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MANGROVES IN CHANGING ENVIRONMENTS

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

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

Keywords *Rhizophora mangle* · Mangrove · *Ucides cordatus* · Sediment salinity

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Introduction

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

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

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

Two morphologically and functionally different groups of crabs are common in North Brazil, fiddler crabs (*Uca* spp., Leach, 1814, Ocypodidae) and *Ucides cordatus* (Linnaeus, 1763, Ucididae). Fiddler crab burrows are usually shallow, typically with a maximum depth of approximately 20 cm, and with a single opening (Lim, 2006). By contrast, burrows of *U. cordatus* reach as deep as 2 m into the sediment and can exhibit up to 2 burrow openings, while one opening is the most common type (Wunderlich et al., 2008). The tidal flushing effect of U-shaped and multiple-loop crab burrows is a well-studied topic (Wolanski & Gardiner, 1981; Stieglitz et al., 2000; Heron & Ridd, 2003, 2008; Lim, 2006; Xin et al., 2009). Crab burrows can facilitate the cycling of nutrients, CO_2 and oxygen, and are therefore considered an important pathway for the export of solutes between the mangrove sediment and the creek and for land–ocean organic and inorganic solute exchange (Stieglitz et al., 2000, 2013; Hollins et al., 2009; Xin et al., 2009; Pülmanns et al., 2014). The desalinating influence of animal burrows has also been investigated (Smith III et al., 1991; Passioura et al., 1992; Stieglitz et al., 2000, 2013). However, the first authors that have addressed specifically the relation between burrows with one opening from larger crabs, like *Ucides cordatus*, and salt contents in rooted sediments were Pülmanns et al. (2015). In a laboratory microcosm study, salinity in mangrove sediment with artificial crab burrows with one opening was significantly lower than in sediment without burrows. However, no evidence for a desalination effect in rooted areas was found for natural *Ucides* burrows in a field study conducted by the same authors during the pronounced North Brazilian rainy season. Pülmanns et al. (2015) suggested that any such effect of the burrows may have been masked by leaching of salt through precipitation. They predicted that the burrows' influence on sediment salinity would be revealed during the dry season. Sediment salinity drives many processes in mangrove sediments (e.g., Kida et al., 2017) and it is important to understand how it is influenced by burrowing crabs, particularly in light of the harvesting pressures that many crab species experience. *Ucides cordatus* for example, our study species, is heavily fished in many areas (e.g., Nascimento et al., 2017), and mass mortalities caused by fungal pathogens (Boerger et al., 2005, 2007) have caused population crashes, possibly affecting ecosystem processes (Schmidt et al., 2013).

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

Material methods

Location

The study was carried out in an intertidal mangrove forest located at the Ajuruteua Peninsula, close to the channel Furo Grande (46°38′W; 0°50′S), at the Caeté Estuary, about 30 km northwest of the city of Bragança in Pará, Brazil (Fig. 1). Situated within the Amazonian Coastal Zone (ZCA), this mangrove forest is part of the largest and best-preserved continuous mangrove belt on earth (Nascimento Jr. et al., 2013). These extensive mangrove forests can extend up to 40 km inland. The Furo Grande channel has a length of approximately 12 km with many smaller tributaries and connections with the Atlantic Ocean (Acheampong, 2001). The Ajuruteua Peninsula has a characteristic well-developed forest made up by the Red

