

1                   **The influence of crab burrows on sediment salinity**  
2           **during the dry season in a *Rhizophora*- dominated mangrove forest**  
3                                   **in North Brazil**

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36 **Abstract**

37 Many ecological processes are influenced by salinity. Burrowing  
38 crabs, abundant fauna of mangrove forests around the world, can facilitate  
39 sediment water fluxes, which may decrease the salinity in mangrove  
40 sediments. We investigated whether and how crab burrow density and  
41 secondary fine root biomass interact to drive sediment salinity during the  
42 dry season in a northern Brazilian mangrove forest. Areas with high density  
43 of *Rhizophora mangle* prop roots and areas free of such roots were  
44 compared. We found no correlation between burrow density and sediment  
45 salinity in areas with dense prop and fine roots, while crab density  
46 correlated negatively with sediment salinity in areas without prop roots,  
47 where fine root density was low. Hence, the strength of sediment  
48 desalination effects of crabs appears to be context-dependent, and high root  
49 density of a salt-excluding mangrove species (*R. mangle*) seems to  
50 counteract the crabs' effects. Our results complement those of a former  
51 study conducted in the same area during the rainy season, highlighting that  
52 the findings are independent from seasonality and should be considered  
53 when evaluating the overall ecological effects of crabs in mangrove  
54 ecosystems.

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57 **Key words:** *Rhizophora mangle*, mangrove, *Ucides cordatus*, sediment  
58 **salinity**

## 59 **Introduction**

60 Mangrove forests are species-rich, highly productive systems, and  
61 they provide numerous ecosystem services. These forests can considerably  
62 affect the biogeochemical cycles of coastal regions (Alongi et al., 1989;  
63 Alongi, 2008; Rivera-Monroy et al., 1995; Sakho et al., 2015;  
64 Schwendenmann et al., 2006), serve as feeding grounds and nursery sites  
65 for oceanic and coastal nekton, and provide habitat for a range of  
66 terrestrial, intertidal and marine fauna and flora (Ellison, 2008; Faunce and  
67 Serafy, 2006).

68 Adaptations of mangrove trees to the intertidal environment include  
69 various mechanisms of handling high salt concentrations in the sediment  
70 pore water. For example, some species (e.g., *Avicennia germinans* (L.) L.,  
71 Acanthaceae, common in Brazil) excrete salt by aboveground tissues, while  
72 others exclude salt upon water-uptake through roots. The latter results in  
73 salt accumulation in the sediment near the roots, potentially producing  
74 deleterious effects on mangrove trees (Passioura et al., 1992). The Red  
75 mangrove, *Rhizophora mangle* L., Rhizophoraceae, the dominant species in  
76 North Brazilian mangrove forests, is one example for a salt-excluding  
77 species (Parida and Jha, 2010; Passioura et al., 1992).

78 Crabs are one of the most abundant faunal groups in mangrove  
79 forests in terms of number and biomass (Legat et al., 2006; Smith III et al.,  
80 1991; Kristensen, 2008; Lee, 2008). Burrowing crabs can play an important  
81 functional role as they can enhance the exchange of nutrients, salt, oxygen,  
82 and pollutants between surface water and sediment.

83 Two morphologically and functionally different groups of crabs are  
84 common in North Brazil, fiddler crabs (*Uca* spp., Leach, 1814,  
85 Ocypodidae) and *Ucides cordatus* (Linnaeus, 1763, Ucididae). Fiddler crab  
86 burrows are usually shallow, typically with a maximum depth of  
87 approximately 20 cm, and with a single opening (Lim, 2006). By contrast,  
88 burrows of *U. cordatus* reach as deep as 2 m into the sediment and can  
89 exhibit up to 2 burrow openings, while one opening is the most common  
90 type (Wunderlich et al., 2008). The tidal flushing effect of U-shaped and  
91 multiple-looped crab burrows is a well-studied topic (Heron and Ridd,  
92 2008; 2003; Wolanski and Gardiner, 1981; Stieglitz et al., 2000; Xin et al.,  
93 2009; Lim, 2006). Crab burrows can facilitate the cycling of nutrients, CO<sub>2</sub>  
94 and oxygen, and are therefore considered an important pathway for the  
95 export of solutes between the mangrove sediment and the creek and for  
96 land-ocean organic and inorganic solutes exchange (Xin et al., 2009;  
97 Stieglitz et al., 2000 and 2013; Hollins et al. 2009; Pülmanns et al., 2014).  
98 The desalinating influence of animal burrows has also been investigated

99 (Pissoura et al., 1992; Smith III et al., 1991; Stieglitz et al., 2000; 2013).  
100 However, the first authors that have addressed specifically the relation  
101 between burrows with one opening from larger crabs, like *Ucides cordatus*,  
102 and salt contents in rooted sediments were Pülmanns et al. (2015). In a  
103 laboratory microcosm study, salinity in mangrove sediment with artificial  
104 crab burrows with one opening was significantly lower than in sediment  
105 without burrows. However, no evidence for a desalination effect in rooted  
106 areas was found for natural *Ucides* burrows in a field study conducted by  
107 the same authors during the pronounced North Brazilian rainy season.  
108 Pülmanns et al. (2015) suggested that any such effect of the burrows may  
109 have been masked by leaching of salt through precipitation. They predicted  
110 that the burrows' influence on sediment salinity would be revealed during  
111 the dry season. Sediment salinity drives many processes in mangrove  
112 sediments (e.g. Kida et al., 2017) and it is important to understand how it is  
113 influenced by burrowing crabs, particularly in light of the harvesting  
114 pressures that many crab species experience. *Ucides cordatus* for example,  
115 our study species, is heavily fished in many areas (e.g. Nascimento et al.,  
116 2017), and mass mortalities caused by fungal pathogens (Boeger et al.,  
117 2007; 2005) have caused population crashes, possibly affecting ecosystem  
118 processes (Schmidt et al., 2013).

