UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"

INSTITUTO DE BIOCIÊNCIAS - CÂMPUS DO LITORAL PAULISTA

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Juan Pardo

São Vicente, SP

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Is bioturbation also reflected on above-ground biogenic sedimentary structures? A hypothesis regarding the estuarine fiddler crab *Uca thayeri*

Juan Carlos Farias Pardo[1] and Tânia Marcia Costa[1]*

Biosciences Institute, São Paulo State University – UNESP, Coastal Campus, Praça Infante Dom Henrique, s/nº, Parque Bitaru, São Vicente, SP, Brasil. P. O, Box 73601-Zip Code 11.380-972

*corresponding author: costatm@clp.unesp.br

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Abstract:

We evaluated the vertical distribution of organic matter promoted by construction and maintenance of *Uca thayeri* biogenic sedimentary structures. By integrating field and laboratory approaches, we estimated the amount of organic matter transported by burrowing activity and chimney building processes. In the laboratory experiment, we used microcosms with different layers of organic matter content: upper (low content/10cm) and lower (high content/10cm). Sediment was physically transported from lower to upper layers in which chimney and burrow profiles reflected organic matter transport after crab activity. In the field experiment, we compared burrow and non-burrow profiles (without visible burrows); chimneys were collected and sediment samples were stratified in the upper (0-4 cm), upper intermediate (4-8 cm), lower intermediate (8-12 cm) and lower layers (12-20 cm), the latter which comprises maximum burrow depth for this species (~20 cm). Burrows had more organic matter than non-burrow layers, acting as traps for sediment and organic compounds. Chimneys showed lower organic matter content when compared to lower burrow layers. Thus, organic matter is disposed (e.g. washed by tides) or consumed (e.g. microbial community) after chimney shaping. The *U. thayeri* biogenic sedimentary structures affect organic matter vertical distribution of mangrove soils. Lab and field experiments seemed to be complementary for a better understanding of the whole process of organic matter distribution. Ecological implications of above-ground biogenic sedimentary structures are discussed.

Keywords: Organic matter. Vertical sediment distribution. Mangrove habitat. Ecosystem engineers. genus *Uca*. Chimney building.

1. Introduction

Estuarine ecosystem act as an important component in coastal zones due to their valuable ecological and economical services (Barbier et al., 2011; Day et al., 2013). Mangroves, salt marshes and other estuarine habitats are characterized by high primary productivity and efficient nutrient cycling (Jennerjahn and Ittekkot, 2002; Caffrey, 2004); for protection of shorelines from erosion and natural disasters (Dahdouh-Guebas et al., 2005; Barbier, 2015), while also providing food and shelter for many species (Robertson and Duke, 1987; Nagelkerken et al., 2000; Huijbers et al., 2015). Owing to their environmental resources, estuaries are a nursery site and refuge for terrestrial, semiterrestrial and marine groups (Colpo et al., 2001; Nagelkerken et al., 2008; Huijbers et al., 2015).

The organism's behaviour is intrinsically related to environment dynamics (Jones et al., 1994; Nagelkerken et al., 2008). Bioturbation, bioirrigation and biodeposition processes promoted by estuary organisms affect soil biogeochemistry factors, which in turn can affect carbon and nitrogen cycles (Kristensen et al., 2001; Wang et al., 2010; Fanjul et al., 2011; Quintana et al., 2015), oxygen, pH, redox potential gradients (Aller, 1994; Araújo Jr. et al., 2012), granulometry and organic matter (Krantzberg, 1985; Penha-Lopez et al., 2010). Remineralization and organic matter lability play an important role in material flow through ecosystems (Jennerjahn and Ittekkot, 2002). Organic matter in estuarine soils is composed of labile (e.g. microbial biomass C) and refractory (e.g. plant dead tissues) organic compounds (McLusky and Elliott, 2004). Thus, organic matter is a valuable energy source in natural processes involving flora and fauna and ecosystem functioning (Alongi, 1996; Barbier et al., 2011).

