

HYPERSALINE TIDAL FLATS (*APICUM ECOSYSTEMS*): THE WEAK LINK IN THE TROPICAL WETLANDS CHAIN

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ABSTRACT

Hypersaline tidal flats (HTF) are transitional ecosystems commonly occurring in arid/semi-arid coastal regions. These ecosystems typically border mangrove forests. HTF perform important functions related to the maintenance of coastal biodiversity as well as support socio-economic and cultural activities in local communities. Despite their importance, HTF are rarely studied, especially with regard to the understanding of their formation and function. From the premise that the knowledge on the formation of HTF and soil contribute to the understanding of ecological relationships occurring in these ecosystems, a review is presented. Flat topography, coastal dynamics, pronounced hydric deficit, limited frequency, and duration of tidal flooding are the key factors for the formation of these coastal wetlands. The active pedogenetic processes (salinization, gleyzation, sulfidization and bioturbation) are highly influenced by these factors and present important ecological roles, specifically in regards to carbon and nutrient dynamics. This review presents evidence for the necessity of further studies on the ecological relationships in HTF's, as well as determining the ecological connection between HTF and other wetlands. Filling this knowledge gap is essential if we are to improve public policies and conservation laws on the protection of all coastal ecosystems.

Key words: tropical semiarid estuaries, saltflats, ecosystem formation, soil formation

51 INTRODUCTION

52 Wetlands are transitional ecosystems between terrestrial and aquatic
53 environments which occur in areas where soils are naturally or artificially saturated by
54 water due to ground or surface water saturation. Furthermore, the saturation may take
55 place during part of or the entire year. These ecosystems are commonly found in river
56 deltas, estuaries, floodplains, and tidal flats (Neue et al. 1997).

57 These ecosystems are important in terms of the global biogeochemistry, water
58 balance, wildlife, food source (Neue et al. 1997, Mitsch et al. 2009) and carbon
59 dynamics (Nelleman et al. 2009) covering, approximately, only 5 to 7% of the world's
60 surface area (Neue et al., 1997) Because of environmental functions, these ecosystems
61 are among the most important, yet vulnerable and endangered ecosystems (Mitsch et al.
62 2009). In fact, in terms of global economics, the degradation of wetlands results in
63 monetary losses in the form of goods and services which total approximately \$630
64 million US Dollars per year (Blankespoor et al. 2012).

65 Mangroves are typical tropical and subtropical wetland ecosystems situated
66 where the land meets the sea and are characterized by a high degree of ecological
67 stability but with interactive components (e.g. channels, ponds, islands, and hypersaline
68 tidal flats) which promote high primary productivity. The biological productivity is
69 stimulated by the exchange of water masses, sediment, nutrients, organic matter, and
70 animal populations (Tomlinson 1986, Kjerfve 1990, Alongi 2002, Lacerda 2002, Lana
71 2003, Alongi 2008). Due to the coupling of multiple components, mangrove ecosystems
72 are key elements for the flow of energy and nutrients between terrestrial environments
73 and the ocean. The result of this coupling of components is the generation of ideal
74 conditions for nurseries and refuge areas (Alongi, 2002; Aburto-Oropeza et al. 2008).
75 Considering the various roles of mangrove ecosystems (fisheries, forestry, coastal

76 protection, recreation and tourism, nutrient retention, carbon sequestration, biodiversity,
 77 and also non-use areas), the estimates suggest that the global economic value of
 78 mangrove ecosystems are approximately \$27,000 US Dollars ha⁻¹ yr⁻¹ (Salem and
 79 Mercer 2012).

80 In Brazil, a geoenvironmental unit called *apicum* (pl. *apicuns*; from indigenous
 81 language Tupi: “apecu” meaning saltwater marsh; Cunha 1999) can commonly be found
 82 associated with mangroves found in arid and semi-arid regions (Meireles et al. 2007,
 83 Lebigre 2007, Hadlich et al. 2010). *Apicuns* are defined as hypersaline tidal flats formed
 84 in marginal areas of mangrove forests (or inside them), with a unique flora composition
 85 (Table 1), particularly when compared to the mangroves (Lebigre 2007). Similar
 86 environments other than “*apicum*” or “*tanne*” (Lebigre 2007) were characterized and
 87 studied in other semiarid regions of the world sharing similar genetic and ecosystemic
 88 traits (Bigarella 1947, Bigarella 2001, Lana 2003, Conesa et al. 2011). The literature
 89 reports the occurrence of these hypersaline tidal flats in Brazil (Lebigre 1999, Hadlich et
 90 al. 2008, Marques 2010), Africa (e.g., Gabon and Madagascar) and Oceania (New
 91 Caledonia; Lebigre 2007).

92 The key characteristic of these ecosystems is that they are hypersaline and may
 93 reach salinity values up to five times greater than those found in the sea water (Ridd and
 94 Sam 1996, Sam and Ridd 1998, Ridd and Stieglitz 2002). Furthermore, the association
 95 of HTFs with mangroves is also a necessary condition for the characterization of this
 96 ecosystem (Lebigre 2007, Hadlich et al 2010).

97 When compared to other coastal ecosystems, the studies of these hypersaline
 98 tidal flats are recent (Lebigre 2007) and began with studies in Senegal (Vieillefon 1969,
 99 1977, Marius 1985). In fact, Lebigre (2007) reported that the first study of hypersaline
 100 tidal flats (*tannes*) was carried out in Senegal and Gambia, followed by studies in

101 Madagascar, Australia, Nicaragua and Ecuador; all located in tropical climates with a
102 three month dry season. According to Marius (1985), the hypersaline tidal flats are
103 formed through flooding and drying cycles which culminate in increases salinities
104 relative to entering sea water with the disappearance of mangroves and the colonization
105 of soils by halophytes. Sadio (1989) reported that pedogenesis in these environments is
106 driven by the water regime conditioning the occurrence of hydromorphism, and also
107 includes gleying and sulfidization processes.

108 In southeast Brazil (the State of Espírito Santo), Marius (1985) performed the
109 first pedological study in environments similar to the Senegalese *tannes*. The author
110 found soils characterized by a sandy clay texture, grey colors, and colonies of
111 *Philoxerus vermicularis*, *Sesuvium portulacastrum*, and *Eleocharis caribaea*. The
112 region identified in southeast Brazil, however covered less area than the hypersaline
113 tidal flats in Africa.