119 Here we investigate whether the density of both *Ucides* and fiddler  
120 crab burrows and/or the density of secondary fine roots affect the salinity  
121 of the upper sediment (up to 50 cm depth) of *Rhizophora mangle* stands  
122 during the dry season. We hypothesize that sediment salinity is lower in  
123 areas with higher crab burrow density due to the tidal flushing of the  
124 burrows.

## 125 **Material Methods**

### 126 **Location**

127 The study was carried out in an intertidal mangrove forest located at  
128 the Ajuruteua Peninsula, close to the channel Furo Grande (46°38'W;  
129 0°50'S), at the Caeté Estuary, about 30 km northwest of the city of  
130 Bragança in Pará, Brazil (Fig. 1). Situated within the Amazonian Coastal  
131 Zone (ZCA), this mangrove forest is part of the largest and best-preserved  
132 continuous mangrove belt on earth (Nascimento Jr. et al., 2013). These  
133 extensive mangrove forests can extend up to 40 km inland. The Furo  
134 Grande channel has a length of approximately 12 km with many smaller  
135 tributaries and connections with the Atlantic Ocean (Acheampong, 2001).  
136 The Ajuruteua Peninsula has a characteristic well-developed forest made  
137 up by the Red mangrove (*Rhizophora mangle*), the Black mangrove  
138 (*Avicennia germinans*), and the White mangrove (*Laguncularia racemosa*  
139 (L.) C. F. Gaertrn, Combretaceae). At the Furo Grande channel, the

140 mangrove forest consists of a mix of *Rhizophora* and *Avicennia*, with a  
141 mean density of 520 trees per ha (Reise, 2003).

142         The tides at the study area are semidiurnal with a range between 3  
143 and 5 m. The forest at the study site is located in the high intertidal zone  
144 which is not flooded during neap high tides (Pülmanns et al., 2015). The  
145 region has two very distinct seasons. The dry season lasts for about 3 to 5  
146 months, generally from August/September until November/December, and  
147 the rainy season lasts from January until June/July (INMET, 2015).  
148 Throughout the year, air temperatures vary between 24°C and 34°C  
149 (Mehlig, 2006; Menezes et al., 2003). No significant precipitation was  
150 recorded during the experiment; the only rain event during the study  
151 occurred on October 5 2014 (5mm; Source: INMET, 2015).

## 152 **Burrowing crabs**

153         *Ucides cordatus* is a semi-terrestrial crab that lives only in  
154 mangrove forests and occurs throughout the western Atlantic Ocean, from  
155 Florida (USA) to Santa Catarina State (Brazil) (Pinheiro and Hattori,  
156 2006). The crabs have a life span of more than 10 years (Ostrensky et al.,  
157 1995; Diele, 2000; Pinheiro et al., 2005), are slow-growing (Diele and  
158 Koch, 2010) and can reach sizes of up to 9 cm carapace width in the Caeté  
159 Estuary (Diele et al., 2005). They construct up to 2 m deep burrows and  
160 feed mostly upon leaf litter (Goes et al., 2010; Nordhaus et al., 2006;

161 Nordhaus et al., 2009). *Ucides cordatus* preferably lives among the roots of  
162 *Rhizophora mangle*, as this tree species provides shelter and food through  
163 litter fall (Diele et al., 2005; Piou et al., 2009). Their density can be  
164 extremely heterogeneous, with very few crab holes in dry habitats,  
165 especially among pneumatophores of *Avicennia germinans* (Schories et al.,  
166 2003), and higher densities in humid habitats and underneath the aerial  
167 roots of *Rhizophora mangle*, with an average of 1.7 crab burrows m<sup>-2</sup>  
168 (Diele et al., 2005).

169 Species of the genus *Uca*, commonly known as fiddler crabs, are  
170 widespread throughout the Western Atlantic and abundant in mangroves  
171 from Southern Florida (USA) to Santa Catarina (Brazil) (Crane, 1975).  
172 Fiddler crabs feed on organic matter that they sieve out from the sediment  
173 (Moura et al., 1998; Twilley et al., 1995). Inside the mangrove forests of  
174 the Caeté Estuary, two species are abundant, *Uca rapax* (S. I. Smith, 1870)  
175 and *Uca vocator* (J. F. W. Herbst, 1804) (Diele et al., 2010), with average  
176 densities of 19 and 18 crabs burrows/m<sup>2</sup> (Koch et al., 2005). Male *Uca*  
177 *rapax* can reach a carapace width of 26 mm, while the females can grow up  
178 to 24 mm (Castiglioni and Negreiros-Fransozo, 2006). *Uca vocator* varies  
179 in size from 13 mm (females) to 17 mm carapace width (males) (Crane,  
180 1975).

181 **Field study area**

182 Two field sampling campaigns were conducted throughout the dry  
183 season of 2014 during slack low tide. The first campaign was held on 15<sup>th</sup>  
184 and 16<sup>th</sup> of October, and the second on 16<sup>th</sup> and 17<sup>th</sup> of November, both  
185 during waning moon phase. At seven sites (up to 200 m apart from each  
186 other), three replicate sediment cores of 50 cm length and 5 cm diameter  
187 were collected with a peat sampler (Eijkelkamp), from two areas with  
188 different root densities: areas with high density of aerial prop roots  
189 (“rooted” areas, samples were collected within an area of approximately  
190 5 m of diameter) and areas without prop roots (“gap” areas, again  
191 approximately 5 m in diameter)