78 Some species construct and maintain sedimentary structures, defined by Frey
79 (1973) as "*a biogenic structure produced by the activity of an organism upon or within*
80 *an unconsolidated particulate substrate*", which are related to bioturbation and
81 consequential biogeochemical effect on estuarine soil. Biogenic sedimentary structures
82 have been described for some estuarine groups, such as elasmobranchs (rays - Howard
83 et al., 1977), annelids (polychaetes – François et al., 2002), fish (mudskipper – Dinh et
84 al., 2014) and crustaceans (lobster - Ngoc-Ho and Saint Laurent, 2009; crabs -
85 Kristensen, 2008; Kim et al., 2011). The shapes of these structures and hence their
86 names vary (e.g. burrows, pillars, chimneys) as do their functions (e.g. sexual attraction,
87 predation risk reduction, reduction of structure loss to an intruder). As well as having an
88 ethological purpose, sedimentary structures are a key-factor in estuarine ecosystems soil
89 conformation (Meysman et al., 2006).
90 The effects of ecosystem engineers are, directly or indirectly, related to resource
91 availability and habitat shaping for other organisms (Bertness, 1985; Jones et al., 1994),
92 from microbial communities (Bertics and Ziebis, 2009) to macrobenthic populations
93 (Widdicombe et al, 2000). The engineer species create, maintain and modify
94 surrounding areas by physical alterations in biotic and abiotic factors (Jones et al.,
95 1994). Filter feeders, grazers and burrowers are influential bioengineers on estuaries;
96 among them, decapod crustaceans predominate in mangrove forests and salt marshes
97 acting as biodiffusors and regenerators of sedimentary matrix (Kristensen et al., 2012).
98 Burrowing crabs and their intrinsic behaviour (i.e. feeding, locomotion) are known to
99 allogenically modify soil characteristics. For instance, by increasing the exposed surface
100 area and sediment-water interface (Koo et al., 2007), enhancing CO2 release from
101 stocked carbon to the atmosphere (Pülmanns et al., 2014), and altering soil nutrient

availability (i.e. ammonium, sulphide, nitrogen) to other species (Smith et al., 1991; Fanjul et al., 2011).

Crabs of the genus *Uca,* also known as fiddler crabs, are semiterrestrial intertidal organisms with widespread distribution in estuarine ecosystems, occupying sandy and muddy substrates (Wolfrath, 1992; Thurman et al., 2013). Fiddler crabs are known for their high numbers in estuarine habitats, which facilitates their use as model organisms in comparative and ecological studies (Crane, 1975). Some of the species build above-ground biogenic sedimentary structures associated or not with their burrows (Crane, 1975). This behavioural strategy also varies in function and morphology, such as reducing aggression between males [hoods: Zucker (1981)], concealing the burrow entrance [chimneys: Slatyer et al. (2008)] and attracting females [pillar: Christy (1998b)]. The fiddler crab *Uca thayeri* (Rathbun, 1900) is one of most abundant in the western Atlantic Ocean (Costa and Negreiros-Fransozo, 2002; Thurman III et al., 2013). This species prefers muddy soils with high organic matter content, mainly in mangrove areas (Costa and Negreiros-Fransozo, 2001, 2003), where they construct and maintain burrows with associated structures in the shape of chimneys (Crane, 1975). The function of chimney-building behaviour in *U. thayeri* was related to territory defence by females in late gonadal stage and possibly to reproductive success (Salmon, 1987); also, Gusmão-Junior et al. (2012) showed that ovigerous females had more developed chimneys, which may be associated with maintenance of internal conditions inside burrows.

Previous studies already recognize the critical role played by fiddler crabs influence on mangrove soils (e.g. Kristensen, 2008; Kristensen et al., 2012; Fanjul et al., 2015). However, the bioturbation potential promoted by estuarine crabs and its bioarrangements has not yet been substantially described. In this context, we

hypothesize that the construction and maintenance of *U. thayeri* biogenic sedimentary structures (burrows and chimney buildings) affects organic matter distribution on mangrove soils. By combining field and laboratory experiments, we estimated the sediment transportation on mangrove soils, evaluating the vertical distribution and amount of organic matter bioturbated by this crab.

2. Material and methods

2.1 Laboratory experiments

2.1.1 Crab and sediment sampling design

Crab and sediment were collected in Portinho Mangrove, Praia Grande - São Paulo/Brazil (23°59'16.74" S 46°24'26.28" W). We used *U. thayeri* adult females as our model species (carapace width larger than 13.9 mm; Negreiros-Fransozo et al., 2003). Only adult females were used because they actively built and maintain chimneys (Gusmão-Junior et al., 2012). Hence, we collected adult females [carapace width (±SE): 17.57±0.41] that occupied burrows with chimney buildings. All crabs were acclimated with constant temperature (25°C) and photoperiod (daily light regime of 12h light/12h dark) for 48h.

Sediment collection was conducted in two different areas with distinct organic matter (%) content and similar granulometry [silty clay (Shepard, 1954) - previous analysis]; both low [3.46 ± 0.22%] and high [20.61 ± 1.12%] organic matter from sediment was sieved (mesh/2mm) in order to remove macrofauna and detritus to avoid organic content overestimation. Afterwards, we removed the excess of water from sediment surface for both samples, since this could affect the stability and structure of the sediment matrix.