114 In spite of the limited number of studies, these ecosystems perform important
115 functions in terms of the maintenance of the biodiversity of flora and fauna in coastal
116 environments, as well as provide socio-economic and cultural activities for local
117 communities (Nascimento 1993, Schmidt 2006). For example, local populations use
118 these areas to harvest crustaceans (such as *Cardisoma guanhumi* [Leitreille]), for
119 recreational activities, and also as grazing sites for domesticated animals (Ackermann et
120 al. 2006). Furthermore, these environments allow access to the mangrove forest
121 (Meireles et al. 2007). Although mangroves and *apicuns* perform a great number of
122 similar social and ecological functions, the latter are still subjected to a great variety of
123 human pressures, especially in northeastern Brazil (Meireles et al. 2007). This negative
124 environmental impact is likely due to the fact that mangroves have always been

125 explicitly protected by Brazilian laws whereas *apicuns* were poorly protected (Ucha et
 126 al. 2008, Hadlich et al. 2008).

127 Despite the importance of these HTF's, a great knowledge gap still exists,
 128 specifically with regard to ecosystem formation and soil genesis (Ucha et al. 2008,
 129 Hadlich et al. 2010). Determining how ecosystem and soil processes function in HTF's
 130 is crucial to understanding their function as a whole on an ecosystem level., Here we
 131 present a literature review in order to provide theoretical analysis on the processes that
 132 occur in these tropical wetlands, with specific reference to soils.

134 **Hypersaline tidal flats: definitions and general characteristics**

135 The Brazilian word "*apicum*" describes sandy areas close to mangroves (Cunha
 136 1999, Hadlich et al. 2008). In reference to the *apicum* ecosystem, the words "*salgado*"
 137 (Salty, briny) and "*areal*" (Sandy area) were also reported by Schmidt (2006) as
 138 synonyms used by local populations to refer to hypersaline tidal flats from NE-Brazil.
 139 In addition, the words "*salt flats*", "*tidal flats*" and "*supratidal flats*" are used to
 140 reference environments which are similar to the Brazilian "*apicuns*", even though, there
 141 is some controversy on the best synonym for these terms in English. According to
 142 Lebigre (2007), the Brazilian *apicum* environments correspond to the French term
 143 "*tannes*", also used to designate HTF's.

144 *Apicuns* are the transition zones found mostly between semiarid mangroves
 145 forests and the adjoining dry upland areas, i.e. Coastal Tablelands in Brazil (Fig. 1 and
 146 2; Hadlich et al. 2008, Ucha et al. 2008, Marques 2010), also occurring within
 147 mangrove forests (Maciel 1991, Schmidt 2006, Hadlich et al. 2008) and whose limits
 148 are set by the mean level of the spring tides (Fig. 1 and 2; Maciel 1991, Pellegrini
 149 2000).

150 The apicuns environments, which are always associated with mangroves
 151 (Schaeffer-Novelli 2002), are subjected to much less frequent tidal flooding periods
 152 compared to mangrove flooding frequency. This different flooding regime coupled with
 153 high evaporation and low precipitation rates causes the formation of hypersaline soils
 154 (Ridd and Sam 1996, Sam and Ridd 1998, Ridd and Stieglitz 2002), which frequently
 155 present salt crusts (Fig. 3A; Lebigre 2007, Hadlich et al. 2008). The less frequent tidal
 156 flooding regime is caused primarily by the transport of sediments into the estuaries by
 157 water and/or wind. Sediment transport promotes the formation of sediment banks and
 158 the subsequent obstruction of tidal creeks, thus limiting the flow seawater to tidal
 159 flooding during the spring tides. The rainfall regimes with long and well defined dry
 160 seasons also contribute to the development of the hyper-salinity.

161 The apicum differs from salt marshes and tidal marshes in that the latter flood
 162 daily on during high tide. The flooding results in strong chemically reducing conditions
 163 (Odum 1988) that dilutes the salinity. The lower salinity conditions in salt marshes and
 164 tidal marshes promote the development of grasses and sedges, while the HTF are
 165 primarily vegetated by extreme halophytes (Table 1; Fig. 3B; Marques 2010), or are
 166 devoid of vegetation (Fig. 3C; Hadlich et al. 2008). The sabakhas, on the other hand, are
 167 hypersaline flats which occur only in arid regions, are colonized by cyanobacteria (Attia
 168 2013) and differ from the apicum in the mineral composition of the sediments,
 169 composed by well developed evaporites (Stanford and Wood 2001, Attia 2013).

170 The soil salinity in the HTF controls the species which colonize the soils: they
 171 are typically halophytic perennial herbaceous succulents (e.g., *Batis maritima*; Table 1;
 172 Fig. 3D), rather than mangrove. However, the seasonal climatic variations influence
 173 plant colonization patterns in hypersaline tidal flats soils. During the rainy season,
 174 rainfall dilutes the salts and allows the colonization of soils by typical mangrove species

(Nascimento 1999, Hadlich et al. 2010). In addition, during dry seasons, which are common along the NE-Brazilian semiarid coast, the expansion of *apicum* species may spread into mangrove ecosystems (Portugal 2002, Filho 2007).

Hypersaline tidal flats may interact with the adjacent ecological systems through ecological, geological, sedimentological, and pedological relationships (Lebigre 1999, Meireles and Silva 2002). However, hypersaline tidal flats clearly differ from other wetland ecosystems (e.g. salt marshes, swamps, mangroves, and lagoons) and therefore are important to the environmental variability and biodiversity in coastal zones.

Socio-ecological roles of hypersaline tidal flats

Hypersaline tidal flats provide refuge, nursery habitat, food resources for different animal species, primarily decapod crustaceans (Nascimento 1993, Schmidt 2006) (Fig. 3E and F, Fig. 4A). According to Nascimento (1993), large populations of fiddler crabs *Uca spp.* may be found in these ecosystems. During the rainy season, the population density of *Uca* may reach up to 250 individuals per square meter (ind m⁻²), while in areas shaded by mangrove trees, the density of young *Ucides* specimens does not exceed 30 ind m⁻².

The *Cardisoma guanhumi* (Leitreille) land crab, which is an important food source for local populations (Fig. 3E and F), burrows in elevated sites where flooding is less frequent, specifically in the *apicum*, contrary to other typical mangrove crab species (e.g., *Uca maracoani* and *Ucides cordatus*; Oliveira 1946). Thus, the conservation and protection of *C. guanhumi* depends on the conservation of *apicuns* (Firmo et al. 2012). In addition, *Gecarcinidae* and juvenile *Callinectes* crabs are also found in these HTF's (Normann and Pennings 1998).

199 With respect to the edaphic perspective, these hypersaline tidal flats act as a
 200 nutrient reservoir to surrounding ecosystems providing organic matter, nutrients and
 201 ions (Nascimento 1999, Marques 2010). Moreover, HTF's represent a strategic region
 202 for protecting mangrove species in response to rising sea level (Portugal 2002) as well
 203 as other natural and/or anthropogenic disturbances.