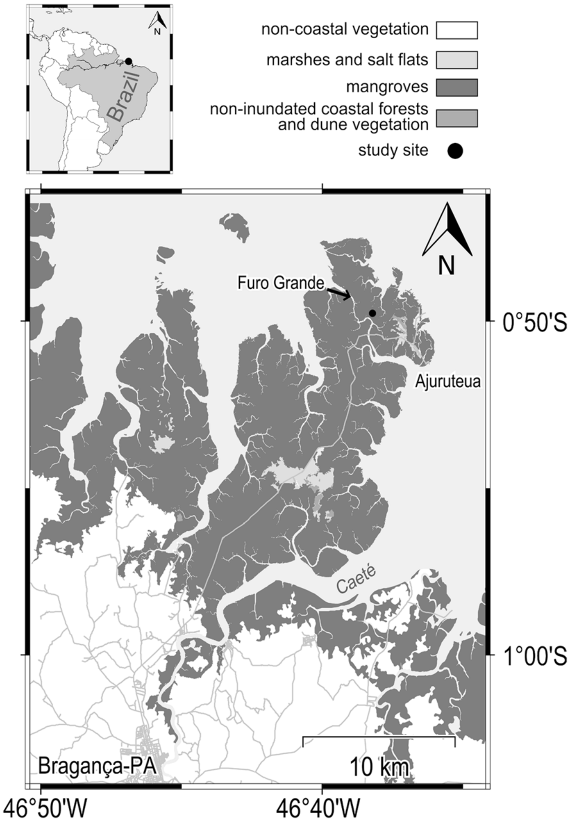

Fig. 1 Location of the study area in North Brazil and the details of the Ajuruteua's Peninsula. *Source* Pülmanns et al. (2014)

mangrove (*Rhizophora mangle*), the Black mangrove (*Avicennia germinans*), and the White mangrove (*Laguncularia racemosa* (L.) C. F. Gaertrn, Combretaceae). At the Furo Grande channel, the mangrove forest consists of a mix of *Rhizophora* and *Avicennia*, with a mean density of 520 trees per ha (Reise, 2003).

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

Burrowing crabs

Ucides cordatus is a semi-terrestrial crab that lives only in mangrove forests and occurs throughout the western Atlantic Ocean, from Florida (USA) to Santa Catarina State (Brazil) (Pinheiro & Hattori, 2006). The crabs have a life span of more than 10 years (Ostrensky et al., 1995; Diele, 2000; Pinheiro et al., 2005), are slow growing (Diele & Koch, 2010), and can reach sizes of up to 9 cm carapace width in the Caeté Estuary (Diele et al., 2005). They construct up to 2-m-deep burrows and feed mostly upon leaf litter (Nordhaus et al., 2006, 2009; Goes et al., 2010). *Ucides cordatus* preferably lives among the roots of *Rhizophora mangle*, as this tree species provides shelter and food through litter fall (Diele et al., 2005; Piou et al., 2009). Their density can be extremely heterogeneous, with very few crab holes in dry habitats, especially among pneumatophores of *Avicennia germinans* (Schories et al., 2003), and higher densities in humid habitats and underneath the aerial roots of *Rhizophora mangle,* with an average of 1.7 crab burrows m^{-2} (Diele et al., 2005).

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

Field study area

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

On both sampling occasions, a 1.0 m × 1.0 m quadrat was placed three times in both “rooted” and “gap” areas at each of the seven sites. The number of crab burrows assigned to either fiddler crabs or *U. cordatus* was estimated within each quadrat. This differentiation was made by the size of the burrow opening. In *R. mangle*-dominated forest stands of the Caeté Estuary, the average and minimum size of *U. cordatus* burrows is 5.08 cm (SD = 1.39) and 1.45 cm, respectively (Korting, 2012). In our study area, most crab burrows were either large, i.e., with a diameter of 5 cm or above, or small, i.e., 1 cm or below. The former could clearly be assigned to *U. cordatus*, whereas all small burrows, often with characteristic chimneys, were assigned to the much smaller fiddler crabs that are abundant in the forest, according to visual observations. In contrast, intermediate and smaller *Ucides* crabs are often more aggregated at the margins of the forest and near creeks (Diele et al., 2005; Schmidt et al., 2013). The few intermediate sized burrows present (approximatively 5%) (Korting, 2012), which could belong to *Ucides* or fiddler crabs, were not considered in this study.