192 On both sampling occasions, a 1.0 m x 1.0 m quadrat was placed  
193 three times in both “rooted” and “gap” areas at each of the seven sites. The  
194 number of crab burrows assigned to either fiddler crabs or *U. cordatus* was  
195 estimated within each quadrat. This differentiation was made by the size of  
196 the burrow opening. In *R. mangle* dominated forest stands of the Caeté  
197 Estuary, the average and minimum size of *U. cordatus* burrows is 5.08 cm  
198 (SD = 1.39) and 1.45 cm, respectively (Korting, 2012). In *our* study area,  
199 most crab burrows were either large, i.e. with a diameter of 5 cm or above,  
200 or small, i.e. 1 cm or below. The former could clearly be assigned to *U.*  
201 *cordatus*, whereas all small burrows, often with characteristic chimneys,  
202 were assigned to the much smaller fiddler crabs that are abundant in the

203 forest, according to visual observations. In contrast, intermediate and  
204 smaller *Ucides* crabs are often more aggregated at the margins of the forest  
205 and near creeks (Diele et al., 2005; Schmidt et al., 2013). The few  
206 intermediate sized burrows present (approximately 5%) (Korting, 2012),  
207 that could belong to *Ucides* or fiddler crabs, were not considered in this  
208 study.

209 From inside each quadrat, one core was sampled for analysis of  
210 sediment salinity and fine root biomass. From the core, samples were taken  
211 at depths of 1, 5, 10, 20, 30, 40, and 50 cm. For salinity, at each of these  
212 depths, 1 cm segments of the sediment core were collected and stored in  
213 sealed plastic tubes until further analysis. For the analyses of the first  
214 sediment layer (1 cm), the segment from 1 to 2 cm was collected; for the  
215 second layer (5 cm), the segment from 5 to 6cm, for the third (10 cm), the  
216 segment from 10 to 11 cm. For the determination of fine root biomass, 4  
217 cm segments of the sediment were collected from the core and stored in  
218 plastic bags until processing. All samples were stored in a styrofoam box  
219 on ice in the field and then transferred into a refrigerator in the laboratory  
220 where they were kept at 4°C until processing.

## 221 **Laboratory Analyses**

### 222 **Salinity and water content**

223 In the laboratory, sediment samples were homogenized and then  
224 divided into two parts, to measure salinity and water content. For salinity, 2  
225 g of the sediment were mixed with 10 mL of distilled water and shaken for  
226 24 hours using a mechanical shaker (MA 136, Marconi). After 24 hours,  
227 salinity was measured with a WTW TetraCon 325 connected to a WTW  
228 portable meter (Multi 340i). The water content was determined through  
229 mass loss upon oven-drying at 104° C to constant mass.

### 230 **Fine Root Biomass**

231 In this study, only the secondary thin roots were considered as fine  
232 root biomass. Due to their small size, no separation between living and  
233 dead material was made. Samples were washed with tap water using a sieve  
234 with 0.5 mm mesh size and stored at 4° C until further processing. Fine  
235 roots (including live and dead ones) were oven-dried at 104°C to constant  
236 mass and weighed. Herein, we report root biomass as grams of dried roots  
237 per unit soil volume (g/cm<sup>3</sup>).

### 238 **Statistical data analyses**

239 The analyses were performed in R (R Core Team 2012, version  
240 2.15.2). The protocol for data exploration from Zuur et al. (2009; 2010)  
241 was followed to check for outliers and collinearity between explanatory  
242 variables. Then a linear mixed effect model (LME) (Pinheiro and Bates,  
243 2000; Zuur et al., 2009) was used to analyze differences in sediment

244 salinity among area types (gap and rooted area) and sediment depths and all  
245 their interaction terms. The random part of the LME model allowed for  
246 heterogeneity among individual sediment cores and different sampling  
247 sites. A variance function was applied to account for variance heterogeneity  
248 between sediment depth levels (Pinheiro and Bates, 2000; Zuur et al.,  
249 2009). For this the package “nlme” (Pinheiro et al., 2012) was used.  
250 Differences in burrow density among area types, sediment salinity and  
251 amount of fine root biomass were tested with a linear model of covariance  
252 (ANCOVA). For this analysis, the density of aerial prop roots (“rooted”  
253 and “gap” areas) was used as a fixed factor, the salinity as a dependent  
254 variable and the fine root biomass and crab density as co-variables.

## 255 **Results**

256 Fine root biomass changed significantly with depth in areas with  
257 high density of aerial prop roots (“rooted”) ( $p < 0.001$ ,  $R^2 = 0.036$ ). No  
258 such significant change was observed within “gap” areas ( $p = 0.583$ ,  $R^2 =$   
259  $0.002$ , Fig. 2). Average fine root biomass was significantly higher in the  
260 “rooted” areas ( $0.274 \text{ g/cm}^3 \pm 0.012 \text{ SE}$ ) than in “gaps” ( $0.163 \text{ g/cm}^3 \pm$   
261  $0.023 \text{ SE}$ ) ( $p < 0.001$ , L Ratio = 36.4,  $df = 1$ ). The difference of fine root  
262 biomass between the “rooted” and “gap” areas at the surface (depth  $\leq 5 \text{ cm}$ )  
263 and the deeper layers ( $\geq 40 \text{ cm}$ ) remained constant, around  $0.1 \text{ g/cm}^3$ , but

264 was more pronounced at intermediate depths, between 10 and 30 cm depth,  
265 being around  $0.4 \text{ g/cm}^3$  at 20 cm depth (Fig. 2).

