry

The connection between sea level rise and microbiology is an emerging area of research with 420 broad implications given the strong connection between hydrology, plant production, soil microbes, and 421 422 soil C storage. Soil microbes are often the first organisms in a wetland to respond to environmental 423 changes due to their large surface-to-volume ratio and rapid turnover rate. Although microbial changes 424 are less visible than vegetation shifts, they often occur within a matter of hours or days following an event 425 and could involve alterations in community function, composition, and diversity. For example, 426 periphyton mats in the Everglades (a mixture of cyanobacteria, algae, and microinvertbrates), are highly 427 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 428 429 coastal wetlands, saltwater intrusion, increased inundation, and storm surge events linked to sea level rise 430 could all directly alter soil microbial community structure, activity, and subsequently the balance of soil C 431 that controls how resilient a wetland is to sea level rise (e.g., Chambers et al. 2011, 2013, Neubauer et al. 432 2013).

433 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 434 must be capable of osmoregulation, which can involve either the accumulation of potassium chloride in 435 the cytoplasm, or the biosynthesis and/or accumulation of compatible solutes (Oren 2008). Salt intolerant 436 437 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 438 439 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 440 CO₂ and CH₄ production (Pattnaik et al. 2000, Muhammad et al. 2006, Gennari et al. 2007). It is believed 441 442 the higher conductivity in the soil-water environment causes osmotic/ionic stress to the organisms and 443 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 444

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 450 451 environmental change may be even more critical than the increase in ionic strength—an increase in the sulfate, SO₄²⁻, concentration. Unlike inland salinity discussed above, seawater contains a consistent ratio 452 of ions, of which $SO_4^{2^2}$ is the third most abundant. Sulfate functions as a terminal electron acceptor 453 454 (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 455 456 commonly used TEA by heterotrophic bacteria is oxygen, which utilizes C as an energy source (electron 457 donor) and produces energy in a relatively efficient manner. The presence of water reduces the diffusion of oxygen into the soil by10,000 times, requiring microbes in wetlands and coastal ecosystems to rely on 458 459 alternative TEAs, which they utilize in a specific sequence based on their availability and potential energy 460 vield (Patrick and DeLaune 1977; Table 1). Sulfate is near the bottom of the energy cascade and is used 461 only when the environment becomes sufficiently reduced (as indicated by an oxidation reduction potential (Eh) of <-100 mV) and produces only $-0.7 \times 10^{-3} \text{ kJ mol}^{-1}$ of energy. 462

463 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 464 that although an increase in ionic strength from seawater intrusion may slightly suppress microbial 465 activity by causing osmotic stress, there will also be a stimulatory effect from the influx of SO_4^{2-} 466 providing an abundance of new TEAs for anaerobic respiration. This was demonstrated under laboratory 467 468 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 soil (Chambers et al. 2011). Additions of 10 ppt 469 seawater to freshwater sediment cores can cause SO_4^{2-} reduction to become the dominant pathway for 470

471 microbial respiration after only 12 days, and account for 95% of all organic C oxidation after 35 days of 472 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 473 474 limiting (Chambers et al. 2011). A longer-term manipulative field study in a freshwater tidal marsh found 475 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-476 microbial interactions (Neubauer et al. 2013). Interestingly, while the stimulatory effect of SO_4^{2-} on 477 respiration appears to be somewhat transient, the suppression of methanogensis through competitive 478 479 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% 480 481 in just 5 days (Chambers et al. 2013). In the field, oligonaline water additions to a freshwater wetland soil 482 caused a 2 to 3-fold decrease in CH_4 production that persisted for 3.5 y (Neubauer et al. 2013). 483 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. 484 During low water (low tide) conditions, more oxygen can diffuse into the soil to promote aerobic 485 486 respiration. For this reason, low tide CO_2 production rates can be between 50-300% higher in coastal 487 wetlands than high tide CO_2 production rates, with the variability attributed to differences in the hydraulic 488 conductivity of the soil (Chambers et al. 2013). However, as sea level rises, we can expect deeper, more 489 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 490 491 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, 492 which tend to be slower and less efficient than aerobic respiration. In a mesocosm study that simulated 493 494 sea level rise in an Everglades mangrove peat soil, soil organic C loss was 90% higher under control 495 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 496

497 increases, promoting soil C storage and accretion. However, the same study also demonstrated that 498 prolonged inundation may actually result in a loss of soil material, as seen by a decrease in surface (0-5 499 cm) soil bulk density (Chambers et al. 2014). While the mechanism for this reduction in bulk density is 500 not known, it was correlated with an increase in porewater dissolved organic C, causing speculation it 501 may be a product of excessive leaching during water-logging or increased shear stress due to the deeper 502 water column above the soil (Chambers et al. 2014).

503 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 504 505 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 506 507 has found a direct correlation between bacterial abundance and salinity in freshwater tidal marshes 508 (Morrissey et al. 2014b). Only one study of microbial community composition has been performed in the 509 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 510 511 secondarily on P availability (Ikenaga et al. 2010).

Ultimately, while soil microbial communities may be rapid indicators of wetland ecosystem 512 513 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., 514 the size of the oxidized rhizosphere), quantity and quality of organic C, and will interact with enzyme 515 synthesis. Under conditions in which salinity drives a decline of plant productivity, vegetation death, or 516 517 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 518 519 coastal peatlands.