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

Laboratory analyses

Salinity and water content

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

Fine root biomass

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

Statistical data analyses

The analyses were performed in R (R Development Core Team, 2008, version 2.15.2). The protocol for data exploration from Zuur et al. (2009, 2010) was followed to check for outliers and collinearity between explanatory variables. Then a linear mixed effect model (LME) (Pinheiro & Bates, 2000; Zuur et al., 2009) was used to analyze differences in sediment salinity among area types (gap and rooted area) and sediment depths and all their interaction terms. The random part of the LME model allowed for heterogeneity among individual sediment cores and different sampling sites. A variance function was applied to account for variance heterogeneity between sediment depth levels (Pinheiro & Bates, 2000; Zuur et al., 2009). For this the package “nlme” (Pinheiro et al., 2012) was used. Differences in burrow density among area types, sediment salinity, and amount of fine root biomass were tested with a linear model of covariance (ANCOVA). For this analysis, the density of aerial prop roots (“rooted” and “gap” areas) was used as a fixed factor, the salinity as a dependent variable, and the fine root biomass and crab density as co-variables.

Results

Fine root biomass changed significantly with depth in areas with high density of aerial prop roots (“rooted”) ($P < 0.001$, $R^2 = 0.036$), No such significant change was observed within “gap” areas ($P = 0.583$, $R^2 = -0.002$, Fig. 2). Average fine root biomass was significantly higher in the “rooted” areas (0.274 g/cm^3 ± 0.012 SE) than in “gaps” (0.163 g/cm^3 ± 0.023 SE) ($P < 0.001$, L ratio = 36.4, df = 1). The difference of fine root biomass between the “rooted” and “gap” areas at the surface (depth ≤5 cm) and the deeper layers (≥40 cm) remained constant, around 0.1 g/cm^3, but was more pronounced at intermediate depths, between 10 and 30 cm depth, being around 0.4 g/cm^3 at 20 cm depth (Fig. 2).

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

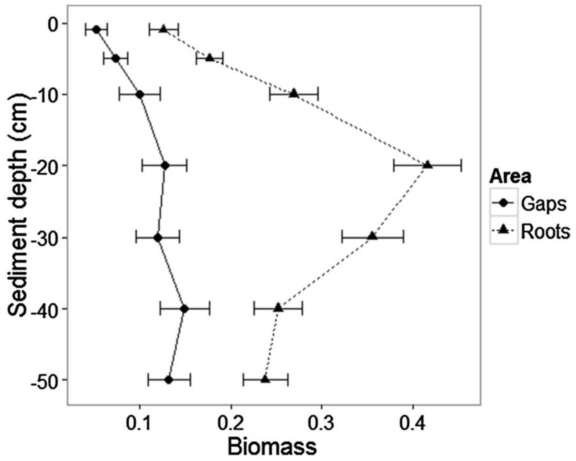

Fig. 2 Relationship between fine root biomass (g) and the sediment depth. Data represent means and standard error (L ratio = 36.4, df = 1, $P < 0.001$)

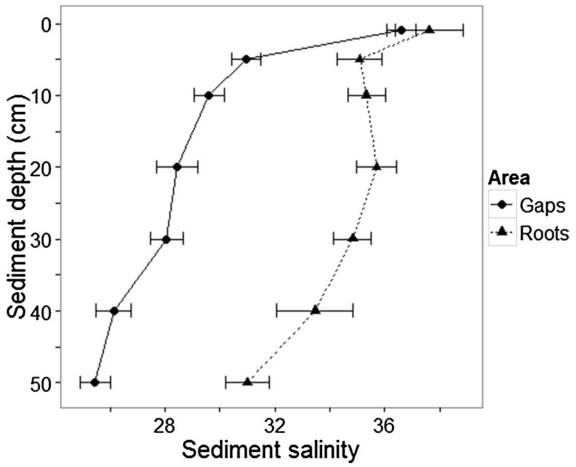

Fig. 3 Relationship between sediment salinity and sediment depth. Data represent means and standard error (L ratio = 23.6, df = 1, $P < 0.001$)