266 Sediment salinity was higher in “rooted” areas than in “gap” areas ( $p$   
267  $< 0.001$ , L. Ratio = 23.6,  $df = 1$ ), with the highest values at the surface,  
268 regardless of the aerial root density (at 1 cm: “rooted”  $38 \pm 1.23$  and “gaps”  
269  $36 \pm 0.52$  SE; Fig. 3). In the “gap” areas, salinity dropped drastically from  
270 1 to 5 cm depth (from  $36 \pm 3$  to  $31 \pm 1$  SE), then decreased gradually until  
271 50 cm depth, where it reached  $25 \pm 1$  SE. In the “rooted” areas the salinity  
272 varied likewise, dropping from  $38 \pm 8$  SE at the surface to  $35 \pm 1$  SE at 5  
273 cm depth, but remained relatively constant between 5 and 30 cm depth.  
274 Below 30 cm, salinity dropped gradually until reaching  $31 \pm 1$  SE at 50 cm  
275 depth in the “rooted” areas,, being significantly higher than at the same  
276 depth in root-free gaps ( $31 \pm 1$  in contrast to  $25 \pm 1$  SE,  $p = 0.002$ ,  $R^2 =$   
277  $0.101$ ,  $df = 1$ ; Fig. 3)

278 Overall, salinity as a function of depth followed a similar pattern in  
279 both areas, despite the higher overall values in the “rooted” areas. Sediment  
280 salinity and fine root biomass were positively correlated, both when  
281 samples from the two areas were pooled together ( $p < 0.05$ ; Fig. 4A) and in  
282 the “rooted” area ( $p = 0.026$ ; Fig. 4B). In contrast, in gap areas without  
283 aerial roots, the correlation was not significant ( $p = 0.398$ ; Fig. 4C). When  
284 comparing fine root biomass and *Ucides* burrow density, no significant

285 relation was found when pooling the two treatments together ( $p = 0.804$ ;  
286 Fig. 5A) and at “gap” areas ( $p = 0.236$ ; Fig. 5C). However, *Ucides* burrow  
287 density and fine root biomass were positively correlated in "rooted" areas  
288 ( $p = 0.028$ ; Fig. 5B). No correlation was observed for fiddler crabs (all  
289 samples:  $p = 0.665$ , “rooted” areas:  $p = 0.797$ , “gaps”:  $p = 0.352$ ; Fig. 6).  
290 Sediment salinity did not show a relation with crab burrow density, when  
291 samples from the two areas were pooled together (*U. cordatus*:  $p = 0.465$ ;  
292 Fig. 7A, Fiddler:  $p = 0.750$ ; Fig. 8A), and there was also no relation  
293 between crab density and sediment salinity in "rooted" areas (*U. cordatus*:  
294  $p = 0.331$ ; Fig. 7B, Fiddler:  $p = 0.673$ ; Fig. 8B). However, in gaps without  
295 aerial roots, sediment salinity decreased with both increasing *Ucides*  
296 burrow density ( $p = 0.026$ ; Fig. 7C) and fiddler crab burrow density ( $p =$   
297  $0.052$ ; Fig. 8C).

298         The area (“rooted” *versus* “gap”) had a significant influence on  
299 salinity ( $p = 4.6 \times 10^{-10}$ ) and on the burrow density of *U. cordatus* ( $p = 0.004$ ),  
300 but did not have a significant effect on fiddler crab burrow density ( $p =$   
301  $0.194$ ). Burrow densities of both *Ucides* and fiddler crabs were higher in  
302 the “rooted” areas than in the “gaps”. In the “rooted” areas the average  
303 density was  $7.4 \text{ m}^{-2}$  ( $\pm 0.4 \text{ SE}$ ) for *Ucides cordatus* and  $7.6 \text{ m}^{-2}$  ( $\pm 0.5 \text{ SE}$ )  
304 for fiddler crabs. In the “gaps” the average density for *U. cordatus* was  $5.5$   
305  $\text{m}^{-2}$  ( $\pm 0.7 \text{ SE}$ ) and  $6.6 \text{ m}^{-2}$  ( $\pm 0.5 \text{ SE}$ ) for fiddlers.

## 306 **Discussion**

307 Salinity influences many processes in mangrove sediments. For  
308 example, Kida et al. (2017) recently demonstrated that high salinity  
309 flocculates and thereby accumulates humic substances, which could be one  
310 of the mechanisms underlying carbon belowground accumulation in these  
311 wetlands. Our understanding of the effects of the abundant crab burrows in  
312 mangrove forests on sediment salinity (and depending processes) is sparse.  
313 Crab burrows extend the contact surface of these sediments. In the case of  
314 *U. cordatus*, this increase in contact surface amounts to 43% to 128%  
315 (Korting, 2012), while it is only approximately 1% per each fiddler crab  
316 burrow (Kristensen, 2008). Any increase in contact surface is likely to  
317 enhance tidal flushing (Katz, 1980; Heron and Ridd, 2003; 2008). By  
318 reworking and bioturbating the sediment (Kristensen, 2008), burrowing  
319 crabs can play an important direct role in carbon storage in mangrove  
320 sediments (Iribarne et al., 1997) and their burrowing also changes the  
321 vertical and horizontal transfer of soil nutrients (Wang et al., 2010), a  
322 further important ecological function of these crabs in mangrove  
323 ecosystems.

324 In our North-Brazilian study, conducted during the dry season,  
325 sediment salinity was higher in areas with a higher *R. mangle* prop root  
326 density (despite higher *Ucides* and fiddler crab burrow densities) than in

327 the gap areas. This refutes our hypothesis of lower sediment salinity at  
328 areas with higher density of crab burrows during this time of year. The  
329 result corroborates the findings of Pülmanns et al. (2015) in the rainy  
330 season, when sediment salinity in “rooted” areas was also higher than in  
331 “gap” areas (27 and 31 in gap areas and rooted areas, respectively, at the  
332 end of the rainy season) Findings by Smith III (1987), demonstrating a  
333 salinity of 57.5 in areas with high amounts of aerial roots *versus* 55.2 in  
334 gaps, are also in concordance with the present results. A microcosm  
335 experiment by Pülmanns et al. (2016), showed lower salinity in treatments  
336 with (41) than without (47) artificial burrows after 6 months (both  
337 treatments started with sediment salinity of 37.5 at the first centimeter),  
338 showcasing that crab burrows can have a desalinating effect.