204 Coastal wetlands, such as mangroves and salt marshes are known to store high
 205 amounts of organic carbon. Despite their relatively low area, in comparison to some
 206 other coastal communities, these environments may store up to 50% of the global
 207 terrestrial organic C (Gorham 1995, Lal 2004, Hopkinson et al. 2012). For example, salt
 208 marshes represent the coastal wetlands with the highest burial rate (mean = 1.51 Ton C
 209 $\text{ha}^{-1} \text{y}^{-1}$), followed by mangroves (mean = 1.39 Ton C $\text{ha}^{-1} \text{y}^{-1}$) and seagrasses (0.83 Ton
 210 C $\text{ha}^{-1} \text{y}^{-1}$ (Nelleman et al. 2009) (Table 3). Unfortunately, at this time data are not
 211 available for the organic carbon burial rate in *apicum* environments. However, since
 212 HTF represent a key role for the preservation of semi-arid mangrove forests, the
 213 anthropogenic impacts on these HTFs would also impact the ability of the mangrove to
 214 act as a carbon sink (Lacerda et al. 2007). Recently, the conception of the term "*Blue*
 215 *Carbon Sink*" was used to describe the importance of coastal wetlands in the global
 216 carbon cycle (Nelleman et al. 2009). The potential for carbon sequestration by *apicuns*
 217 occurs via mangrove burial processes during genesis; and therefore highlights the
 218 importance of protecting these and other coastal wetlands (Chmura et al. 2003,
 219 Nelleman et al. 2009).

220 The HTF also has a great socio-economic and cultural importance. The local
 221 populations (e.g., indigenous peoples, fishermen, shell fishermen) collect crustaceans,
 222 fish, and shellfish necessary to their diets from mangroves and associated areas;
 223 furthermore, they use the *apicum* regions to access the mangroves (Meireles et al

224 2007). However, some crustaceans, such as *Cardisoma guanhumi* (Leitreille), which
 225 have great economic value, are often collected primarily from *apicum* regions. In
 226 addition, the *apicums* close to the fishers' houses may be used for goat and cattle
 227 husbandry (Fig. 4B; Ackermann et al. 2006, Lebigre, 2007), as well as for recreational
 228 activities.

229 Despite its social and ecological importance, hypersaline tidal flats have been
 230 subjected to a great variety of anthropogenic stresses in different parts of the world due
 231 to economic activities, such as aquaculture (e.g. shrimp farming) and salterns (Fig. 1,
 232 and 2; Wilke and Fortuna 2003, Lebigre et al. 1990, Lebigre 2007, Ucha et al. 2008,
 233 Hadlich et al. 2008). According to Meireles et al. (2007), in the Brazilian states of Rio
 234 Grande do Norte and Ceará, where shrimp farming activity is intense, the deployments
 235 of production ponds occurs on hypersaline tidal flats (Fig. 1 and 2).

236 The Brazilian Forest Code (Brazil 1965) and the National Council of the
 237 Environment (CONAMA; Brazil 2002) consider the mangrove forests as permanent
 238 preservation areas. However, due to the legal interpretation, the enforcement of laws
 239 governing for the protection of *apicum* regions have been inadequately described
 240 (Schaeffer-Novelli 2002). Considering the close relationship between mangroves and
 241 *apicuns*, the latter should be considered as part of the mangrove ecosystem with regards
 242 to the applicability of conservation laws (Schaeffer-Novelli 2002). Although the New
 243 Brazilian Forest Code (NBFC; Brazil 2012) has included *apicum* regions, it also has
 244 allowed for an occupancy rate of 10 to 35% by shrimp farms and salterns, respectively.
 245 Furthermore, the saltern and shrimp farm activities initiated prior to July 22nd 2008 in
 246 *apicuns* were legalized (Brazil 2012).

247 Due to the reduced number of studies focusing on *apicuns* ecological functions,
 248 within their ecological boundaries and associated mangroves, it is virtually impossible

249 to protect *apicuns* in Brazil (Rovai et al. 2012). Therefore, once anthropogenic activity
 250 is allowed to occur within these ecosystems, mangrove forests may also become
 251 threatened (Rovai et al. 2012).

252

253 **Geomorphological aspects of hypersaline tidal flats**

254 Apicuns and mangroves are contiguous ecological systems which present
 255 contrasting soils, with very different physical, chemical and mineralogical
 256 characteristics (Ucha et al. 2008, Marques 2010). From a geomorphological point of
 257 view, the HTF's are considered active areas which constantly receive sediments from
 258 dunes and adjacent higher terrains (e.g., Coastal Tablelands from the Brazilian coast).
 259 Sediments are delivered via three possible mechanisms: (1) wind action, which also
 260 affects mangroves and estuarine channels; (2) waves that deposit sediment during ebb
 261 flow; and (3) the riverine system which transports sediments from inland areas and
 262 deposits it along the coastal plains (Fig. 5; Meireles et al. 2007).

263 The sedimentary material forming HTF soils ranges from fine (clay and silt) to
 264 coarse (sand). However, the sand fractions composed of quartz and feldspars (Table 2;
 265 Marques 2010), may have different origins than the sediments deposited by the above
 266 mentioned processes. According to Hadlich and Ucha (2009), after the sediment
 267 deposition, the dispersion of colloids by sodium in seawater, combined with the high
 268 energy of tides and rainfall events, result in the clay removal, particularly in surface
 269 layers (Table 2). The relatively high sand content in Brazilian hypersaline tidal flat soils
 270 may also be related to the evolution of the coast during the Quaternary period. Many
 271 studies suggest that during the evolution of the Brazilian coastal plains, areas with lower
 272 elevation, such as the riverine plains, were covered with sand deposits from the

273 Pleistocene and were later reworked during a subsequent transgression (5,100 years BP;
 274 Funceme 2009, Villas Boas et al. 2001, Meireles and Raventos 2002).

275 Some studies using proxies, such as pollen (Behling et al. 2004), tannin (Benner
 276 et al. 1990), and pyrite (Roychoudhury et al. 2003, Nielsen et al. 2011), also suggest
 277 that HTF's originated from the burial of ancient mangroves. This hypothesis is
 278 supported by the presence of traces of mangrove plant tissues buried beneath different
 279 HTF's in Brazil and other parts of the world (Table 2; Fig. 4C). The expansion and
 280 regression dynamic between the mangrove forests and the HTF can also be confirmed
 281 based on the presence of remnants of oyster shells in deeper layers of HTF soils
 282 (Nascimento 1999, Hadlich et al. 2010) and preserved mangrove roots (Nascimento
 283 1999, Hadlich et al. 2010, Marchand et al. 2011).