152 **2.1.2 Experimental design**

153 We investigated the effect of crab bioturbation promoted by the construction and
154 maintenance of biogenic sedimentary structures on vertical sediment distribution.
155 Microcosms [35 cm (Ø) x 30 cm (h)] were established with low organic matter content
156 in the top layer (upper 10 cm) and high organic matter content (lower 10 cm) in the
157 bottom layer. The sediment layers were based on the maximum and mean depth of
158 burrows constructed by *U. thayeri* (19.4 cm and 11.88 ± 3.2 cm, respectively – Moreto,
159 unpublished data). The experiment had three experimental groups (n = 8/each
160 treatment): (1) control - absence of crabs, (2) burrow sampling and (3) next to burrow
161 sampling.

162 Before allocation of crabs to the microcosms (To), we core-collected (diameter:
163 three cm) three sediment layer samples with 10 cm depth (upper region) in each
164 microcosm for posterior comparison. We carefully closed the holes with surrounding
165 sediment. Then, we allocated four adult females per microcosms (proportionally to the
166 field density for this species), except for the control treatment, which we did not allocate
167 any crab. Each microcosm was randomly allocated in the laboratory.

168 After 72h of experiment (T1), chimney buildings [mean structure height (±SE):
169 20.67±1.21 mm; mean structure width (±SE): 26.6±1.32 mm] of crab inclusion
170 treatments and sediment samples (10 cm/upper region) (n=3/each microcosm) were
171 collected, identified and frozen for posterior analysis. Corer collection (~3 Ø)
172 comprised the whole burrow aperture for this species. Burrow architecture may vary in
173 shape but is usually comprised of a single J-shaped structure (Wolfrath, 1992; Machado
174 et al., 2013; Wang et al., 2015). Since the corer is thus able to sample the burrow in its
175 vertical entirety (from top to bottom), its characteristic shape does not affect core
176 collection. All samples of control (Figure 1a), burrow and next to burrow (Figure 1b)

variables were referred to the upper sediment layer (10 cm), except for the chimneys buildings (Figure 1b, 1c). Posteriorly, samples were dried in oven (60°C, 72h) and 10g portions were burned in a muffle (500°C, 4h) by loss on ignition (Heiri et al., 2001) to obtain a measure of organic matter content and the percentage of ash free dry weight (AFDW).

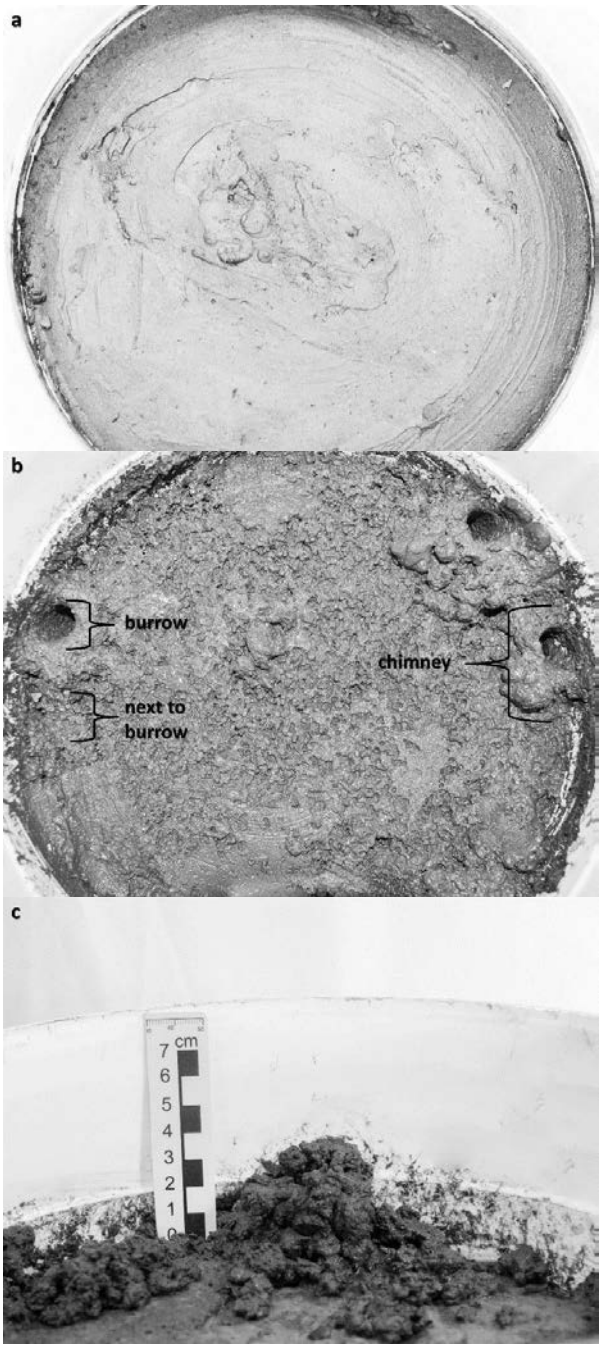


Figure 1: Overview of microcosms and its variables: a) Control treatment after 72h of experiment (T1); b) Sampling location of the variables (chimney, burrow and next to