339 In our study, secondary fine root biomass was highest at a sediment  
340 depth of 20 cm in areas with aerial roots, roughly coinciding with the  
341 average depth of fiddler crab burrows (Lim, 2006). Fiddler crab densities  
342 were higher than *U. cordatus* in both “rooted” and “gap” areas, whereas  
343 previous studies state that fiddler crabs preferentially colonize areas with a  
344 less dense canopy, since they feed on microphytobenthos (Miller, 1961;  
345 Bouillon et al., 2002). By contrast, *Ucides cordatus* preferably settles in  
346 areas with high density of *R. mangle* aerial roots, probably due to the

347 shelter and burrow structure stability that these roots provide (Piou et al.,  
348 2009).

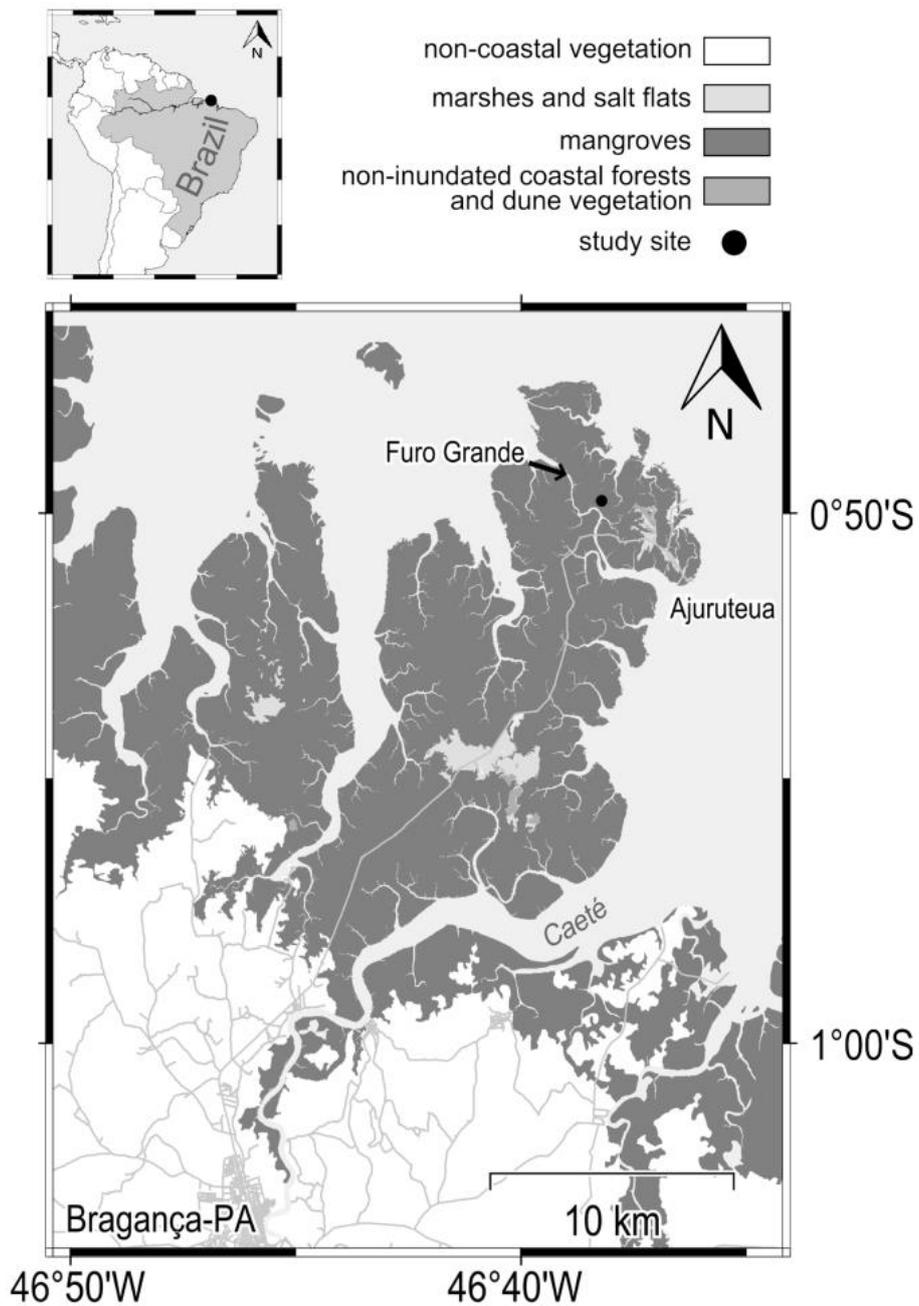
349         According to Heron and Ridd (2008), a multiple-loop crab burrow  
350 can decrease sediment salinity by up to 5 units within one week. In the  
351 present study, sediment salinity decreased with increasing density of  
352 *Ucides* burrows in gap areas with low density of fine roots. In “rooted”  
353 areas, no such effect of crab burrows on salinity was found, indicating that  
354 any potential existing crab effect was overruled (masked) by the salt-  
355 accumulating effects of the activity of the fine roots. Overall, our results  
356 indicate that the magnitude of the desalinating effects of the crab burrows  
357 seems to be context dependent, driven by the density of *Rhizophora* fine  
358 roots.