284 Bigarella (1947) studied the coastal plain from the Brazilian southern state of
 285 Paraná and described an environment similar to the HTF with a marked contrast
 286 between the rainy and dry seasons. The described HTF's were composed of sandy-clay
 287 soils, which evolved to sandy tablelands in response to the high inputs of sediments
 288 followed by colloid dispersion and removal. At the subsurface, an ancient buried
 289 mangrove called "*mangrovito*" was found. Further studies in Paraná reaffirmed that the
 290 HTF studied in 1947 was previously vegetated by a mangrove species. During a drier
 291 and hotter period past, a thin layer of salt crust precipitated on the soil surface (burying
 292 the mangrove), and thus promoting the establishment of the herbaceous vegetation
 293 present today (Bigarella 2001).

294 In Brazil, these ancient mangrove forests are located in upper physiographic
 295 position (due to transgressive processes) and were probably displaced by the restriction
 296 of tidal flooding and lower sea levels that occurred during the last regression period
 297 (Fig. 5B; Hadlich et al. 2010, Marques 2010). This last regression would also be

298 responsible for the production of sediments present in diverse geomorphological
 299 features (e.g. dunes and fluviomarine plains; Tomazelli et al. 2008).

300 Another factor that is considered to contribute to the formation of HTF's, though
 301 detrimental to mangroves, is the input of sediment from adjacent elevated areas (e.g.
 302 Brazilian Coastal Tablelands). In the long term, terrestrial sediment transport may cause
 303 mangrove dieback (Ucha et al. 2004, Ackermann et al. 2006). The flat topography of
 304 hypersaline tidal flats, with slopes up to 0.4% when compared to the steeper slopes (>
 305 3%) of contiguous areas, reinforces the hypothesis that HTF develops from the
 306 deposition of sediments from higher positions in the landscape (Hadlich et al. 2008).

307 Some authors suggest that the formation of HTF's may also be due to the
 308 formation of sand banks as a result of trapping of sediments by mangrove root
 309 structures (e.g. *Rhizophora mangle*; Cintrón 1978). The constant sediment input would
 310 raise the topographic level in relation to the mangrove, impeding tidal waters and
 311 promoting salt accumulation in soils (Vieillefon 1969, Pellegrini 2000). Other authors
 312 propose that the construction of dams in semiarid inland river basins would reduce
 313 freshwater delivery to estuaries, and therefore increasing the salt intrusion into
 314 freshwater regions (Knoppers et al. 2006, Hadlich and Ucha 2009). Similarly, shrimp
 315 farming activity and marine salt exploration in the salterns could also contribute to the
 316 development of HTF's, due to the fact that both activities promote changes in water
 317 flow in mangroves because of pond construction. After abandonment the regions
 318 affected by ponds construction may develop hypersaline soils (Meireles et al. 2010).

319

320 **Pedogenesis in HTF's**

321 In Brazil HTF's are frequently found in the states of Ceará and Bahia, due to the
 322 favorable climatic conditions (tropical arid and semiarid) for the formation of these

ecosystems (Fig. 1). In fact, global HTF's are associated with semiarid climates (Table 2; Schaeffer-Novelli et al. 1990, Shaeffer-Novelli 2002, Hadlich et al. 2008, Ridd and Stieglitz 2002). At these sites, during the rainy season the amount of freshwater that supplies the aquifer is sufficient to dissolve salts and favors the reduction of soil salinity. However, during the dry seasons evaporation and capillary rise of water enhances the salinization process (Lebigre 2007; Table 2; Fig. 5) and may result in the formation of salt crusts (Fig. 3A) with the precipitation of calcium carbonate (CaCO_3), dolomite ($\text{CaMg}(\text{CO}_3)_2$), gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$), halite (NaCl) and sylvite (KCl ; Ridd et al. 1997, Barbiéro et al. 2002). Thus, as a reflection of the marked climatic seasonality, the salinity in these environments presents significant seasonal variation, with an increase in salt concentration during dry periods (Hadlich et al. 2008, Lebigre 1983). According to Lebigre (2007), the translocation of salts associated with the formation of these HTF's may be referred to tannification, in reference to *tannes*.

The high content of exchangeable Na in HTF soils (Marques 2010) may also be a result of the salinization process, which would initially promote the precipitation of less soluble salts (e.g. CaCO_3), and the replacement of exchangeable Ca^{2+} by Na^+ (Langmuir 1997). The remaining high concentrations of sodium and bicarbonate would increase the concentration of CO_3^{2-} , and therefore leading to high pH values and clay dispersion (Table 2; Miller and Pawluk 1994, Barbiéro et al. 2002, Marques 2010). The occurrence of alkalization has been described in other wetlands (e.g. mangroves and salt marshes) due to the fact that high pH is characteristic of HTF's where precipitation of carbonates is known to occur (Marques 2010).

The hypersaline conditions and tidal regime also determine some of the morphological features of soil and the vegetation. The structure of hypersaline tidal flat soils (Table 2) indicate that these soils are subjected to incipient soil ripening

348 (dehydration, shrinkage, development of crack, and an increase in permeability and
 349 development of soil structure; see Ellis and Atherton 2003, Vermeulen et al. 2003) in
 350 response to tidal waters and a natural drainage deficit. Due to the hypersaline soils
 351 HTF's are heavily colonized by herbaceous succulents in a patchy vegetation pattern.
 352 The spatial distribution of vegetation may also act as a limiting factor for structure
 353 development in soils as well as for the input of organic carbon to these soils (Table 2;
 354 Pennings and Richards 1998). In some cases the first few millimeters of the HTF soils
 355 are characterized by a higher content of organic matter than in the subsequent layers.
 356 The higher concentrations in the surface layers is likely due to microalgae biomass
 357 found as a coherent-laminated structure known as microbial mats (Fig. 4D; Ridd et al.
 358 1997, Meireles et al. 2007, Huerta-Díaz et al. 2011, Marchand et al. 2011). These
 359 structures, dominated by cyanobacteria, are widespread in nature but typically limited to
 360 extreme environments (Huerta-Díaz et al. 2011) and play an important role in bio-
 361 mineralization and nutrient dynamics (Pires and Lacerda 2008, Reimer and Huerta-Díaz
 362 2011, Huerta-Díaz et al. 2011). On the other hand, the patchy vegetation cover may be
 363 related both to nutrient availability and flooding patterns which determine the spatial
 364 extent of salinity and redox conditions (He et al. 2011). Thus, site-specific soil
 365 conditions combined with tidal flow patterns may be the primary factors determining
 366 ecological relationships between plants and soil in an HTF.