187 burrow) from treatment I (chimney and burrow) and/or treatment II (chimney and next
188 to burrow); c) chimney building constructed by the female *Uca thayeri*.
189
190 **2.2 Field experiment**
191 **2.2.1 Study site**
192 The experiment was conducted in a mangrove area (23°50'16.57" S; 46°
193 9'10.11" W) at the Itapanhaú River, the main tributary of the Bertioga channel, which is
194 associated to the Santos estuarine complex system, central coast of São Paulo State,
195 Brazil. The Itapanhaú river discharges approximately 10 m^3s^{-1} of freshwater
196 (semidiurnal tide flow) and is fringed by mangrove areas characterized by the typical
197 mangrove vegetation in Brazil (*Rhizophora mangle*, *Avicennia shaueriana,* and
198 *Laguncularia racemosa)* (Eichler et al., 2006).
199
200 **2.2.2 Experimental design**
201 We carried out a field experiment to verify the distribution of organic matter in
202 biogenic sedimentary structures (burrows and chimney buildings) and in the
203 surrounding area, without visible burrows (non-burrow profile). Surveying was
204 conducted between August and September 2012. The field experiment had two
205 treatments (20 replicates each one): (1) non-burrow profile and (2) burrow profile. We
206 collected burrows with chimneys that were occupied by ovigerous females. We
207 carefully collected the crabs, measured their carapace length (mm), and sampled all
208 chimneys [mean structure height (±SE): 23.10±1.59 mm; mean structure width (±SE):
209 39.37±1.01 mm]. All core-collected samples (20 cm) were stratified *in situ* in four
210 layers: upper (0-4 cm), upper intermediate (4-8 cm), lower intermediate (8-12 cm) and
211 lower layer (12-20 cm). Chimney buildings were compared with upper and lower layer

212 of both treatments to prevent data dependence (see details in data analysis). We chose a
213 deeper lower layer based on the maximum and mean depth of *U. thayeri* burrows (19.4
214 cm and 11.88 ± 3.2 cm, respectively – Moreto, unpublished data), which included the
215 bottom surface. AFDW of all samples was obtained in the same way described for the
216 laboratory experiment (see above), with crabs and sediment reallocated following the
217 experiment.

218

219 **2.3 Data analysis**

220 In the laboratory experiment, differences between before and after crab
221 bioturbation and the comparison between chimney structures and the upper layer (To)
222 were evaluated using a Paired t test (Underwood, 1997). The field data were
223 randomized to assure the independence of superior and inferior layers when compared
224 with chimneys. Collection of a vertical sediment sample using a core may promote
225 dependence of layers; thus, we analysed ten samples of each layer and treatment
226 (control and burrows). We applied an Independent t test to relate burrow and control
227 layers and an One-way ANOVA followed by Tukey's *post hoc* to compare chimney and
228 upper and lower layers (Underwood, 1997).

229 Data were checked for normality (Shapiro-Wilk's test) and homoscedasticity
230 (Lavene's test) and, when necessary, transformed with $\text{logit}(x) \equiv \log[x/(1-x)]$ to meet
231 assumptions (Warton and Hui, 2011). Outliers were removed for laboratory and field
232 data by Chauvenet's test (Wilkinson et al., 1996). Differences were considered
233 significant if $p < 0.05$ (Zar, 1999). All the analyses were performed with IBM SPSS
234 Statistics 20 and graphics were made in ORIGIN 2015.

235

3. Results

3.1 Laboratory experiment

Burrows with chimneys were checked after 72h. Chimneys showed higher organic matter content than the upper layer (Paired t test, df = -17,88, F = 84, p = 0.0001) (Figure 2).