359         We conclude that neither *Uca* spp. nor *Ucides cordatus* are the key  
360 drivers for sediment salinity underneath mangrove trees in the studied  
361 mangrove forest. The areas where these crabs do have a clear desalinating  
362 effect, the gaps, are much smaller in area coverage than the rooted areas in  
363 the *Rhizophora* dominated mangrove forest in Northern Brazil, part of the  
364 largest continuous mangrove ecosystem of the world. These results need to  
365 be considered when evaluating the overall ecological effect(s) of crabs in  
366 mangrove ecosystems.

367

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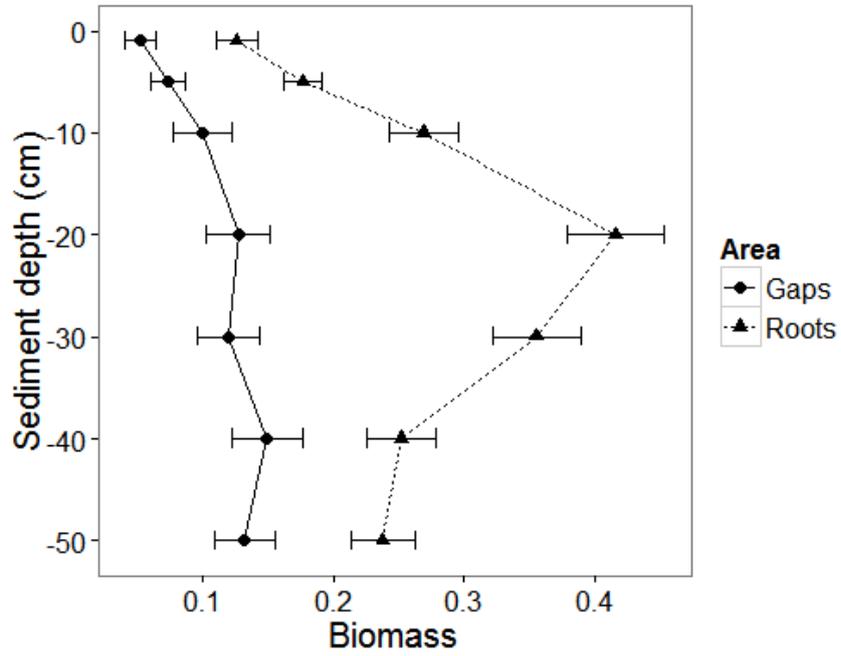
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377

378 Figure 1: Location of the study area in North Brazil and the detail of

379 the Ajuruteua's Peninsula. Source: Pülmanns. 2014.

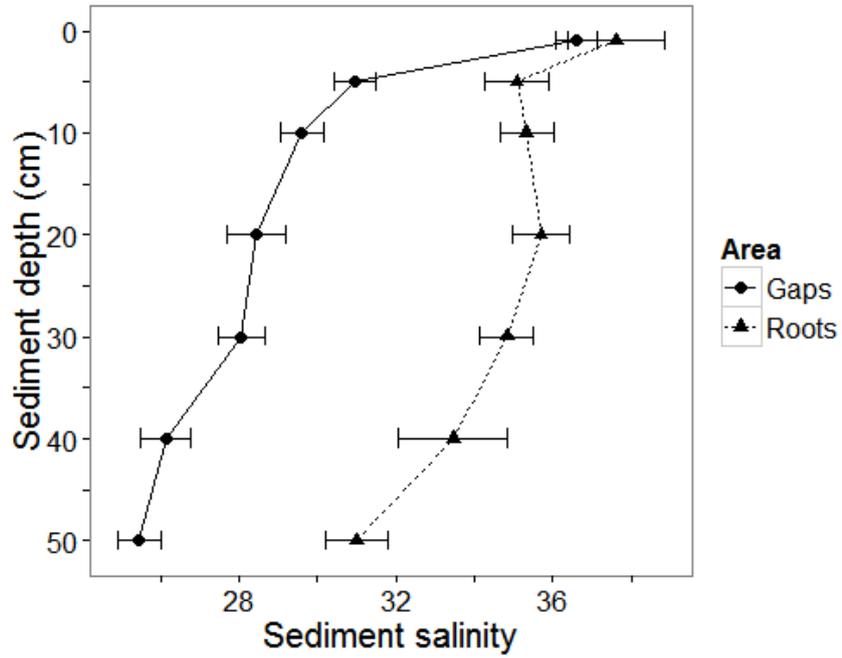


380

381 Figure 2: Relationship between fine root biomass (g) and the sediment  
 382 depth. Data represent means and standard error (L. Ratio = 36.4, df = 1, p <  
 383 0.001).

384

385



386

387 Figure 3: Relationship between sediment salinity and sediment depth.

388 Data represent means and standard error. (L. Ratio = 23.6, df = 1, p <

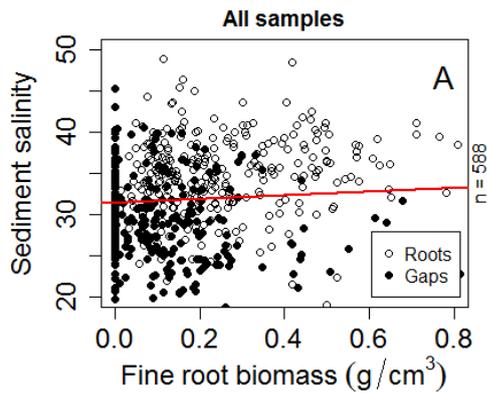
389 0.001).