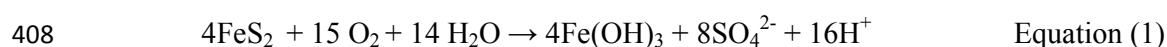
367 In an HTF the water input occurs primarily during spring tides or due to
 368 drainage of adjacent continental areas (Hadlich et al. 2009, Marques 2010). The water
 369 regime in these soils is characterized by periodic water saturation and therefore
 370 hydromorphic conditions (Marques 2010). In response to waterlogging, HTF soils are
 371 prone to the anaerobic organic matter decomposition (Marchand et al. 2011). In the
 372 absence of O₂, the decomposition of organic compounds takes place with alternative

373 electron acceptors (e.g. Fe^{3+} ; Mn^{4+} ; SO_4^{2-}) in a sequential cascade which reflects the
 374 energetic efficiency of the process ($\text{O}_2 > \text{NO}_3^- > \text{Mn}^{4+} > \text{Fe}^{3+} > \text{SO}_4^{2-} > \text{CO}_2$; Reddy et al.
 375 1986, Canfield et al. 2005).

376 In HTF soils the reduction of Fe (III) minerals (e.g. ferrihydrite; goethite;
 377 lepidocrocite; through the bacterial reduction of iron) causes the development of grey or
 378 neutral colored soils (with or without mottling). These soil colors are typical of reducing
 379 environments and of the gleying processes (or gleyzation; Fig. 5; Marques 2010). The
 380 variation in the water table may also result in the formation of brownish and reddish
 381 mottles (Fig. 4E). After Fe reduction the decomposition of organic matter occurs via
 382 sulfate reduction (or sulfidization; Fig. 5); which results in the formation of metallic
 383 sulfides, such as Acid Volatile Sulfide (AVS) and pyrite (Berner 1984, Rickard and
 384 Morse 2005). Sulfate reduction is an important microbial metabolic pathway in
 385 mangroves and coastal wetland soils (Table 2; Alongi 2002, Lambais et al. 2008, Otero
 386 et al. 2009), and may be evident in sea water as in the high concentrations of dissolved
 387 sulfate detected during tidal flooding (Otero and Macías 2002). The presence of iron
 388 sulfides in these soils may also be due to inheritance from pre-existing buried mangrove
 389 soils, rather than from active/recent sulfidization processes (Marques 2010). Therefore,
 390 iron sulfide formation (sulfidization), may be restricted to the deeper layers in HTF
 391 soils. Sulfidization may also occur in response to anoxic conditions caused by higher
 392 water levels in combinations with sulfate input by seawater, iron from ground and
 393 surface waters, as well as to the presence of existing organic matter (from ancient
 394 mangroves). Sulfidization is an important process in HTF's as it occurs with less
 395 intensity in comparison to other wetlands that undergo constant flooding (Marques
 396 2010, Marchand et al. 2011).

397 Sulfidization may also play an important ecological role as it controls trace
 398 metal biogeochemistry and bioavailability through the co-precipitation of metals with
 399 pyrite or via the formation of metallic sulfides (Morgan et al. 2012, Huerta-Diaz and
 400 Morse 1990). However, these metallic sulfides are highly unstable under oxidizing
 401 conditions and may lead to oxidation and the release of associated metals: therefore
 402 increasing bioavailability of trace metals. Therefore, any natural or anthropogenic
 403 disturbance of the system may increase the contamination risk of the adjacent mangrove
 404 ecosystems (Morgan et al. 2012). Sulfides oxidation, due to changing in redox
 405 conditions, is also responsible for marked decreases in soil pH (typically to values less
 406 than 3.5; Equation 1; Otero et al. 2008, Burton et al. 2006).

407



409

410 The oxidation of iron sulfides (which results in the formation of iron
 411 oxyhydroxides; Langmuir 1997; Otero et al. 2008, Burton et al. 2006) is the primary
 412 pathway for the accumulation iron oxyhydroxides in HTF soils (Marques 2010).
 413 Furthermore, the oxidation of dissolved iron (Fe^{2+}) in continental drainage waters is due
 414 to aerobic conditions and may also result in the accumulation ferric compounds in the
 415 superficial sediment layers.

416 Another conspicuous process in HTF soils is bioturbation (Fig. 5). This process
 417 causes the dispersion and/or displacement of soil particles by benthic organisms or plant
 418 species, and determines the biogeochemical state of the substrate (Gabet et al. 2003,
 419 Ferreira et al. 2007, Maire et al. 2008). In wetland soils, bioturbation leads to changes in
 420 the functioning of ecosystems by modifying physical, chemical, and biological
 421 characteristics of soils and sediments, oxygen diffusion, nutrient flow and, rates of

organic matter mineralization (Jones et al. 2006, Meysman et al. 2006, Maire et al. 2008). Bioturbation differs from others pedogenetic processes because it promotes considerable changes not only due to biochemical processes, but also by the mobilization of particles and by the construction of channels (made by interstitial and superficial fauna) in the sediments through which water flows.

Kristensen et al. (2008) consider crabs to have a considerable impact on ecosystem functioning as they are responsible for the transfer of nutrients, for maintaining high functional diversity, and promote considerable biogeochemical heterogeneity within wetland soils. Similarly, it would be expected that the high density of crabs typically found in HTF's would also cause changes in its soils, as is indicated by observations of morphological features (Fig. 4F). However, to our knowledge, no studies are presently published on the effects of crab bioturbation in HTF soils. Therefore, while the importance of faunal activity is well established for other wetland soils (Smith et al. 1991, Thongtham and Kristensen 2003, Ferreira et al. 2007, Wang et al. 2011, Casariego et al. 2011, Araujo-Junior et al. 2012), studies on the effects of bioturbation specifically in HTF's are still not available.

Floral bioturbation results from the interaction between roots and soil due to root growth, root expansion, channel opening, water extraction, and exudate release (Schaetzl et al. 1989). Additionally, in the microregion of the soil rhizosphere, high rates of chemical and biological processes affect nutrient biogeochemical cycles (e.g., carbon, nitrogen, and phosphorus), greenhouse gases emission rates, and the immobilization of pollutants (Toal et al. 2000, Liangpeng et al. 2007, Richter et al. 2007, Dantas et al. 2009). Biogeochemical processes in sediment surface horizons are strongly influenced by rhizosphere activity. The relevant soil biogeochemical reactions between plant roots and the mineral phase of sediments of HTF's are: ion absorption,

447 production of organic acids, changes on redox conditions and CO₂ production (Richter
448 et al. 2007, Caçador et al. 2000).