Overall, salinity as a function of depth followed a similar pattern in both areas, despite the higher overall values in the “rooted” areas. Sediment salinity and fine root biomass were positively correlated, both when samples from the two areas were pooled together ($P < 0.05$; Fig. 4A) and in the “rooted” area ($P = 0.026$; Fig. 4B). In contrast, in gap areas without aerial roots, the correlation was not significant ($P = 0.398$; Fig. 4C). When comparing fine root biomass and *Ucides* burrow density, no significant relation was found when pooling the two treatments together ($P = 0.804$; Fig. 5A) and at “gap” areas ($P = 0.236$; Fig. 5C). However, *Ucides* burrow density and fine root biomass were positively correlated in “rooted” areas ($P = 0.028$; Fig. 5B). No correlation was observed for fiddler crabs (all samples: $P = 0.665$, “rooted” areas: $P = 0.797$, “gaps”: $P = 0.352$; Fig. 6). Sediment salinity did not show a relation with crab burrow density, when samples from the two areas were pooled together (*U. cordatus*: $P = 0.465$; Fig. 7A, Fiddler: $P = 0.750$; Fig. 8A), and there was also no relation between crab density and sediment salinity in “rooted” areas (*U. cordatus*: $P = 0.331$; Fig. 7B, Fiddler: $P = 0.673$; Fig. 8B). However, in gaps without aerial roots, sediment

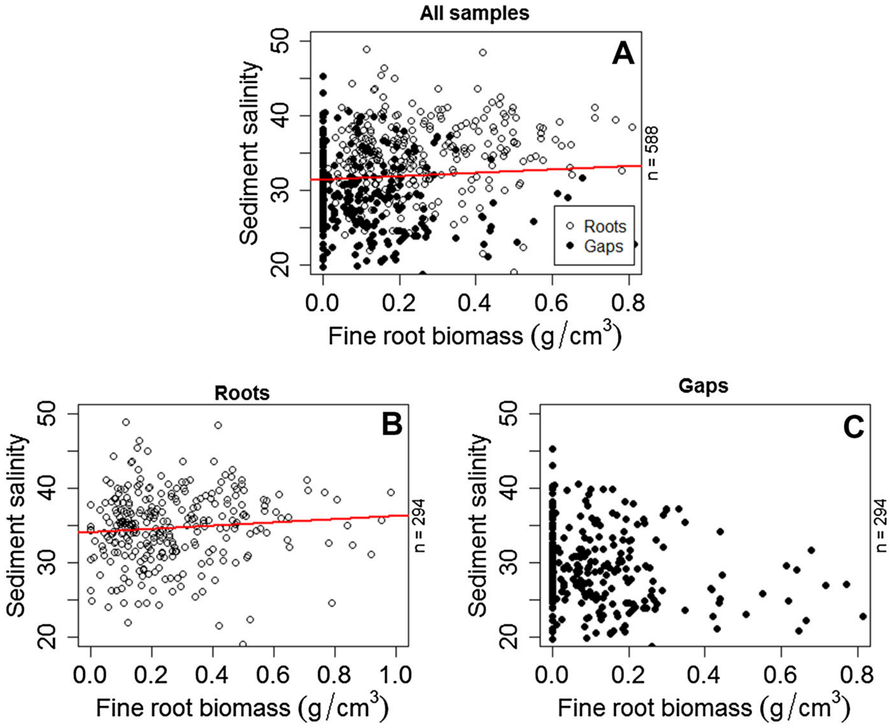

Fig. 4 Relationship between fine root biomass (g) and sediment salinity. **A** All samples ($P = 0.004$, $R^2 = 0.011$), **B** densely rooted areas ($P = 0.0266$, $R^2 = 0.094$), and **C** root-free gaps ($P = 0.398$, $R^2 = -0.006$). The *red line* indicates the trend line, when significant. "*n*" indicates the number of measurements