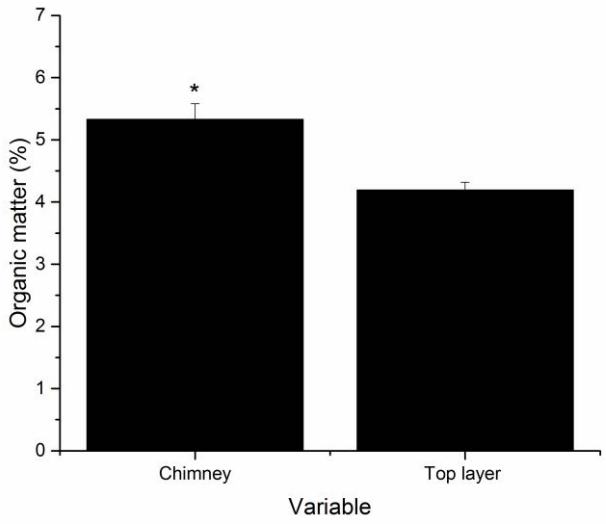


Figure 2: Mean (±SE) of organic matter content of chimney structures and top layer after 72 h. Asterisk (*) indicates statistical difference between variables (Paired t test, p = 0.0001).

Vertical sediment transportation was reflected on female crab burrows, showing an increase in organic matter content in the upper layer (Paired t test, t = -2.46, df = 19, p = 0.02). However, there were no significant differences between To and T1 next to the burrows (t = - 0.641, df = 22, p = 0.52). Also, organic matter content did not differ in the control treatment (Paired t test, t = 1.72, df = 20, p > 0.09) (Figure 3).

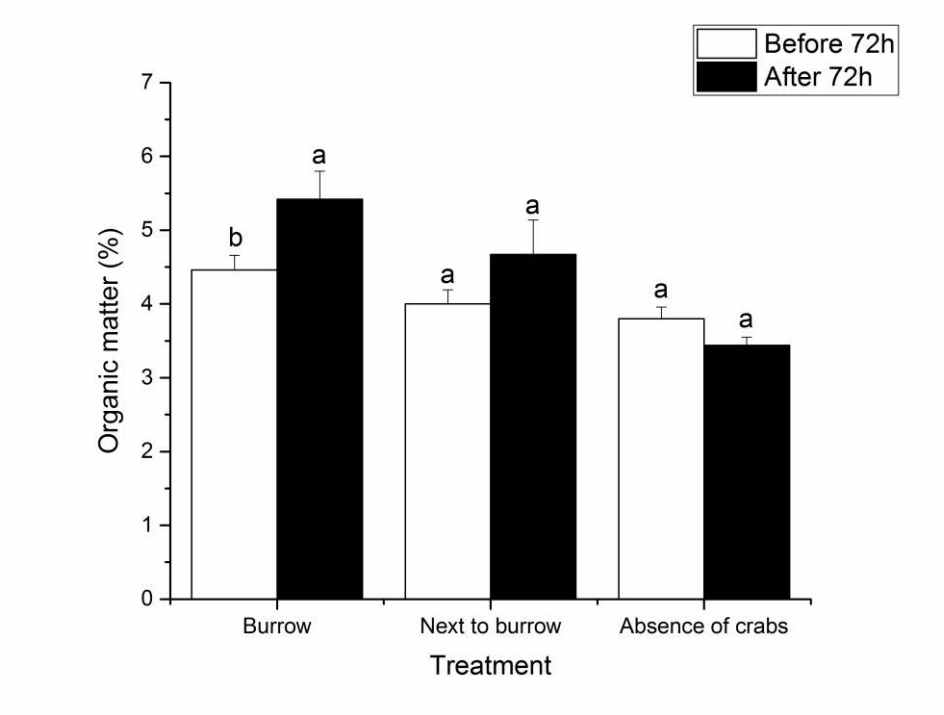


Figure 3: Mean (±SE) of organic matter content in the upper layer of sediment before and after 72 h in the three experimental groups: burrow, next to burrow and control (absence of crabs). Different letters indicate statistical difference within treatment (Paired t test, $p < 0.05$). Outliers were removed from this data ($n = 21$-24).

3.2 Field experiment

All burrow layers had more organic matter content than the non-burrow layers (Independent t test: $p < 0.05$) with a mean difference of 3.93-fold between layers (Figure 4).