449

450 **CONCLUSIONS**

451 Apicuns are HTF's and are unique ecosystems located adjacent to mangrove
452 forests along arid and semi-arid coasts. These ecosystems are directly influenced by the
453 coastal dynamic which control both past and present ecosystem processes. The available
454 literature presents different theories on the formation of these ecosystems. The reduced
455 tidal flooding associated to an evaporative environment and a hydric deficit seems to be
456 the primary controlling factors for the formation of these hyper-saline coastal wetlands.
457 Pedogenesis, salinization, gleyzation, sulfidization and bioturbation are the main
458 processes that seem to occur in the soils from these ecosystems. Despite the great
459 ecological and socio-economic importance of HTF's, very a few studies have focused
460 on these endangered ecosystems; more specifically on the ecological relationships
461 between soils, plants, and fauna. Further studies are necessary to delineate the
462 ecological connection between HTF's and other highly ecologically important wetlands
463 in order to improve public policies and conservation laws which should strive for the
464 protection of the whole coastal ecosystem chain.

465

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960 **FIGURE CAPTIONS**

961 **Figure 1.** Hypersaline tidal flat ecosystems located in NE-Brazilian states which are
 962 known to be influenced by various anthropogenic impacts. (1) Maranhão; (2) Piauí; (3)
 963 Rio Grande do Norte; (4) Paraíba; (5) Pernambuco; (6) Alagoas; (7) Sergipe; and (8)
 964 Bahia.

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966 **Figure 2.** (A) Schematic of geophysical distribution along a transect through a
 967 hypersaline tidal flat in northeast Brazil (*apicum*): from the mangrove forest at the land-
 968 sea interface up to the Coastal Tableland. The numbered positions are in reference to:
 969 the spring tide level (1), mean high tide level (2) and mean low tide level (3). (B)
 970 Satellite image of a hypersaline tidal flat ecosystem in the transition between Coastal
 971 Tablelands and mangrove forests (Ceará State, NE-Brazil); (C) A general panorama of
 972 a hypersaline tidal flat ecosystem.

973

974 **Figure 3.** (A) Typical salt crusts commonly found in hypersaline tidal flat ecosystems;
 975 (B) “patchy” vegetation pattern in a hypersaline tidal flat; (C) region with poor
 976 vegetation cover; (D) *Batis maritima*; (E) *Cardisoma guanhumi* (land crab) burrow;
 977 and (F) *Cardisoma guanhumi* (land crab) and trap used to collect land crabs; a dietary
 978 staple of local populations.

979

980 **Figure 4.** (A) *Ucides cordatus* found in hypersaline tidal flats; (B) domestic animals
981 grazing in a hypersaline tidal flats; (C) typical sediment layer with preserved mangrove
982 residue; (D) microbial mats found on the surface of sediments; (E) reddish mottling
983 indicating variations in the redox conditions in sediments; (F) iron oxide precipitation in
984 sediments as a result of bioturbation. by crabs.

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986 **Figure 5.** General characteristics of hypersaline tidal flats; (A) sediment accumulation
987 from dunes and adjacent areas; (B) flooding period during spring tides; (C) seawater
988 evaporation and salt accumulation during low tides.

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1001 **TABLE CAPTION**1002 **Table 1.** Floral composition of *apicum* and *tannes*.
1003

1004 **Table 2.** Site location, climatic characteristics (temperature, precipitation, and climate
1005 classification), mean organic carbon content, granulometric composition (sand, silt, and
1006 clay), pH, electrical conductivity (EC), presence of mangrove plant tissues and sulfidic
1007 material of different hypersaline tidal flats around the world.

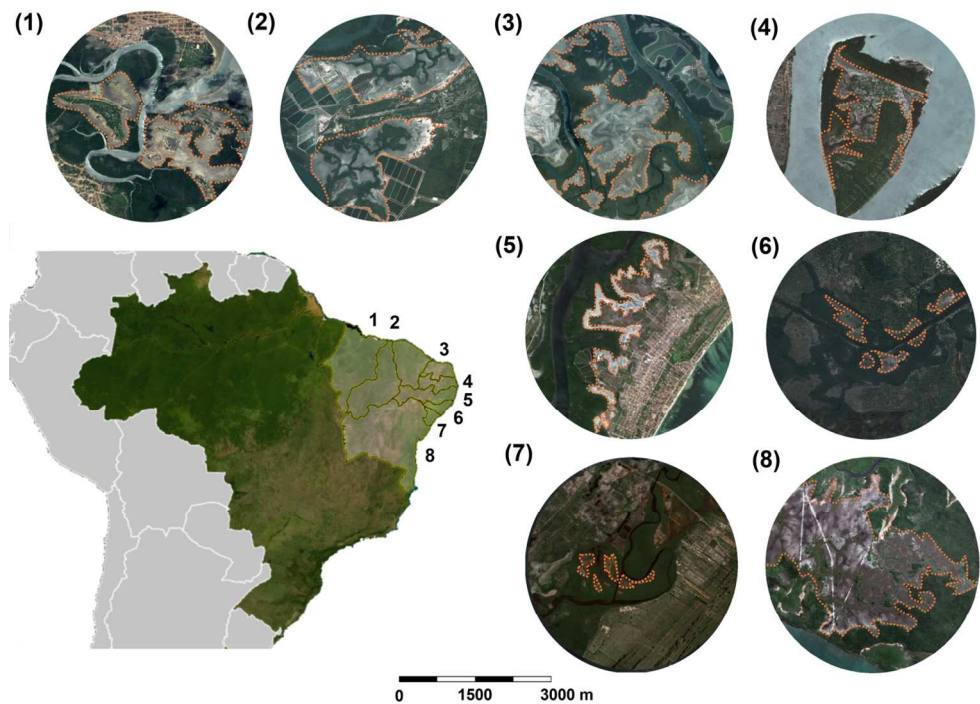


Figure 1. Hypersaline tidal flat ecosystems located in NE-Brazilian states which are known to be influenced by various anthropogenic impacts. (1) Maranhão; (2) Piauí; (3) Rio Grande do Norte; (4) Paraíba; (5) Pernambuco; (6) Alagoas; (7) Sergipe; and (8) Bahia.
128x91mm (300 x 300 DPI)