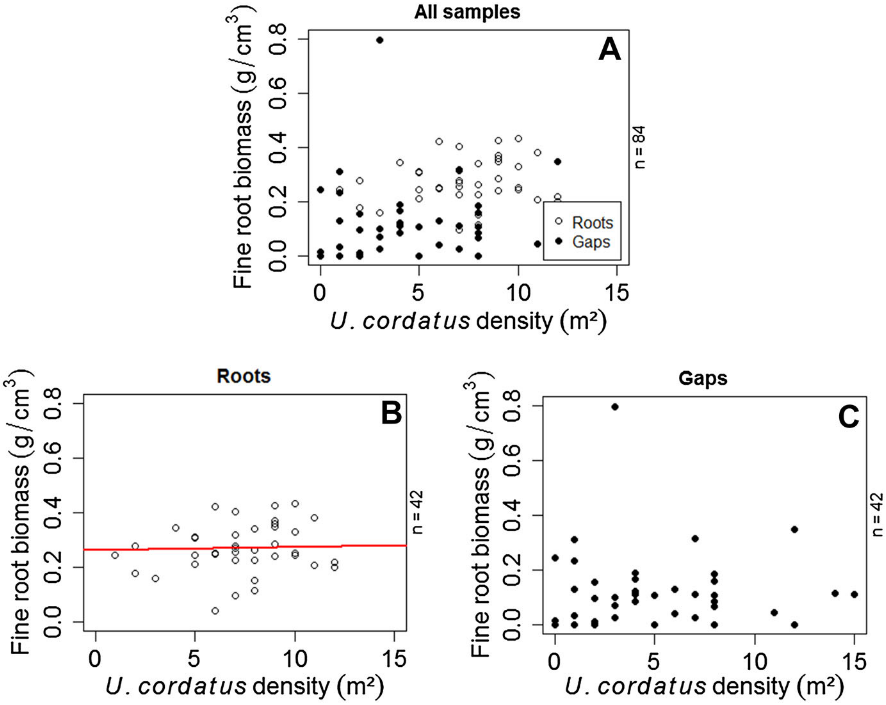

Fig. 5 Relationship between fine root biomass (g) and *Ucides cordatus* density. **A** All samples ($P = 0.804$, $R^2 = -0.011$), **B** densely rooted areas ($P = 0.028$, $P^2 = 0.092$), and **C** root-free gaps ($P = 0.236$, $R^2 = 0.010$). The *red line* indicates the trend line, when significant. "*n*" indicates the number of measurements

salinity decreased with both increasing *Ucides* burrow density ($P = 0.026$; Fig. 7C) and fiddler crab burrow density ($P = 0.052$; Fig. 8C).

The area ("rooted" *versus* "gap") had a significant influence on salinity ($P = 4.6\,\mathrm{e}^{-10}$) and on the burrow density of *U. cordatus* ($P = 0.004$), but did not have a