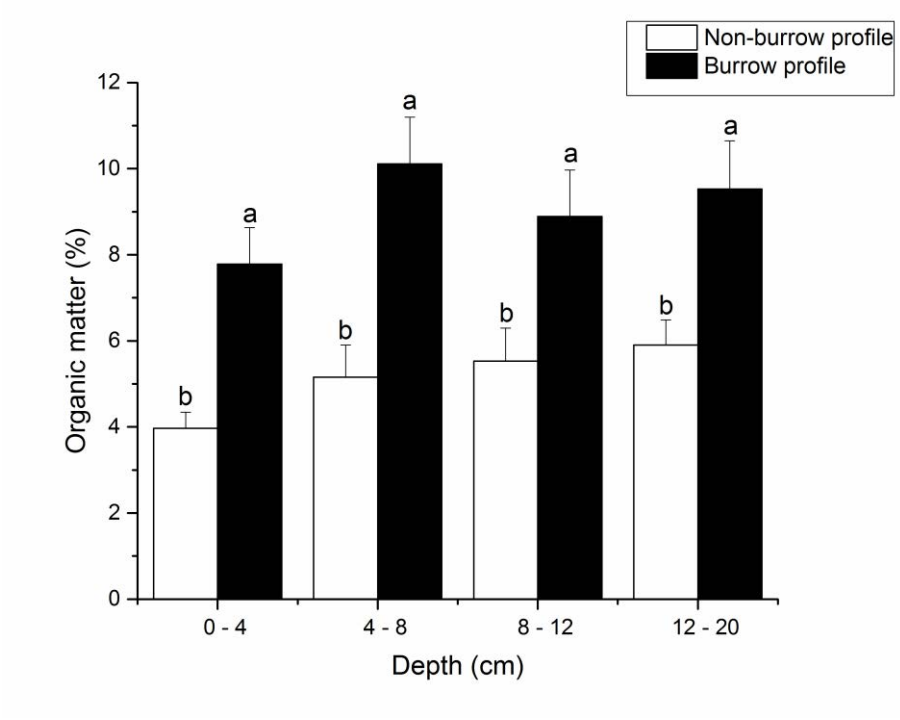
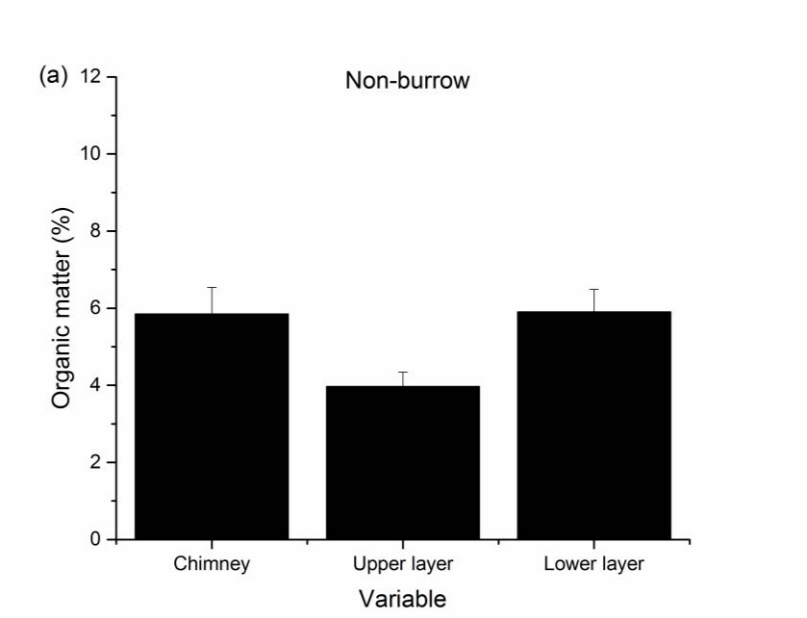


Figure 4: Mean (±SE) of organic matter content of different layers [upper (0-4 cm), upper intermediate (4-8 cm), lower intermediate (8-12 cm) and lower (12-20 cm)] from non-burrow (area without visible crab burrows) and burrow profiles. Different letters indicate statistical difference within treatment (Paired t test: upper*upper, $t = 4.12$, $df = 18$, $p = 0.001$; upper intermediate*upper intermediate, $t = 3.74$, $df = 18$, $p = 0.0001$; lower intermediate*lower intermediate, $t = 2.53$, $df = 18$, $p = 0.02$; lower*lower, $t = 2.86$, $df = 18$, $p = 0.01$). Outliers were removed from this data ($n = 18$-20).

Chimneys showed a mean organic matter content of 5.94±1.93%. Organic matter did not differ between chimneys of ovigerous females [carapace width (±SE): 17.37±0.39] and non-burrow layers (One-way ANOVA, $df = 2$, $F = 3.218$, $p = 0.055$) (Figure 5a). However, there was a significant difference when compared to burrow layers (One-way ANOVA, $df = 2$, $F = 4.165$, $p = 0.02$). *Post hoc* analysis (Tukey's test) revealed that organic matter content in chimneys was significantly lower than in the

276 lower burrow layer ($p < 0.05$), which was not observed for the upper burrow layer ($p >$

277 0.05) (Figure 5b).