520 The Future of the Coastal Everglades

521 As salinity and inundation patterns in the Everglades change in response to sea level rise and 522 human-driven alterations in hydrology, coastal zone ecology is changing as well. The movement of

523 ecotones (regions bridging two distinct community types) is often a reliable way of monitoring 524 environmental change because ecotones develop and migrate in response to specific environmental gradients. Several studies have used historical aerial photography and various bio-indicators to document 525 526 shifts in the location of coastal ecotones in the Everglades over time. This provides a glimpse of how the 527 ecosystem has responded to past sea level changes and a basis for predicting future ecosystem responses. 528 The land boundary of the Everglades, and all of Florida, has changed significantly throughout 529 geologic time in response to sea level. Soil cores indicate the current seaward edge of the Everglades 530 formed from red mangrove (*R. mangle*) derived peats that began accumulating approximately 3,500 years 531 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 532 mangroves to expand in the seaward direction, creating mangrove islands (Parkinson et al. 1989). The 533 534 distribution of mangroves, and peat accumulation from relic mangrove forests, are considered good 535 indicators of historic sea level because they always occupy the upper portion of the tidal range (Scholl 1964). 536

Current research shows that mangroves within the Everglades are continuing to respond to 537 changing sea levels, mainly through the expansion of their coverage at the expanse of inland marsh 538 539 habitat (Doyle et al. 2003). A look at aerial photographs of the Ten Thousand Islands National Wildlife 540 Refuge on the western edge of the Everglades has shown a 35% increase in mangrove coverage in the 541 past 78 years. The construction of canals near the coast is a driving force in the expansion of mangroves 542 within previously low salinity marshes because they provide a conduit for saltwater intrusion and 543 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 544 boundary between the mangrove-graminoid community and the interior sawgrass marsh has shifted inland 545 3.3 km, which is believed to be in response to a combination of reduced freshwater flows and encroaching 546 547 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 548

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 555 Everglades are migrating landward with rising sea levels, there are large uncertainties about how the 556 557 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 558 documented erosional events accompanying hurricanes (Doyle et al. 2003, Wanless et al. 1994). At 559 present, mangrove soil accretion rates are exceeding sea level rise rates in at least one area of the 560 561 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 562 al. 2006) suggests that saltwater intrusion could increase productivity (Chen and Twilley 1999), and 563 subsequently soil accretion. However, increasing salinity may have the opposite effect due to the 564 565 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 566 peats and mangrove transition is also worth considering as a driver shaping the coastal Everglades of the 567 568 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 restabilize the soil, they may continue to grow larger and transition directly into subtidal habitat as sea

levels continue to rise. With 8,744 km² of south and southwest Florida being located below the 1.5m
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.

578 Conclusion

579 Overall, there is ample evidence to support the idea that coastal ecology in the Everglades is 580 changing in concert with rising sea levels. In the southeast Everglades, the signature of sea level rise has 581 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 582 583 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 584 altering the physical and chemical environment. However, the structure and function of microbial 585 586 communities will likely respond far in advance of vegetation shifts. Few studies have addressed the 587 direct impacts of sea level rise on soil micro-biota, but evidence such as changes in soil respiration rates (CO₂ production) suggest seawater intrusion can accelerate heterotrophic microbial activity for the short-588 589 term and suppress methanogenesis for the long-term. The important question is how changes in 590 vegetation type, productivity, and microbial activity will affect the overall balance of C in coastal 591 wetlands. An increase in C inputs and net decrease in microbial respiration would create a positive 592 feedback to promote vertical accretion and increase wetland resilience. In the most likely scenario, 593 different regions of the Everglades will have unique responses to sea level based on the current health of 594 the ecosystem, the supply of inorganic sediments, nutrient availability, topography, and occurrence of 595 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 596 the stability of coastal peatlands vulnerable to sea-level rise, such as the Everglades. 597

598 Acknowledgements

We are grateful to all FCE LTER scientists for their contributions to discussions of this topic and
acknowledge financial support provided by National Science Foundation grants DEB- 1237517 and DBI-

601 0620409. This is contribution number 668 from the Southeast Environmental Research Center at Florida
602 International University.

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

Alternative Electron	Dominant C	Eh Range	Theoretical Energy
Acceptor	End-Product	(@ pH 7)	Yield (ΔG^{o}_{R})
NO ₃	$\overline{CO_2}$	250 to 350 mV	$-14.5 \text{ x } 10^{-3} \text{ kJ mol}^{-1}$
Mn ⁴⁺	CO_2	220 to 300 mV	-3.0 x 10 ⁻³ kJ mol ⁻¹
Fe ³⁺	$\overline{CO_2}$	120 to 180 mV	-1.7 x 10 ⁻³ kJ mol ⁻¹
SO_4^{2-}	CO_2	-100 to -250 mV	-0.7 x 10 ⁻³ kJ mol ⁻¹
CO_2	CH_4	< -250 mV	-0.1 x 10 ⁻³ kJ mol ⁻¹

922 Figures

- 923 Figure 1. A generalized depiction of the carbon cycle in wetlands, including the major storage reservoirs
- 924 and transformations.



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



Modified from: K. R. Reddy, and R. Delaune 2008

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



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