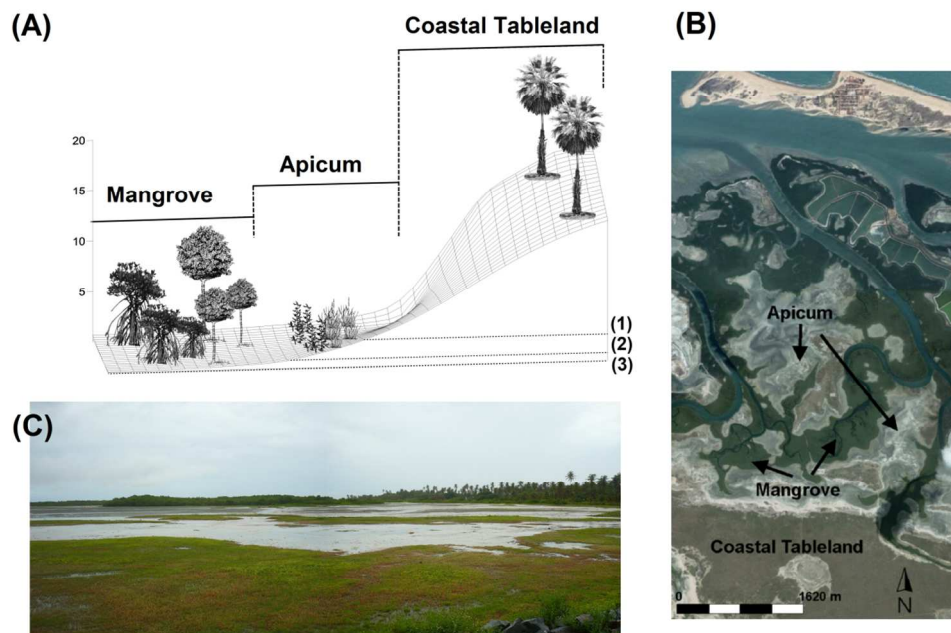


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112x75mm (300 x 300 DPI)

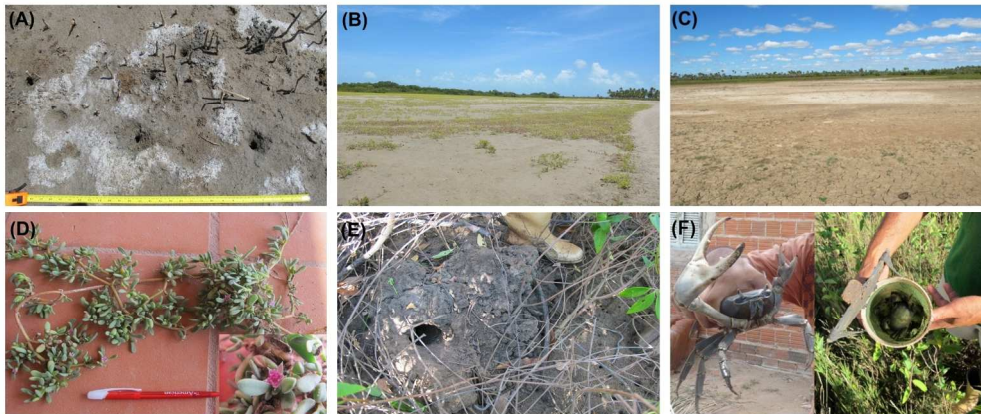


Figure 3. (A) Typical salt crusts commonly found in hypersaline tidal flat ecosystems; (B) “patchy” vegetation pattern in a hypersaline tidal flat; (C) region with poor vegetation cover; (D) *Batis maritima*,; (E) *Cardisoma guanhumi* (land crab) burrow; and (F) *Cardisoma guanhumi* (land crab) and trap used to collect land crabs; a dietary staple of local populations.
162x69mm (300 x 300 DPI)

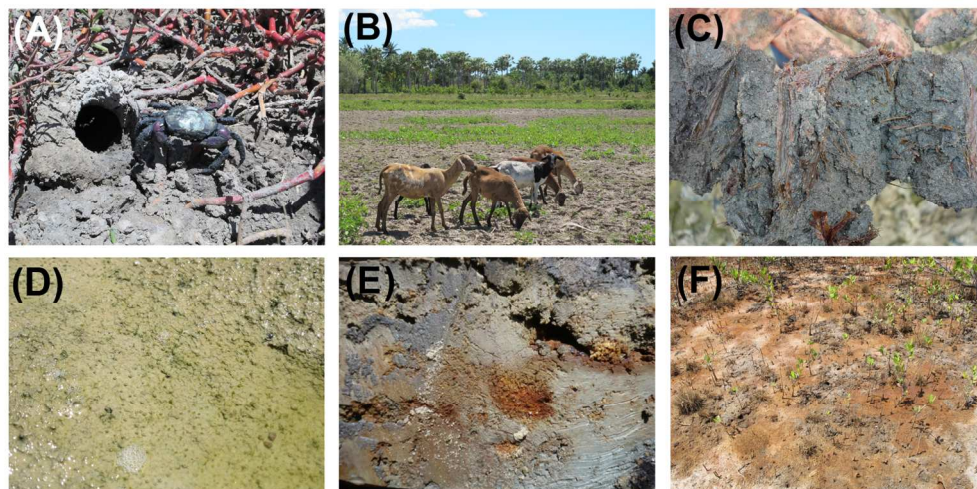
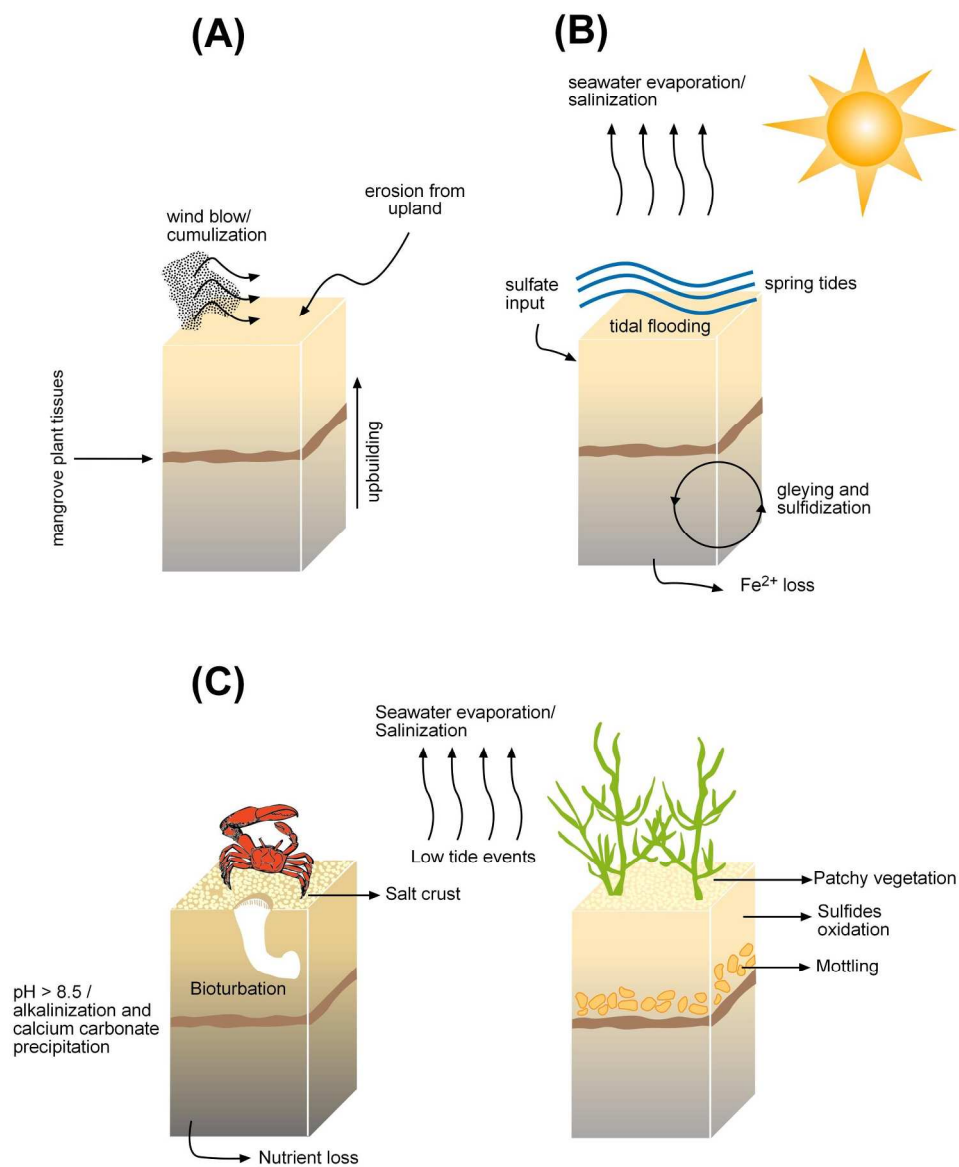