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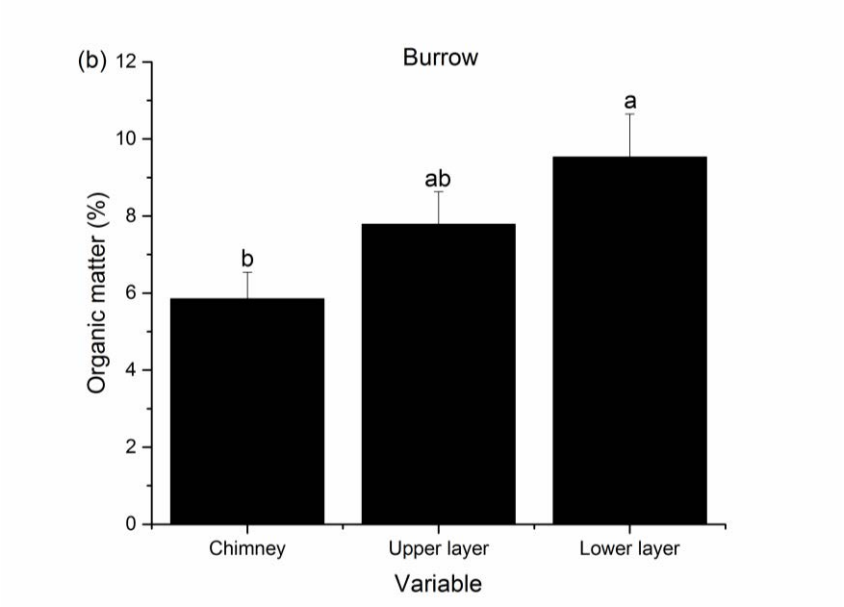

279

280 **Figure 5**: Mean (±SE) of organic matter content of chimneys and upper and lower layer

281 in both treatments [(a) non-burrow and (b) burrow profiles)]. Different letters indicate

282 statistical difference between variables (One- way ANOVA, $p < 0.05$).

283

4. Discussion

Construction and maintenance of both burrow and chimneys promotes vertical sediment distribution, which in turn modifies organic matter disposition in mangrove soil. Laboratory and field experiments showed complementary results regarding the bioturbation processes. Unquestionably, fiddler crabs behaved as ecosystems engineers in estuarine areas (Kristensen, 2008). In the laboratory experiment, it was evident that *U. thayeri* transport sediment from lower to upper layers. This physical behaviour indirectly affects biogeochemical cycles, which appears to be a key geomorphological factor in mangrove areas (Gabet et al., 2003, Kristensen and Alongi, 2006).

Our field results also showed that organic matter inside fiddler crab burrows is higher than in surrounding areas. Burrows act as surface traps, causing organic compounds (i.e. carbon sources) and sediment to be continually incorporated into deeper layers (Botto and Iribarne, 2000; Botto et al., 2006). Estuarine detritus is passively deposited onto the burrow mainly by tide action (Hemminga et al., 1996). Fanjul et al. (2015), observing the crab *Chasmagnathus granulata*, concluded that trapped organic compounds are remineralized and exported to the soil surface by distinct pathways (e.g. CO2). DePrata and Levin (1989) showed that meiofauna, mostly nauplii and adult copepods, are also passively deposited onto fiddler crab burrows. Moreover, inhibition of aerobic microbial decomposition and lixiviation processes enhance organic matter content in deeper layers (Davis et al., 2006). In this context, a depth variation in organic matter content between treatments (burrow and non-burrow profile) was already expected; however, we did not find significant differences between upper and lower layers for the same treatments. Botto and Iribarne (2000) also did not find any depth variation of organic matter in *U. uruguayensis* beds and control areas. Despite beliefs that burrowing crabs promotes transportation of sediment materials (e.g.

309 organic compounds, nutrients) (Botto and Iribarne, 2000, Kristensen and Alongi, 2006),
310 the construction and maintenance of crab burrows tend to homogenize the vertical
311 sediment distribution and organic compounds (see Fanjul et al., 2015); in this sense, the
312 organic matter content of fiddler crabs burrows may not vary substantially according to
313 depth (~20cm – *U. thayeri*) in mangrove soil.