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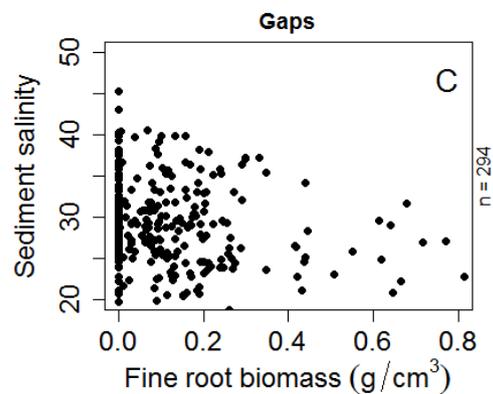
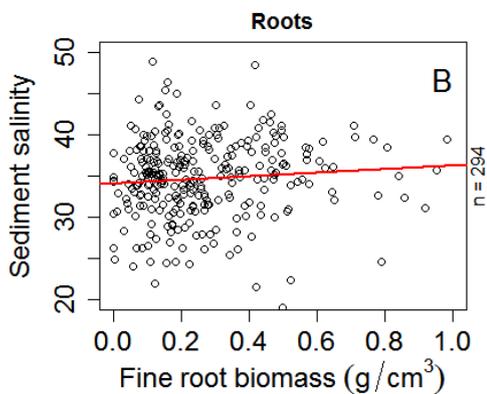
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396 Figure 4: Relationship between fine root biomass (g) and sediment salinity.

397 A) all samples ( $p = 0.004$ ,  $R^2 = 0.011$ ), B) densely rooted areas ( $p = 0.0266$ ,

398  $R^2 = 0.094$ ), C) root-free gaps ( $p = 0.398$ ,  $R^2 = -0.006$ ). The red line

399 indicates the trend line, when significant. “n” indicates the number of

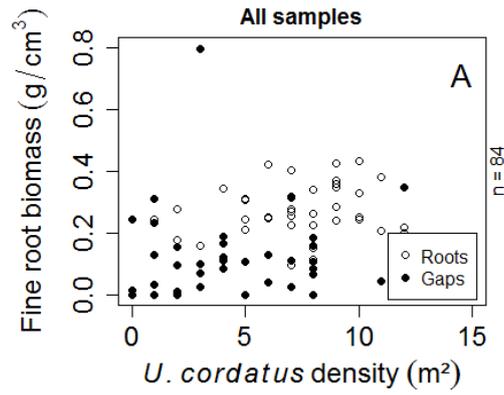
400 measurements.

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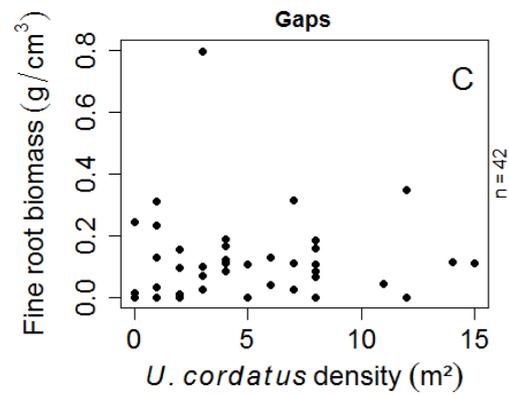
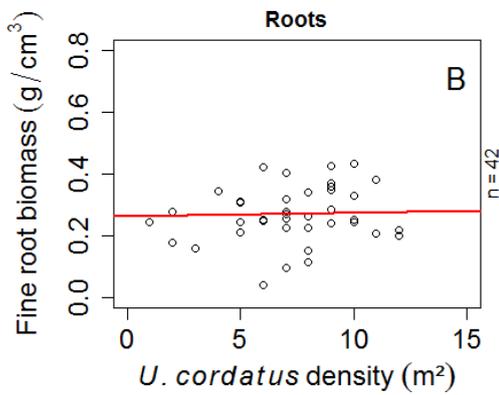
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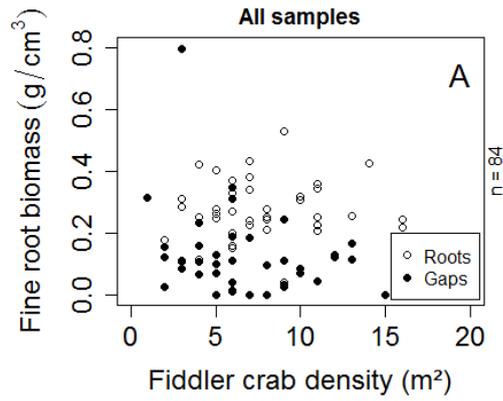
407 Figure 5: Relationship between fine root biomass (g) and *Ucides cordatus*  
 408 density. A) all samples ( $p = 0.804$ ,  $R^2 = -0.011$ ), B) densely rooted areas ( $p$   
 409  $= 0.028$ ,  $R^2 = 0.092$ ), C) root-free gaps ( $p = 0.236$ ,  $R^2 = 0.010$ ). The red line  
 410 indicates the trend line, when significant. “n” indicates the number of  
 411 measurements.

412

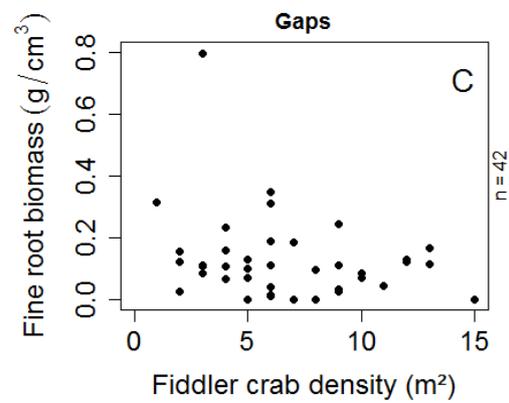
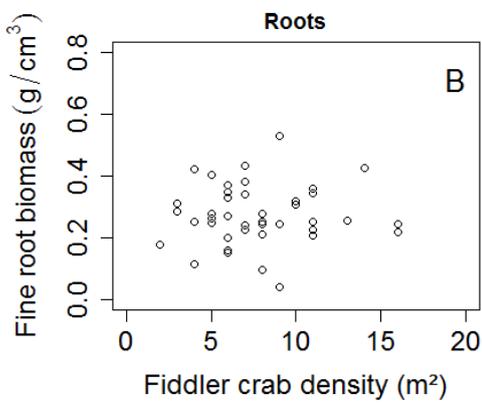
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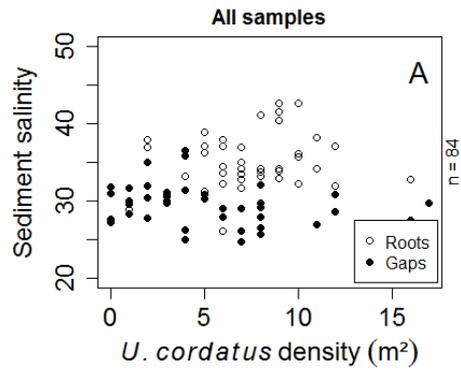
417