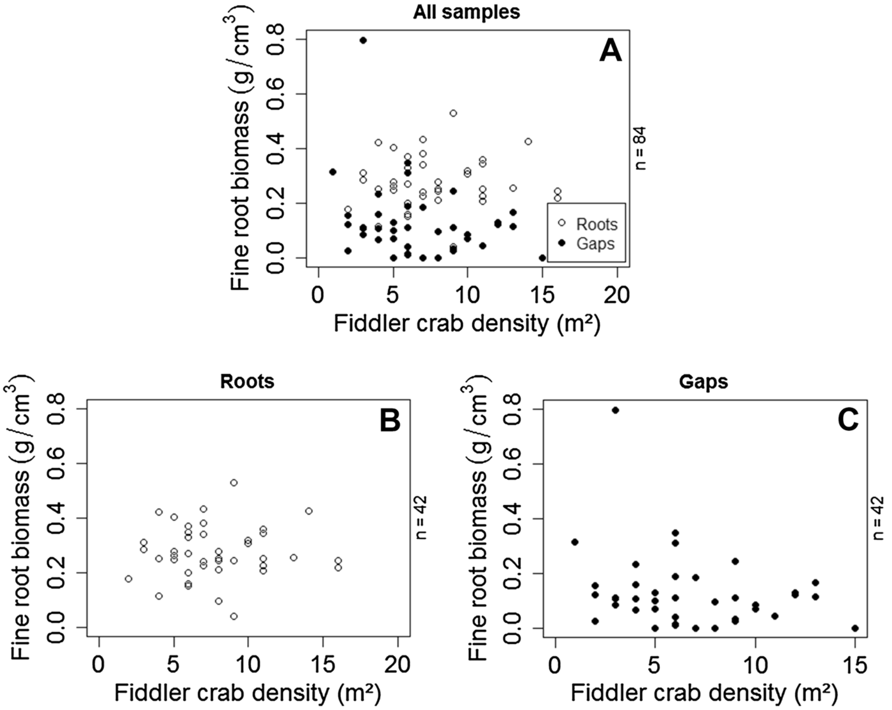

Fig. 6 Relationship between fine root biomass (g) and Fiddler crab density. **A** All samples ($P = 0.665$, $R^2 = -0.009$), **B** densely rooted areas ($P = 0.797$, $R^2 = -0.023$), and **C** root-free gaps ($P = 0.352$, $R^2 = -0.002$). The *red line* indicates the trend line, when significant. "*n*" indicates the number of measurements

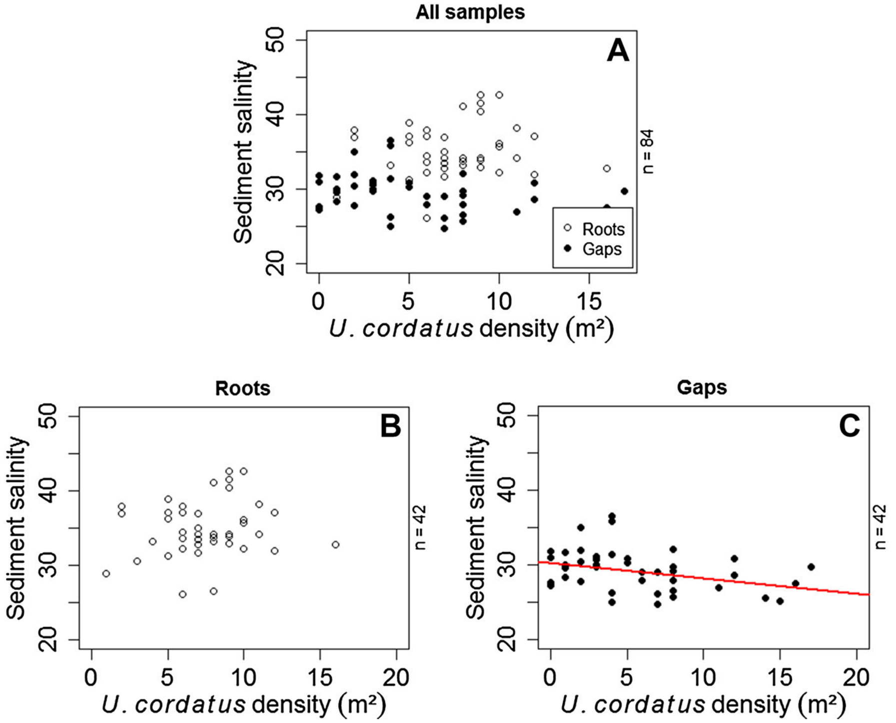

Fig. 7 Relationship between sediment salinity and *Ucides cordatus* density. **A** All samples ($P = 0.465$, $R^2 = -0.005$), **B** densely rooted areas ($P = 0.331$, $R^2 = 0.008$), and **C** root-free gaps ($P = 0.026$, $R^2 = 0.0957$. "*n*" indicates the number of measurements

significant effect on fiddler crab burrow density ($P = 0.194$). Burrow density of *Ucides* was higher in the "rooted" areas than in the "gaps." In the "rooted" areas, the average density was 7.4 m^{-2} (±0.4 SE) for *Ucides cordatus* and 7.6 m^{-2} (±0.5 SE) for fiddler crabs. In the "gaps," the average density for