314 Chimney construction is similar in all fiddler crab builders (Crane, 1975; Shih et
315 al., 2005; Slatyer et al., 2008; Gusmão-Junior et al., 2012). Gusmão-Junior et al. (2012)
316 provided extensive detail on this building process; *U. thayeri* crabs dig and deposit mud
317 from the substrate at the edge of the burrow entrance; they also collect, drag and stack
318 sediment from the superficial layer surrounding the burrow and modify its structure
319 with their pereiopods and chelipeds. In our laboratory experiment, we did not observe a
320 significant increase of organic matter content next to the burrows, which may be related
321 to their collection of surrounding sediment and consequent dragging of excavated
322 pellets from bottom layer to chimney shaping. Most chimney builders and other fiddler
323 crabs that construct distinct sedimentary structures (i.e. mudball, rim and hood
324 buildings) shape their biogenic sedimentary structures with material within the burrow
325 (Crane, 1975; Burford et al., 2001; Shih et al., 2005). In turn, crabs carry sediment from
326 deeper layers and into the soil surface. Thus, mangrove soil compounds (e.g. organic
327 matter and its remineralization products) tend to be reincorporated and retained in
328 above-ground biogenic sedimentary structures, as observed in the laboratory results.

329 We showed that organic matter content of chimneys in a natural environment
330 (field experiment) was inferior than the lower burrow layer. Fiddler crab burrows are
331 continuously constructed and maintained, and occasionally abandoned (Kristensen,
332 2008). The same applies to chimneys (Gusmão-Junior et al., 2013). In turn, organic
333 matter from the bottom of the burrows is constantly up-taking by physical forces (Botto

et al., 2006). It was consequently expected, without natural biotic and abiotic forces, similar organic matter content in chimney structures. Furthermore, the typical oxic thin layer of estuarine muds is inhabited by microphytobenthos, a rich source of organic matter components (Underwood and Kromkamp, 1999; Cloernet al., 2014), which are also carried with the sediment collected by fiddler crabs during construction and maintenance of above-ground biogenic sedimentary structures. However, chimneys are exposed to tide action and washed by semidiurnal tide flows (personal observation), which may drag aggregated organic compounds through the mangrove soil surface. Additionally, chimneys buildings are exposed to oxygen, which increases oxidation and may contribute to the aerobic decomposition processes. Similarly to our results, Fanjul et al. (2015) observed that mounds of the mudflat crab *N. granulata* promote spatial heterogeneity of organic matter in which mounds showed lower organic content (labile carbon fraction) than deep sediment layers.

Several studies have worked with sedimentary mounds on the seafloor (biogenic bottom features) (see references in Murray et al., 2002). Biogenic bottom features affect erosion, transport and sedimentation patterns and, in greater scales (> 50m), geomorphological processes (e.g. mass transfer from seabeds to other environments) (Murray et al., 2002). Despite the physical similarities in sediment transportation (bioturbation activity) between burrowing crabs and burrowing seafloor organisms, environmental factors (biotic and abiotic) differ among ecosystems and their influence on anoxic estuarine sediment may affect soil in a different manner. Interestingly, above-ground biogenic sedimentary structures and their construction process are similar for other estuarine groups. The mud lobster *Thalassina* spp. shape complex burrows which may be associated with chimneys (Ngoc-Ho and Saint Laurent, 2009), the manicure crab *Cleistostoma dilatatum* builds cone-shaped towers at the entrance of their burrows

(Kim et al., 2011), and the goby fish *Periophthalmodon septemradiatus* constructs muddy volcanic cone-like structures (Bhatt et al., 2009), for example. In this sense, sediment vertical transportation and distribution of organic matter may have similar functioning on estuarine species regardless of species.

In conclusion, we demonstrated that burrows and chimneys in the fiddler crab *U. thayeri* influence organic matter vertical distribution of mangrove soils. Organic matter from lower layers (anoxic strata) is carried to the surface and upper layers (Kristensen, 2008). In turn, organic compounds are retained in chimney buildings and then involved in soil biogeochemical and physical processes (e.g. microbial decomposition, lixiviation and/or tide action). These results provide further support for the hypothesis that the construction and maintenance of above-ground biogenic sedimentary structures affects organic matter distribution on estuarine soils. In order to develop a full picture of above-ground biogenic sedimentary structure effects on ecosystem functioning, additional studies will be needed on biological communities and organic compounds aggregated in above-ground biogenic sedimentary structures through time. Along with their ethological functioning (e.g. sexual attraction, territory landmark), these structures could play an important role in biogeochemical processes and may also create a new and unexplored ecological niche for microbial communities (Bertics and Ziebis, 2009) and meiofauna (DePrata and Levin, 1989).

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TABLE OF CONTENTS

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DISCENTE: Juan Carlos Farias Pardo

ORIENTADOR: Profa. Dra. Tânia Marcia Costa

HABILITAÇÃO: Biologia Marinha

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