Figure 4. (A) *Ucides cordatus* found in hypersaline tidal flats; (B) domestic animals grazing in a hypersaline tidal flats; (C) typical sediment layer with preserved mangrove residue; (D) microbial mats found on the surface of sediments; (E) reddish mottling indicating variations in the redox conditions in sediments; (F) iron oxide precipitation in sediments as a result of bioturbation. by crabs.

458x231mm (96 x 96 DPI)



192x234mm (300 x 300 DPI)

Table 1. Floral composition of *apicum* and *tannes*.

Family	Species	References
Aizoaceae	<i>Sesuvium portulacastrum</i> (L.) L.	Marius (1981); Marius (1987); Lebigre (2007)
Chenopodiaceae	<i>Arthrocnemum indicum</i> (Wild.) Moq.	Lebigre (2007)
	<i>Atriplex</i> spp. (L.)	Lebigre (2007)
	<i>Halosarcia indica</i> subsp. <i>leiostachya</i> (Benth.) Paul G. Wilson	Lebigre (2007)
	<i>Salicornia</i> spp. (L.)	Lebigre (2007)
	<i>Salsola littoralis</i> Moq.	Lebigre (2007)
	<i>Sarcocornia</i> sp. (A.J. Scott)	Lebigre (2007)
	<i>Suaeda</i> spp. Scop.	Lebigre (2007)
Poaceae	<i>Aeluropus lagopoides</i> (L.)	Lebigre (2007)
	<i>Cynodon dactylon</i> (L.) Pers.	Lebigre (2007)
	<i>Paspalum vaginatum</i> Sw.	Marius (1981)
	<i>Sclerodactylon macrostachyum</i> (Benth.) A. Camus	Lebigre (2007)
	<i>Sporobolus robustus</i> Kunth	Lebigre (2007)
Convolvulaceae	<i>Sporobolus virginicus</i> (L.) Kunth	Lebigre (2007); R. L. Cabral (personal communication, 2013)
	<i>Cressa australis</i> R. Br.	Lebigre (2007)
Cyperaceae	<i>Cyperus laevigatus</i> (L.)	Lebigre (2007)
	<i>Eleocharis caribaea</i> (Rottb. Blake)	Marius (1981); Marius (1987)
	<i>Eleocharis mutata</i> (L.)	Marius (1981)
	<i>Fimbristylis</i> sp. Vahl	Lebigre (2007)
Amarantaceae	<i>Blutaparion portulacoides</i> (A. St.-Hil.) Mears	R. L. Cabral (personal communication, 2013)
	<i>Philoxerus vermicularis</i> (Linn.) P. Beauv	Marius (1981); Marius (1987); Lebigre (2007)
Bataceae	<i>Batis maritima</i> (L.)	R. L. Cabral (personal communication, 2013)

Table 2. Site location, climatic characteristics (temperature, precipitation and climate classification), mean organic carbon content, granulometric composition (sand, silt and clay), pH, electrical conductivity (EC), presence of mangrove plant tissues and sulfidic material of different hypersaline tidal flats around the world

Site location	Temperature	Precipitation	Climate	Organic carbon	Sand	Silt	Clay	pH	EC	MPT	Sulfidic material	Reference
	°C	mm		----- g kg ⁻¹ -----					dS m ⁻¹			
Madagascar	30,0	500	BSh	-	-	-	-	7±1	12±11	-	-	Lebigre et al., 1990
Bahia, Brazil	26,5	1650	Awi	7±1*	758±36	93±17	149±28	6±0	-	yes	-	Hadlich; Ucha; Celino 2008
Ceará, Brazil	34,0	1.131	BSh	7±8	712±177	135±89	153±92	8±2	33±6	yes	yes	Marques 2010
TerembaBay, New Caledonia	28,1	83	Cfa	59±50	-	-	-	7±0	-	yes	yes	Marchand; Lallier-Vergès; Allenbach 2011
Murcia.Spain	19,1	24	BSh	41±16	225±149	365±92	145±134	7±0	11±8	-	-	Conesa et al., 2011

*Organic Carbon value = organic matter divided by1.724;
** Standard deviation calculated according to the mean values in the references.
MPT- mangrove plant tissues; Awi- Tropical hot and humid; BSh- Semi-arid hot; Cfa- Subtropical humid; (-) not analyzed