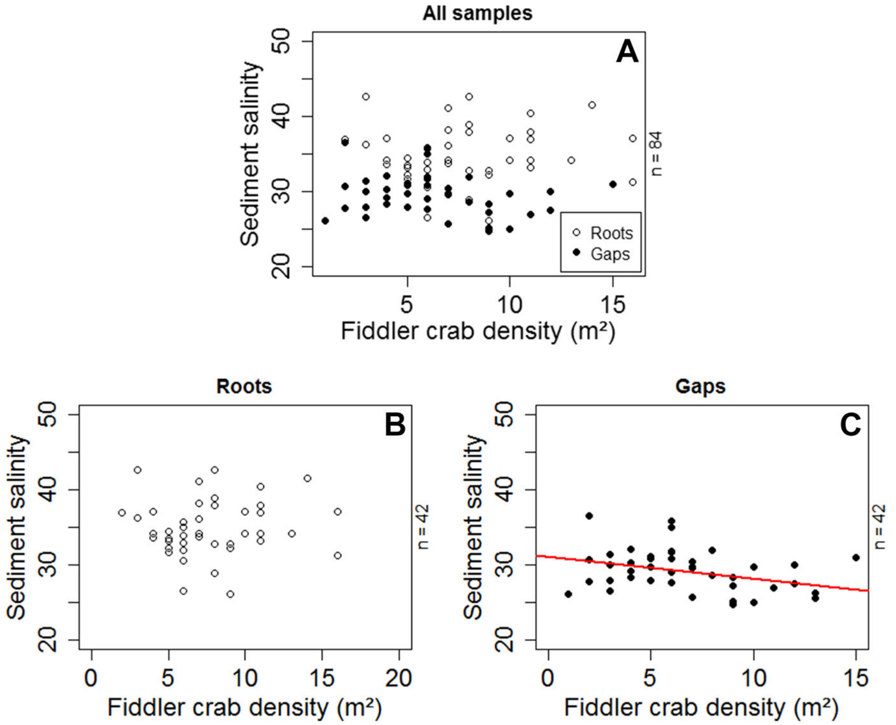

Fig. 8 Relationship between fine root biomass (g) and Fiddler crab density. **A** All samples ($P = 0.750$, $R^2 = -0.010$), **B** densely rooted areas ($P = 0.673$, $R^2 = -0.020$), and **C** root-free gaps ($P = 0.052$, $R^2 = 0.068$). The *red line* indicates the trend line, when significant. "*n*" indicates the number of measurements

U. cordatus was 5.5 m^{-2} (±0.7 SE) and 6.6 m^{-2} (±0.5 SE) for fiddlers.

Discussion

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

In our North Brazilian study, conducted during the dry season, sediment salinity was higher in areas with a higher *R. mangle* prop root density (despite higher *Ucides* and fiddler crab burrow densities) than in the gap areas. This refutes our hypothesis of lower sediment salinity at areas with higher density of crab burrows during this time of year. The result corroborates the findings of Pülmanns et al. (2015) in the rainy season, when sediment salinity in "rooted" areas was also higher than in "gap" areas (27 and 31 in gap areas and rooted areas, respectively, at the end of the rainy season). Findings by Smith III (1987), demonstrating a salinity of 57.5 in areas with high amounts of aerial roots *versus* 55.2 in gaps, are also in concordance with the present results. A microcosm experiment by Pülmanns et al. (2016) showed lower salinity in treatments with (41) than without (47) artificial burrows after 6 months (both treatments started with a sediment salinity of 37.5 at the first centimeter), showcasing that crab burrows can have a desalinating effect.

In our study, secondary fine root biomass was highest at a sediment depth of 20 cm in areas with aerial roots, roughly coinciding with the average depth of fiddler crab burrows (Lim, 2006). Fiddler crab densities were higher than *U. cordatus* in both "rooted" and "gap" areas, whereas previous studies state that fiddler crabs preferentially colonize areas with a less dense canopy, since they feed on microphytobenthos (Miller, 1961; Bouillon et al., 2002). By contrast, *Ucides cordatus* preferably settles in areas with high density of *R. mangle* aerial roots, probably due to the shelter and burrow structure stability that these roots provide (Piou et al., 2009).

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

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

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