418 Figure 6: Relationship between fine root biomass (g) and Fiddler crab  
 419 density. A) all samples ( $p = 0.665$ ,  $R^2 = -0.009$ ), B) densely rooted areas ( $p$   
 420  $= 0.797$ ,  $R^2 = -0.023$ ), C) root-free gaps ( $p = 0.352$ ,  $R^2 = -0.002$ ). “n”  
 421 indicates the number of measurements.

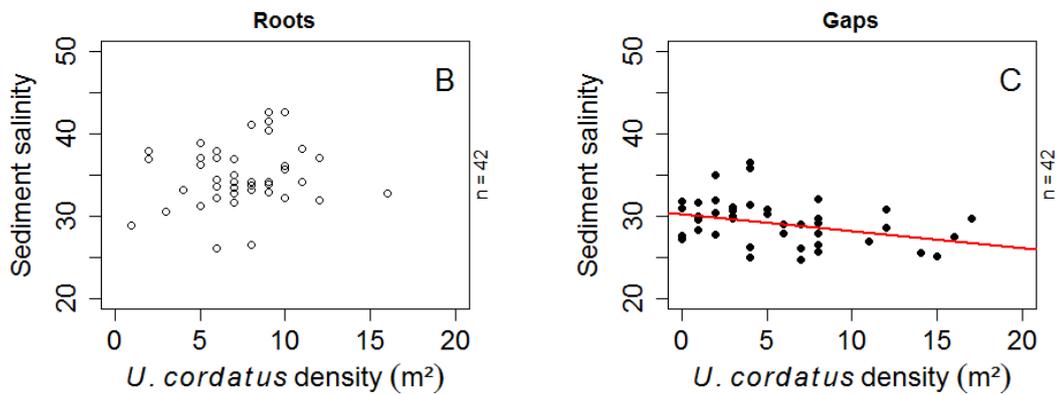
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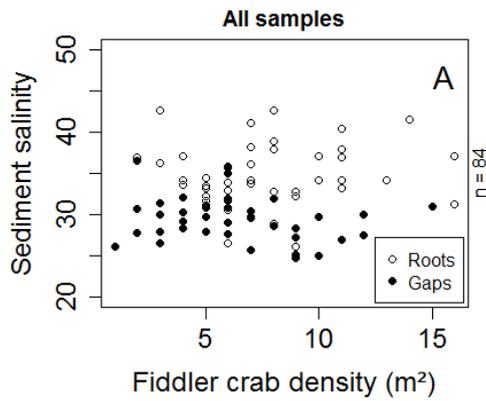


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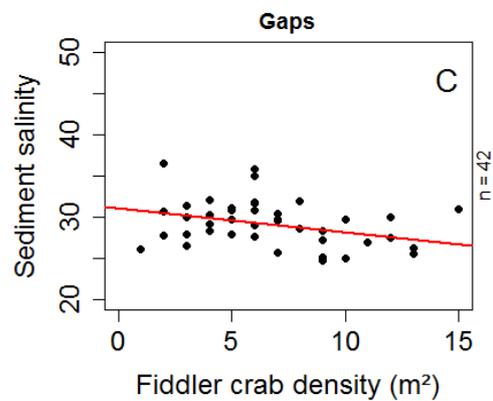
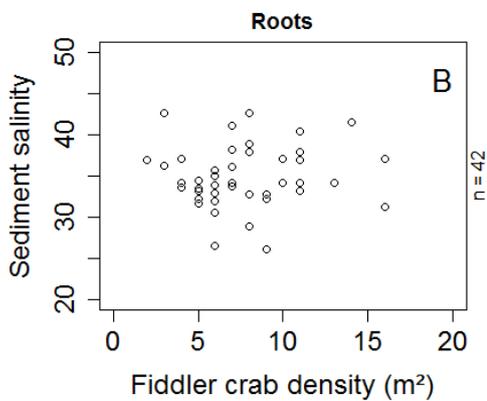
427 Figure 7: Relationship between sediment salinity and *Ucides cordatus*  
 428 density. A) all samples ( $p = 0.465$ ,  $R^2 = -0.005$ ), B) densely rooted areas ( $p$   
 429  $= 0.331$ ,  $R^2 = 0.008$ ), C) root-free gaps ( $p = 0.026$ ,  $R^2 = 0.0957$ ). The red line  
 430 indicates the trend line, when significant. “n” indicates the number of  
 431 measurements.

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436 Figure 8: Relationship between fine root biomass (g) and Fiddler crab  
 437 density. A) all samples ( $p = 0.750$ ,  $R^2 = -0.010$ ), B) densely rooted areas ( $p$   
 438  $= 0.673$ ,  $R^2 = -0.020$ ), C) root-free gaps ( $p = 0.052$ ,  $R^2 = 0.068$ ). The red  
 439 line indicates the trend line, when significant. “n” indicates the number of  
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